TRADITIONAL ORCHARD ABANDONMENT IN DIFFERENT LANDSCAPE CONTEXTS: EFFECTS ON BENEFICIAL ARTHROPOD COMMUNITIES IN OLIVE AND ALMOND ORCHARDS AND CONSERVATION IMPLICATIONS

ABANDONO DE CULTIVOS TRADICIONALES EN DIFERENTES CONTEXTOS PAISAJÍSTICOS: EFECTOS SOBRE LAS COMUNIDADES DE ARTRÓPODOS BENEFICIOSOS EN PARCELAS DE OLIVO Y ALMENDRO E IMPLICACIONES PARA LA CONSERVACIÓN

VNiVERSiDAD
D SALAMANCA

FACULTAD DE BIOLOGÍA

DEPARTAMENTO DE BIOLOGÍA ANIMAL, PARASITOLOGÍA, ECOLOGÍA,
EDAFOLOGÍA Y QUÍMICA AGRÍCOLA

ÁREA DE ZOOLOGÍA

TESIS DOCTORAL

TRADITIONAL ORCHARD ABANDONMENT IN DIFFERENT LANDSCAPE CONTEXTS: EFFECTS ON BENEFICIAL ARTHROPOD COMMUNITIES IN OLIVE AND ALMOND ORCHARDS AND CONSERVATION IMPLICATIONS

ABANDONO DE CULTIVOS TRADICIONALES EN DIFERENTES CONTEXTOS PAISAJÍSTICOS: EFECTOS SOBRE LAS COMUNIDADES DE ARTRÓPODOS BENEFICIOSOS EN PARCELAS DE OLIVO Y ALMENDRO E IMPLICACIONES PARA LA CONSERVACIÓN

Memoria presentada por el graduado en Biología Víctor de Paz Pérez para optar al título de Doctor en Biología por la Universidad de Salamanca.

Salamanca 2023

VNiVERSiDAD
Ð SALAMANCA

Departamento de Biología
Animal, Ecología, Parasitología,
Edafología y Química Agrícola

Área de Zoología

Los Doctores **Dña. Laura Baños Picón,** Profesor Contratado Doctor de la Universidad de Salamanca; y **D. Josep Daniel Asís Pardo**, Catedrático de Zoología de la Universidad de Salamanca

Certifican que:

la Tesis Doctoral titulada "**Traditional orchard abandonment in different landscape contexts: effects on beneficial arthropod communities in olive and almond orchards and conservation implications** (Abandono de cultivos tradicionales en diferentes contextos paisajísticos: efectos sobre las comunidades de artrópodos beneficiosos en parcelas de olivo y almendro e implicaciones para la conservación)" que presenta **D. Víctor de Paz Pérez** para optar al título de Doctor en Biología por la Universidad de Salamanca, ha sido realizada bajo su dirección, en el Área de Zoología de la Facultad de Biología de la Universidad de Salamanca y reúne todos los requisitos científicos y formales necesarios para su defensa.

En Salamanca, a 16 de junio de 2023.

BAÑOS PICON LAURA - 16604041L
Firmado digitalmente por BAÑOS PICON LAURA - 16604041L
Fecha: 2023.06.16 10:59:33 +02'00'

Fdo.: Laura Baños Picón

ASIS PARDO JOSEP DANIEL - 24319492M
Firmado digitalmente por ASIS PARDO JOSEP DANIEL - 24319492M
Fecha: 2023.06.15 16:50:27 +02'00'

Fdo. Josep D. Asís Pardo

Agradecimientos

Lo cierto es que, aunque sea mi nombre el que aparece en la portada, esta tesis es el resultado del esfuerzo y el trabajo conjunto de muchas personas que me han ayudado y han estado a mi lado durante el largo camino que ha llevado hasta aquí.

En primer lugar, quiero dar las gracias a mis directores, Laura y Josep, que me llevan acompañando y enseñando desde hace casi una década, primero a través de sus clases, pasando por un TFG y un TFM y finalmente dirigiendo mi tesis. Gracias por todo lo que me habéis enseñado, por toda la ayuda y guía que me habéis prestado y por todo el tiempo que habéis dedicado a este trabajo. Sin vosotros no sería quien soy ahora.

También quiero dar las gracias a mis compañeras de laboratorio, quienes, junto con Josep y Laura, han creado un ambiente de trabajo insuperable. Gracias por todo lo que me habéis enseñado y por todos los momentos que hemos compartido. Habéis hecho que el lugar de trabajo sea un sitio al que apetece ir y donde puede suceder cualquier cosa, desde historias de secuestros, a personas saliendo de cajas o envueltas en papel de regalo. Y ojo, ojo, OJO, no nos olvidemos de los grandes hits musicales que he conocido gracias a vosotras, a ver en cuántos lugares se puede trabajar al ritmo de sopa de caracol…

Agradecer al Ministerio de Educación y Formación Profesional por concederme un contrato de formación de profesorado universitario (FPU), fundamental para llevar a cabo este trabajo de investigación.

Gracias a todas las personas que me han acogido durante las estancias en Rumanía y Alemania, así como durante las visitas a la Universidad de Valencia y al ITACyL. Gracias por incluirme en vuestros grupos de investigación y enseñarme tantas cosas.

Quiero dedicar una mención especial a Pepe Tormos, que me inició en el fascinante mundo de los himenópteros parasitoides y se ha peleado a mi lado con un buen puñado de alisinos. En la misma línea, agradecer a todas las personas que me han enseñado y ayudado con la identificación de otros grupos de parasitoides, en especial a Lucian Fusu, Jesús Selfa, Juli Puyade, Vicent Falcó, Ovidiu Popovici y Mircea-Dan Mitroiu; y a Félix Torres por su identificación de las abejas.

Gracias a toda mi familia, que siempre me ha apoyado y ha creído en mí más que yo mismo (es imposible sentirse como un impostor con vosotros detrás de mí), y en especial a mis tíos Laura y José, que han ayudado a que creciera en mi la llama de la biología.

Pero, principalmente, a mis padres, sin ellos nunca habría llegado hasta aquí. Gracias por vuestro apoyo incondicional, por acompañarme y ayudarme siempre, incluso aunque eso significara pasar horas al sol de julio en una charca, vigilando por si venían mastines, mientras yo cogía mil y una libélulas. Gracias por todo. No me olvido de mi hermanita pequeña, que en algún momento se ha convertido en una mujer admirable y con una mejor ética de trabajo que la mía, gracias por siempre estar ahí.

Muchas gracias a Javi y a Jesús por aguantar mis "lo siento no puedo quedar tengo que identificar/entregar/revisar…" y por siempre escuchar mis batallitas de tesis en el Eurogrill. Gracias a mi panda de frikis, nuestras rutas y viajes han sido un desahogo imprescindible durante todos estos años, espero que continúen, como poco, hasta que encontremos al vilano de la película.

Y, finalmente, gracias a ti Sara. Me faltan las palabras para agradecerte por todo el apoyo y ayuda que me has prestado todo este tiempo. Sin ti no habría tesis. Gracias por venir a todos los muestreos, a pesar de salir herida en alguno…, gracias por revisar mis textos, por escucharme barallar sobre introducciones y discusiones sin fin para que se me ocurrieran ideas, gracias por cuidar de mí y de Yin Yang y Haku estos últimos meses, que, a pesar de ser los más duros, han sido fáciles de llevar por toda tu ayuda y compañía. Esta tesis también es tuya. Gracias por acompañarme.

Index | Índice

Introduction

Introducción

Chapter I

Chapter II

Effects of Traditional Orchard Abandonment and Landscape Context on the Beneficial Arthropod Community in a Mediterranean Agroecosystem

Efectos del abandono de cultivos tradicionales y del contexto paisajístico sobre la comunidad de artrópodos beneficiosos en un agroecosistema mediterráneo

Chapter V

Description of the first brachypterous *Lonchidia* species (Hymenoptera: Figitidae: Figitinae), with a key to European species

Descripción de la primera especie braquíptera del género Lonchidia (Hymenoptera: Figitidae: Figitinae), con una clave para las especies europeas

Introduction

1. Traditional farming systems

The term "traditional farming system" encompasses all those farming systems whose management practices have changed very little over long periods of time, usually centuries (Fischer et al., 2012). They are characterized by relatively low nutrient inputs, relatively low output per hectare, and limited mechanization and are generally referred to as low-intensity farming systems (Baldock et al., 1994; Bignal and Mccracken, 1996; Plieninger et al., 2006). Traditional farming systems exist throughout the world, but they are particularly abundant in Europe (Fig. 1), where the long history of land-use since the retreat of the last glaciation has created traditional landscapes with high associated biodiversity (Fischer et al., 2012; Grass et al., 2021; Plieninger et al., 2006). In this region, traditional farming systems are identified as High Nature Value farmland (i.e., "areas in Europe where agriculture is a major (usually the dominant) land use and where that agriculture supports or is associated with either a high species and habitat diversity or the presence of species of European conservation concern, or both" (Andersen et al., 2003)).

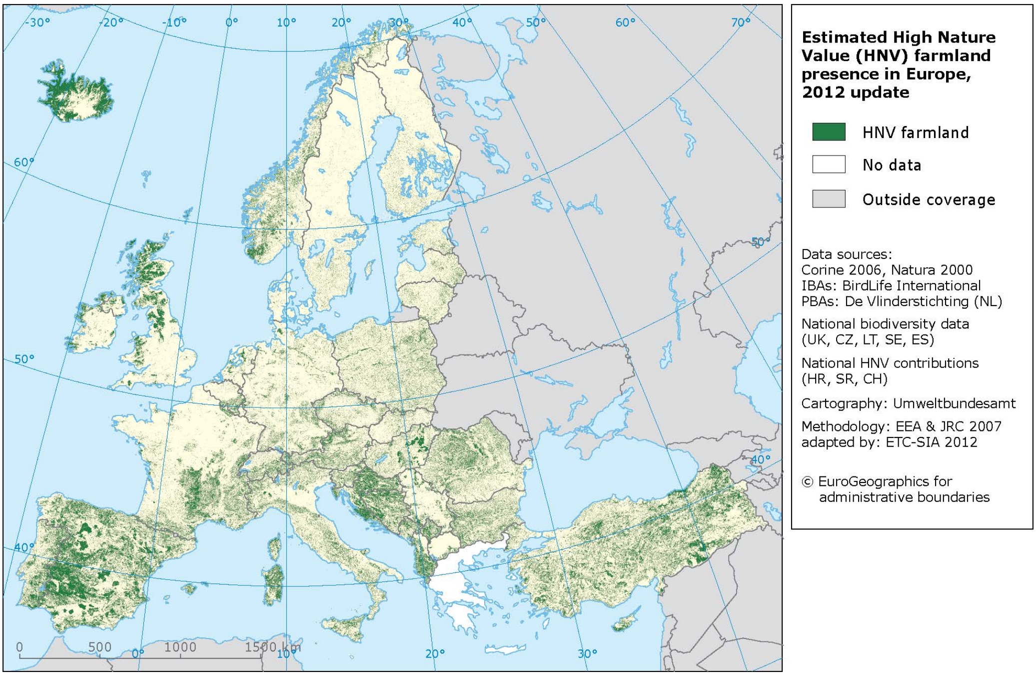

Figure 1: Estimated High Nature Value farmland presence in Europe (European Environment Agency, 2015).

Landscapes under traditional agriculture generally occur in marginal areas, where biophysical characteristics constrain crop productivity (e.g., poor soils, steppe slopes, low rainfall, or high altitude) (Keenleyside et al., 2014). These landscapes typically maintain a high cover of semi-natural habitats (SNH) and a high diversity of land uses (e.g., different crops, fallows, pastures, and landscape elements such as field margins, stone walls, or hedgerows), creating complex mosaics that harbor a high biodiversity of synanthropic species just as valuable as wild biodiversity (Keenleyside et al., 2014; Phillips, 1998; Plieninger et al., 2006; Plieninger and Bieling, 2013). However, traditional farming landscapes are quite vulnerable as they depend on intermediate levels of human disturbance, being threatened by both abandonment and intensification (Baldock et al., 1994; Keenleyside et al., 2014; Plieninger et al., 2006). For instance, in the period between 1973 and 1992, 245 000 ha of low-intensity farmland were abandoned and lost to shrub encroachment in Portugal, while 1 400 000 ha were converted into highly intensified irrigated fields in Spain, two of the countries with a higher coverage of traditional farming systems (Bignal and Mccracken, 1996; Keenleyside et al., 2014). This duality, with the abandonment of traditional agriculture located in more marginal areas and the intensification of those located on more fertile soils, represents the main threat to the persistence of traditional farming landscapes of exceptional conservation value (Fischer et al., 2012; Grass et al., 2021; Plieninger and Bieling, 2013).

The Mediterranean region accounts for a large part of the European HNV farmland and has the greatest diversity of traditional farming systems (Baldock et al., 1994). Among them, permanent crops (mainly olive groves, but also vineyards, almond and fruit orchards) stand out for their stability, complexity and the biodiversity they harbor (Horak et al., 2013; Keenleyside et al., 2014; Nielsen et al., 2011; Potts et al., 2006; Rosas-Ramos et al., 2020a). These permanent crops, and particularly olive groves (considered the most traditional tree crop in the Mediterranean Basin), have been particularly intensified and the remaining low-intensity systems have been relegated to marginal areas where they are at risk of abandonment (Bignal and Mccracken, 1996; Kizos and Koulouri, 2006; Martínez-Sastre et al., 2017; Wolpert et al., 2020).

2. Agricultural intensification: characteristics, consequences, and alternatives

Since World War II, there has been a rapid expansion and intensification of agriculture globally, driven by the need to meet increased demand for food and other crop-derived goods (Ratnadass, 2020; Sandhu et al., 2010) and by the availability of new machinery and synthetic pesticides and fertilizers (Raven and Wagner, 2021). This new method of agricultural production differs from its predecessors in its higher degree of mechanization, larger crop fields and monoculture systems, use of optimized seed varieties, and reliance on pesticides, herbicides, and synthetic fertilizers (Johnston et al., 2011; Raven and Wagner, 2021).

In Europe, land-intensification is occurring at the expense of traditional agricultural systems (Fig. 2), replacing the heterogeneous landscapes of abundant food and shelter resources with which associated biodiversity has evolved over centuries, with simplified, homogeneous landscapes with minimal uncultivated area and where arthropods, plants and other organisms encounter scarce resources and the threats of agrochemicals (Batáry et al., 2015; Benton et al., 2003; Cardoso et al., 2020; Tscharntke et al., 2005). As a result, agricultural intensification has serious consequences for biodiversity conservation and, in fact, is considered the main cause of global biodiversity loss (Feber et al., 2015; Tscharntke et al., 2005) and of the severe decline in arthropod populations (Raven and Wagner, 2021; Seibold et al., 2019). Furthermore, landscape simplification and low-biodiversity levels associated with intensive agriculture impairs ecosystem services, such as natural pest control (Bianchi et al., 2006; Estrada-Carmona et al., 2022; Rusch et al., 2016) and pollination (Estrada-Carmona et al., 2022; Kremen et al., 2002; Potts et al., 2010), turning intensive crops into vulnerable ecosystems whose maintenance depends on a high investment in management (Rusch et al., 2016; Swift and Anderson, 1994).

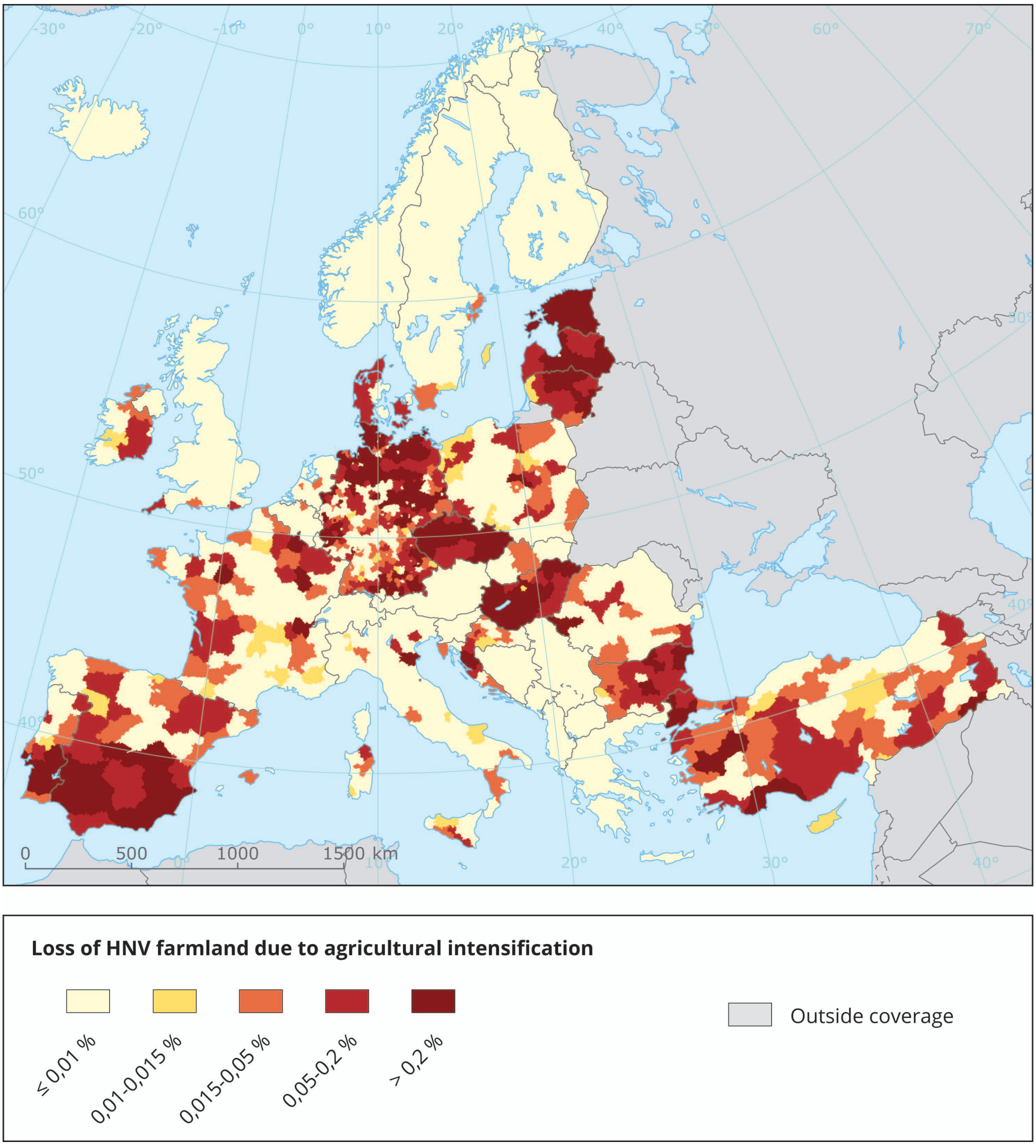

Figure 2: Loss of High Nature Value Farmland due to agricultural intensification (European Environment Agency, 2019).

Concerns over these negative effects on biodiversity and ecosystem services have led to the development of alternatives to intensive agriculture, among which organic farming stands out (Rahmann, 2011). This method of agricultural production eliminates or almost completely avoids the use of pesticides, herbicides, and synthetic chemical fertilizers (Tuck et al., 2014) and promotes practices considered beneficial to the ecosystem, such as crop rotation, the use of native seeds, and the integration of livestock into cropping systems (Emeana et al., 2018; Macfadyen et al., 2009).

There is growing evidence that, compared to intensive agriculture, organic farming leads to significant biodiversity benefits, increasing local species richness by approximately 34% and abundance by approximately 50% (Bengtsson et al., 2005; Hole et al., 2005; Tscharntke et al., 2021). Groups such as plants and bees benefit the most from organic farming, while other arthropods and birds are favored to a lesser extent (Seufert and Ramankutty, 2017). Furthermore, the positive effects of organic farming also vary according to landscape context, being generally higher in simplified landscapes with high cover of intensively farmed agricultural land (Seufert and Ramankutty, 2017); and according to crop type, with more benefits provided in cereal crops than in vegetable crops and orchards (Bruggisser et al., 2010; Macfadyen et al., 2009; Tuck et al., 2014). Organic farming is not the only extensification measure to counteract the negative consequences of intensive agriculture: small fields, crop diversification, or the maintenance of semi-natural habitat patches are other management options that may even be more beneficial for biodiversity than implementing organic farming (Batáry et al., 2017; Tscharntke et al., 2021).

3. Agricultural abandonment: consequences for biodiversity

The total area dedicated to agriculture has declined slightly over the last 20 years, but this decrease has been uneven across the world, with Europe losing the largest percentage of agricultural land (5%) (FAO, 2022). This means that, in Europe, more than 18.5 million ha have been released from agriculture, mainly due to land abandonment (FAOSTAT, 2022; Pereira and Navarro, 2015). This process is mainly driven by socio-economic factors such as rural-urban migration in search of better economic opportunities (Benayas et al., 2007).

Agricultural abandonment can be seen as an opportunity for nature restoration (i.e., rewilding, defined as the "passive management of ecological succession with the goal of restoring natural ecosystem processes and reducing human control of landscapes" (Gillson et al., 2011; Pereira and Navarro, 2015)) or as a threat to the rich biodiversity found in traditional farming systems (Fischer et al., 2012; Plieninger and Bieling, 2013).

Some studies have found positive outcomes to agricultural abandonment. For example, forest regrowth, through vegetation succession, can lead to increased carbon sequestration, increased provision of wood resources, soil recovery, and higher nutrient availability (Benayas et al., 2007; Pointereau et al., 2008; Pugh et al., 2019). Others show negative impacts such as soil erosion, increased wildfire risk and reduced water availability (Benayas et al., 2007; Bentley and Coomes, 2020; Moreira and Russo, 2007; Stanchi et al., 2012).

Several relevant reviews and meta-analyses have been developed to understand the consequences of agricultural abandonment on biodiversity. However, the main conclusion is that there is no *one-size-fits-all* answer to that question, as these consequences seem to be region, taxa, scale, climate, and local context dependent (Plieninger et al., 2014; Queiroz et al., 2014; Quintas-Soriano et al., 2022). In a global review, Benayas et al. (2007) found 77 studies reporting negative effects and 39 reporting positive effects on biodiversity. Queiroz et al. (2014) found that 65 % of studies assessing the effects of agricultural abandonment on biodiversity in Europe reported negative effects and only 6 % positive effects, with large differences between taxa. In a review focused on the Mediterranean region, Plieninger et al. (2014) found slight increases in plant and animal richness and abundance after abandonment, although their results were highly heterogeneous, and they reported a generally negative trend after abandonment periods of 50 years or more. Katayama et al. (2019) focused their review on permanent crops (orchards and vineyards), including 12 studies that compared biodiversity in conventional and abandoned agroecosystems (mostly apple orchards), and found generally positive effects on alpha, beta, and gamma diversity. The last and most recent of these reviews was conducted by Quintas-Soriano et al. (2022) in the Mediterranean region and, while this work had a broader focus on the effects of abandonment on nature's contributions to people, they also analyzed the effects of agricultural abandonment on biodiversity and found mostly negative consequences (although 80 % of the studies they considered were focused on plants and birds).

It seems clear that more research is needed to disentangle the effects of agricultural abandonment on biodiversity in general, and arthropods in particular, especially in underrepresented agroecosystems such as traditional orchards (Kajtoch, 2017; Quintas-Soriano et al., 2022).

4. Landscape context: the role of semi-natural habitats

Agroecosystems, whether traditional or intensive, do not exist in isolation from surrounding habitats, rather they are affected by them. The biodiversity they harbor as well as the consequences of management practices or agri-environmental schemes such as organic farming, depend on the landscape context (Concepción et al., 2012; Tscharntke et al., 2012). The landscape context can be defined on the basis of two main characteristics: landscape composition and landscape configuration (Fig. 3) (Duelli, 1997; Fahrig et al., 2011; Martin et al., 2019). Landscape composition refers to the availability and relative amounts of different land covers, such as grasslands, orchards, arable land, forests, or semi-natural habitats (Martin et al., 2016). On the other hand, landscape configuration focuses on the spatial arrangement of land cover types and on the shape of each land cover patch, providing information on the density of ecotones between land cover types and their degree of interspersion (Fahrig et al., 2011; Martin et al., 2016). There are numerous parameters for measuring landscape configuration, among which edge density or length and average patch size are most frequently used (Fahrig et al., 2015; Martin et al., 2016).

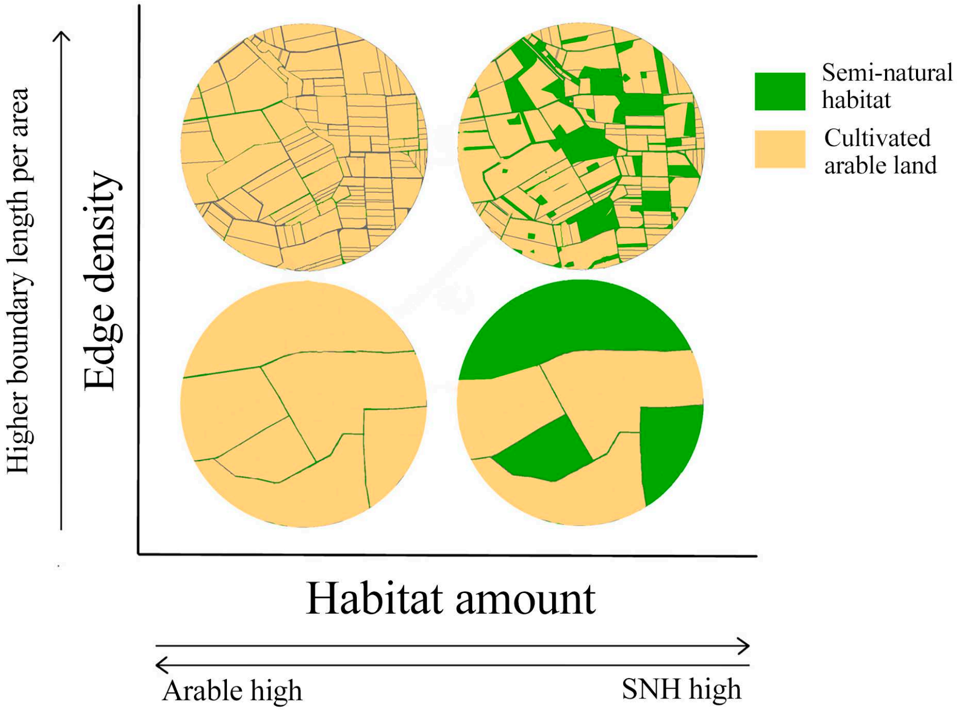

Figure 3: Conceptual representation of the distinction between landscape composition and configuration (modified from Martin et al. (2019)). Four theoretical agricultural landscapes are represented, differing in landscape composition (habitat amount) and configuration (edge density).

Landscape composition and configuration effects on biodiversity are varied and taxon-specific (Bottero et al., 2023). However, it can generally be assumed that landscapes with several different habitats are able to sustain a broader diversity of species than landscapes dominated by one or two land cover types, because different habitats may favor different species (Bianchi et al., 2006; Sirami et al., 2019). In addition, increasing configurational heterogeneity (i.e., smaller fields and higher edge density) favors richness and abundance across taxa (Fahrig et al., 2011; Sirami et al., 2019).

Biodiversity responses to landscape composition and configuration also depend on the scale considered, as different species tend to respond to the landscape context at different scales (Holland et al., 2004; Martin, 2018; Martin and Fahrig, 2012). Different environmental variables can affect a given species' response at different spatial scales (Coffey and Fahrig, 2012; McGarigal et al., 2016; Patenaude et al., 2015). Also, the scale of effect of a given environmental variable seems to depend on the type of response (e.g., a species abundance responding to landscape composition at a different scale than that species occurrence or fecundity) (Martin, 2018). However, the main predictor of the spatial scale at which a species responds is generally its dispersal capacity, the higher the dispersal distance or home range the higher the scale of the response (Jackson and Fahrig, 2012; Miguet et al., 2016), although this relationship might not be as straightforward as previously though (Arroyo-Rodríguez et al., 2023). Therefore, it is important to evaluate biodiversity responses to landscape composition and configuration at different spatial scales (Arroyo-Rodríguez et al., 2023; Jackson and Fahrig, 2015).

The majority of the studies evaluating landscape composition effects on biodiversity in agricultural landscapes have focused on the cover of semi-natural habitats (SNH) as a proxy of landscape complexity (e.g., Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Gkisakis et al., 2016; Marja et al., 2022; Rusch et al., 2016). SNH, defined as "any habitat within or outside of the crop containing a community of non-crop plant species" (Holland et al., 2017) are essential for the maintenance of biodiversity in agricultural landscapes (Estrada-Carmona et al., 2022; Gámez-Virués et al., 2015; Marja et al., 2022; Tscharntke et al., 2021), with up to 65 % of animal species depending on the presence of SNH (Duelli and Obrist, 2003). Several studies have shown decreases in species diversity with the loss of SNH or with increased distance to these habitats (e.g., Batáry et al., 2011; Garibaldi et al., 2011). Semi-natural habitats provide a broad range of microhabitats and microclimatic conditions, alternative resources (e.g., foraging resources, prey and hosts, nesting resources), refuge, and overwintering sites for beneficial arthropods and other groups (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Duelli and Obrist, 2003; Estrada-Carmona et al., 2022; Hevia et al., 2021; Kennedy et al., 2013; Marino and Landis, 1996; Maurer et al., 2022; Tscharntke et al., 2021; Zhu et al., 2023). In addition, SNH generally have a more complex structured vegetation, an important variable for different arthropod groups (e.g., parasitoids (Bartual et al., 2019; Finke and Denno, 2002; Meyhofer and Hindayana, 2000) or spiders (Benhadi-Marín et al., 2020; Rosas-Ramos et al., 2019, 2018; Uetz et al., 1999)) and other taxa (e.g., birds (Kajtoch, 2017)).

More complex landscapes (i.e., those with a higher SNH cover) host larger species diversity, counteracting biotic homogenization, and promote stability of population dynamics through increased resilience and capacity to recover from disturbance (Bengtsson et al., 2003; Estrada-Carmona et al., 2022; Feit et al., 2021; Gámez-Virués et al., 2015; Oliver et al., 2010; Tscharntke et al., 2012). Furthermore, landscape complexity can mediate biodiversity responses to local management, as proposed by the *intermediate landscape complexity hypothesis* (Concepción et al., 2012; Tscharntke et al., 2012). This hypothesis states that "landscape-moderated effectiveness of local conservation management is highest in structurally simple, rather than in cleared (i.e., extremely simplified) or in complex landscapes" (Tscharntke et al., 2012); meaning that in both cleared (<1% of non-crop habitat) and complex landscapes (>20% of non-crop habitat), only small positive responses to local extensification measures (such as organic farming or abandonment) can be expected because of poor species pools and high immigration from semi-natural habitats, respectively, and that only simple landscapes, with intermediate levels of complexity, respond positively to these measures. Therefore, considering the landscape context is fundamental in studies assessing management or land-use change effects on the biodiversity associated with agricultural landscapes (Beaumelle et al., 2021; Karp et al., 2018; Tscharntke et al., 2012).

5. Arthropod biodiversity in agroecosystems

Biodiversity refers to the variety of living organisms, the genetic differences among them, the communities and ecosystems in which they occur, and the ecological and evolutionary processes that keep them functioning, yet ever changing and adapting (Noss and Cooperrider, 1994). In agricultural ecosystems, biodiversity depends on several factors, among which four stand out: the diversity of vegetation within and around the agroecosystem; the permanence of the various crops within the agroecosystem; the intensity of management; and the degree of isolation of the agroecosystem with respect to natural vegetation (Altieri and Nicholls, 2004; Southwood and Way, 1970).

Both the planned biodiversity of agroecosystems (i.e., crop or livestock species intentionally included by the farmer) and the associated biodiversity (i.e., species that colonize crops from adjacent areas and that thrive in them depending on their structure and type of management) are involved in the functioning of the ecosystem and provide important ecosystem services (Altieri and Nicholls, 2004), which are defined as the benefits that humans obtain from ecosystems (Millennium Ecosystem Assessment, 2005).

Arthropods constitute one of the main components of biodiversity associated with agroecosystems. This extremely diverse and abundant group has key implications for agricultural productivity, as it includes some of the main providers of fundamental ecosystem services, such as pollination, natural pest control, and decomposition (Isaacs et al., 2009; McCravy, 2018; Noriega et al., 2018). However, arthropods can also cause serious disservices, since many of their groups constitute agricultural pests capable of causing significant impacts on production (Vansynghel et al., 2022). Other arthropod-mediated disservices have been reported, such as predation of natural enemies and pollinators and damage or transmission of pathogens to plants (Barbercheck and Wallace, 2021; Pereira et al., 2004; Way and Khoo, 1992).

5.1 Bactrocera oleae and its natural enemies

Bactrocera oleae (Rossi, 1790) (Diptera: Tephritidae), the olive fruit fly, is the main pest of olive orchards globally (Ortega et al., 2016). In the Mediterranean Basin, where 98% of the world's olive cultivation takes place (Bueno and Jones, 2002), this pest causes losses of up to 40% of production (Pereira et al., 2004) or, in rare cases, nearly 100 % (Boccaccio and Petacchi, 2009), in addition to a reduction in fruit quality for both table olives and oil (Nardi et al., 2005).

Generally, adults of *B. oleae* emerge in early spring, reproduce, disperse, and deposit their eggs inside olives around July (Marchini et al., 2017). In this period, they are especially vulnerable to generalist predators such as spiders (Picchi et al., 2017a) and birds (Bigler et al., 1986). Larvae emerge from eggs after 2-3 days (Marchini et al., 2017) and develop by feeding on the olive mesocarp, a phase during which they are mainly susceptible to attack by parasitoids (Boccaccio and Petacchi, 2009; Ortega et al., 2016). From summer to mid-autumn, larvae complete the cycle inside the olives, with adults emerging in 10-15 days (Marchini et al., 2017; Pereira et al., 2004); while from mid-autumn, third instar larvae leave the olives and pupate in the surface layer of the soil (~ 3 cm) (Dimou et al., 2003), remaining quiescent until spring (Delrio and Lentini, 2016). In the soil, this pupal stage is vulnerable to generalist edaphic predators, especially carabids, staphylinids, spiders, and ants (Dinis et al., 2016). In the Mediterranean region, the olive fruit fly can complete between 3 and 5 cycles per year (Preu et al., 2020).

Carabid and staphylinid beetles are generalist predators abundant in agroecosystems that provide a valuable pest control service by reducing the populations of several arthropod pests (Albertini et al., 2017; MacLeod et al., 2004). Ants, the most abundant group of edaphic arthropods in olive groves, can also act as pest-control agents, in addition to participating in other ecosystem processes and serving as bioindicators (Campos et al., 2011; Peck et al., 1998; Santos et al., 2007); although they can also cause disservices such as predation of natural enemies (Pereira et al., 2004).

In addition to these predation and parasitism by natural enemies, *B. oleae* populations can be affected by other factors, directly and indirectly, such as climate, landscape context or crop management practices (Delrio and Lentini, 2016; Ortega et al., 2018). For example, Picchi et al. (2017b) showed that organic farming can cause a decrease in *B. oleae* pupae, due to a greater presence of natural enemies in comparison with conventionally managed plots.

5.2 Spiders

Spiders are abundant and ubiquitous generalist predators (with some exceptions) in terrestrial ecosystems, where they comprise a major share of all invertebrate predators (Wise, 1993). Spiders are a diverse group of arthropods, with slightly over 51 000 species (World Spider Catalog, 2023), which primarily attack insects, but also a wide range of other arthropods, including other spiders, being able to affect prey density and community structure dynamics (Wise, 1993). Furthermore, they are one of the most abundant groups of predators in agroecosystems, where they can significantly reduce the populations of several insect pests (Benamú et al., 2017; Marc et al., 1999; Michalko et al., 2019; Nyffeler and Sunderland, 2003).

Spiders present an array of foraging strategies, web structures, prey preference, or activity periods, that allow for their classification into guilds (i.e., as "a group of species that exploit the same class of environmental resources in a similar way" (Root, 1973)) (Cardoso et al., 2011; Uetz et al., 1999). This has important implications for spiders' role in natural and agricultural ecosystems as syntopic species of different guilds may show great prey variability and could exploit different resources, complementing each other (Nyffeler et al., 1989; Sunderland and Samu, 2000; Uetz et al., 1999). The main spider guilds, proposed by Uetz et al. (1999) and later modified by Cardoso et al. (2011) are foliage runners, ground runners, stalkers, ambushers, sheet-web builders, orb weavers, and space-web builders.

Spiders are affected by local habitat features (Barton et al., 2017; Theron et al., 2020), being particularly sensitive to environmental physiognomy (e.g., vegetation architectural complexity or diversity) (Dennis et al., 2015; Gómez et al., 2016; Spears and MacMahon, 2012; Uetz et al., 1999; Wise, 1993) and prey availability (Halaj et al., 1998; Markó et al., 2009; Spears and MacMahon, 2012). Within agroecosystems spiders are affected by management measures at the local scale and by the landscape context. For instance, spiders are favored by organic management (Bengtsson et al., 2005; Cardenas et al., 2015; Kolb et al., 2020; Rosas-Ramos et al., 2020b; but see Bruggisser et al., 2010) and complex ecological infrastructures (Cardenas et al., 2015; Rosas-Ramos et al., 2019, 2018), and negatively affected by pesticide application (e.g., Picchi et al., 2017a). In addition, several studies have shown greater spider diversity in complex or configurationally heterogeneous landscapes (Bianchi et al., 2006; Kolb et al., 2020; Mestre et al., 2018; Rischen et al., 2023; Schmidt and Tscharntke, 2005; Shackelford et al., 2013; but see Picchi et al., 2017a).

5.3 Hymenopteran parasitoids

Parasitoids are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects, eventually killing them. They differ from predators in that they only need a single host on which to mature, and from parasites in that the host always dies (Godfray, 1994). There are parasitoid species in many insect orders, which in decreasing number of species are as follows: Hymenoptera, Diptera, Coleoptera, Neuroptera, Lepidoptera, Strepsiptera, and Trichoptera (Godfray, 1994; Heraty, 2017). Hymenopteran parasitoids comprise around 75 % of all parasitoid species, with approximately 80 000 species described (Belshaw et al., 2003; Huber, 2017). However, hymenopteran parasitoids are one the most poorly know group of insects and the estimated number of extant species ranges from 176 000 to as many as 6 million, although more likely estimates range between 630 000 and 1.6 million species (Godfray, 1994; Heraty, 2017; LaSalle and Gauld, 1991).

Considering how they interact with their host parasitoids can be divided into several categories, useful to describe major types of parasitoid biology (Godfray, 1994; Nastasi et al., 2023). Attending to their host preference parasitoids can be regarded as polyphagous when they can attack a wide variety of non-related hosts (from different families or orders), oligophagous when they are restricted to a few closely related hosts, and monophagous if they parasitize a single host species. Parasitoids can be ectoparasitoids or endoparasitoids if they develop externally o within the bodies of their hosts, respectively. Idiobiont parasitoids paralyze their hosts and stop their development, while koinobiont parasitoids do not stop their hosts' development. Depending on the number of individuals developing on a single host they can be generally classified as solitary (only one egg per individual host) or gregarious (several larvae develop within each host), although more complex interactions exist, including hyperparasitism (parasitoids that use other parasitoids as hosts) (Godfray, 1994; Nastasi et al., 2023). Parasitoids of holometabolous insects can be further classified attending to the stage they attack, differentiating between egg, larval, pupal and adult parasitoids. Some koinobiont parasitoids lay their eggs in one host stage but emerge from another, for example egg-larval parasitoid or larval-pupal parasitoids (Godfray, 1994).

The hosts of parasitoids are almost exclusive insects, although some species attack spiders, acari or even centipedes (Godfray, 1994; Nastasi et al., 2023). Parasitoids have a fundamental role in the natural regulation of host populations, and thus in the functioning and stability of terrestrial ecosystems, where they take part in many trophic interactions (LaSalle and Gauld, 1993, 1991; Shaw and Hochberg, 2001). Moreover, their capacity to regulate populations of phytophagous insects make them one of the main groups responsible for natural pest control (ecosystem service valued in over $20 billion annually only in the US), being widely used in biological control programs (Hajek and Eilenberg, 2018; Henri and Van Veen, 2011; LaSalle and Gauld, 1993; Pennisi, 2010).

Several characteristics make hymenopteran parasitoid a group particularly prone to extinction: they belong to a high trophic level, being particularly sensitive to environmental disturbances; they can have chronically small populations; and are often dependent on unreliable resources, for instance when they effectively regulate their hosts at low population density (LaSalle and Gauld, 1993, 1991; Shaw and Hochberg, 2001). Despite their importance and high extinction risk, parasitoids are generally ignored in insect conservation strategies (Shaw and Hochberg, 2001).

In agricultural landscapes, parasitoids are particularly vulnerable to intensive management practices (e.g., pesticide use) but they benefit from the presence of feeding resources (nectar, pollen, and honeydew) and hosts, including crop pests (Bianchi et al., 2006; Cronin and Reeve, 2005; Kishinevsky et al., 2017; Mates et al., 2012; Shaw, 2006). Several studies have shown higher parasitoid diversity in complex landscapes with a high cover of SNH and high connectivity between patches, as parasitoids benefit from the structurally more complex habitats, shelter and feeding resources, overwintering sites and alternative hosts that SNH provide (Bianchi et al., 2006; Boccaccio and Petacchi, 2009; Chaplin-Kramer et al., 2011; Holland et al., 2016; Marino and Landis, 1996; Marja et al., 2022; Martin et al., 2019).

5.4 Bees

Bees are a diverse group of insect pollinators with over 20 000 species worldwide (Danforth et al., 2019). They are the main pollinators of both wild and cultivated plants and, as such, they play a fundamental role in the maintenance of biodiversity and ecosystem processes, since about 90 % of angiosperms and a significant number of gymnosperms depend on animal pollination (Ollerton, 2017; Ollerton et al., 2011; Potts et al., 2016, 2010). Of all bee species only 50 are currently managed, 12 of them specifically for crop pollination (mainly the European honey bee *Apis mellifera* Linnaeus 1758), however both wild and managed bees have a similar contribution to crop pollination, being crucial for food security, valued around $3 000/ha (Kleijn et al., 2015; Klein et al., 2018; Potts et al., 2016). Despite this importance, only about 2 % of all wild bee species significantly contribute to crop pollination, most of the remaining species being unable to survive in intensive agricultural landscapes (Kleijn et al., 2015). Many studies have shown a significant decrease in wild bee diversity and abundance that could limit pollination services (Ollerton et al., 2011; Potts et al., 2010; Zattara and Aizen, 2021). Land-use change and management intensity, climate change, pesticides and genetically modified organisms, pollinator management and pathogens, and invasive alien species have been identified as the major drives of bee decline (Potts et al., 2016).

Most managed bees are social (i.e., they have a reproductive division of labor were only some females (queens) reproduce, while others (workers) forage pollen and nectar, build and protect the nest, and help to rear the queen's offspring), but the majority of wild bees are solitary (> 75 %), only 13 % being kleptoparasitic (i.e., brood parasites) and 9 % are social (with a wide range of sociality levels) (Danforth et al., 2019). Each solitary bee has the ability to reproduce, builds and maintains its own nest, and collects the floral resources (mainly pollen and nectar) needed to provision its brood cells (Danforth et al., 2019; Michener, 2007). Wild bees also differ in their nesting behavior, presenting diverse strategies regarding where they build their nests, the type of substrate they use, and the material they require to construct the nest (Danforth et al., 2019; Michener, 2007; Potts et al., 2005). These characteristics allow for the categorization of wild bees (with some exceptions) into three major nesting guilds: species that excavate their nests in the ground (most species belong to this guild), species that nest in preexisting cavities (e.g., hollow plant stems, rock cavities, abandoned insect burrows, snail shells), and species that excavate their nests in woody substrates (Danforth et al., 2019; Michener, 2007; Potts et al., 2005). In addition, bees differ in their foraging specialization differentiating monolectic bees, collecting pollen on only one plant species; oligolectic bees, which collect pollen from several species within a genus or family; and polylectic bees, which forage pollen from several distinct families (Cane and Sipes, 2006; Müller and Kuhlmann, 2008). They can be further divided in subcategories depending on the breadth of their diet within each category into narrow and broad oligolectic and polylectic (Cane and Sipes, 2006; Müller and Kuhlmann, 2008). Another factor that affects foraging specialization is tongue length, with long-tongued bees been able to access deeper flowers with long corollas, and short-tongued bees being restricted to flowers with shallow corollas and more exposed nectar and pollen (Michener, 2007). Furthermore, bees are central place foragers, and they need to access all of the resources they require to complete their life cycle within their flight range and period (Ogilvie and Forrest, 2017; Westrich, 1996).

Within agroecosystems, bee traits and resource needs determine their response to local management and landscape composition and configuration (Hall et al., 2019; Kennedy et al., 2013; Williams et al., 2010; Williams and Kremen, 2007). For example, several studies have shown that bees depend on the resources provided by SNH, being favored by higher SNH cover in the landscape (Estrada-Carmona et al., 2022; Kennedy et al., 2013; Maurer et al., 2022; Roth et al., 2023) and negatively affected by isolation from these habitats (Garibaldi et al., 2011; Ricketts et al., 2008); while they tend to be positively affected by increased configurational heterogeneity (e.g., higher edge density) (Hass et al., 2018; Holzschuh et al., 2010; Martin et al., 2019; but see Maurer et al., 2022).

6. Aims of the thesis

The main focus of this thesis is to analyze the consequences of traditional orchard abandonment under different scenarios of farming system and landscape context on the associated communities of beneficial arthropods and an important agricultural pest. Specific goals are:

1. To analyze the effect of traditional olive grove abandonment and organic management on the population of *Bactrocera oleae* and on the natural enemy community composition, diversity metrics, and dominant families (Chapter I).
2. To evaluate spider, bee, and parasitoid community composition, richness, and abundance differences between abandoned and active almond orchards under traditional management in simple and complex landscapes, assessing their responses to semi-natural habitat cover at 150 m and 500 m (Chapter II).
3. To assess how the landscape context and community turnover may mediate parasitoid genus-level community composition and diversity metrics responses to traditional almond orchard abandonment and land-use cover at 150 m and 500 m (Chapter III).
4. To investigate bee taxonomic and guild responses to traditional almond orchard abandonment in landscapes with contrasting percentages of semi-natural habitats, and to land-use composition at different scales, evaluating the role of species turnover in mediating these responses (Chapter IV).
5. To describe a new species from the genus *Lonchidia* (Hymenoptera: Figitidae) and provide a determination key to separate the European species (Chapter V).

Introducción

1. Sistemas agrícolas tradicionales

El término "sistema agrícola tradicional" engloba todos aquellos sistemas agrícolas cuyas prácticas de manejo han cambiado muy poco durante largos periodos de tiempo, normalmente siglos (Fischer et al., 2012). Estos sistemas se caracterizan por unos aportes de nutrientes, una producción por hectárea y un grado de mecanización relativamente bajos y suelen denominarse sistemas agrícolas de baja intensidad (Baldock et al., 1994; Bignal y Mccracken, 1996; Plieninger et al., 2006). Los sistemas agrícolas tradicionales existen en todo el mundo, pero son especialmente abundantes en Europa (Fig. 1), donde se ha explotado la tierra desde el retroceso de la última glaciación, creando paisajes tradicionales con una elevada biodiversidad asociada (Fischer et al., 2012; Grass et al., 2021; Plieninger et al., 2006). En esta región, los sistemas agrícolas tradicionales se identifican como tierras agrícolas de alto valor natural (es decir, "zonas en Europa en las que la agricultura es uno de los principales usos del suelo (normalmente el dominante) y en las que esa agricultura sustenta o está asociada a una elevada diversidad de especies y hábitats o a la presencia de especies cuya conservación está amenazada en Europa, o a ambas cosas" (Andersen et al., 2003)).

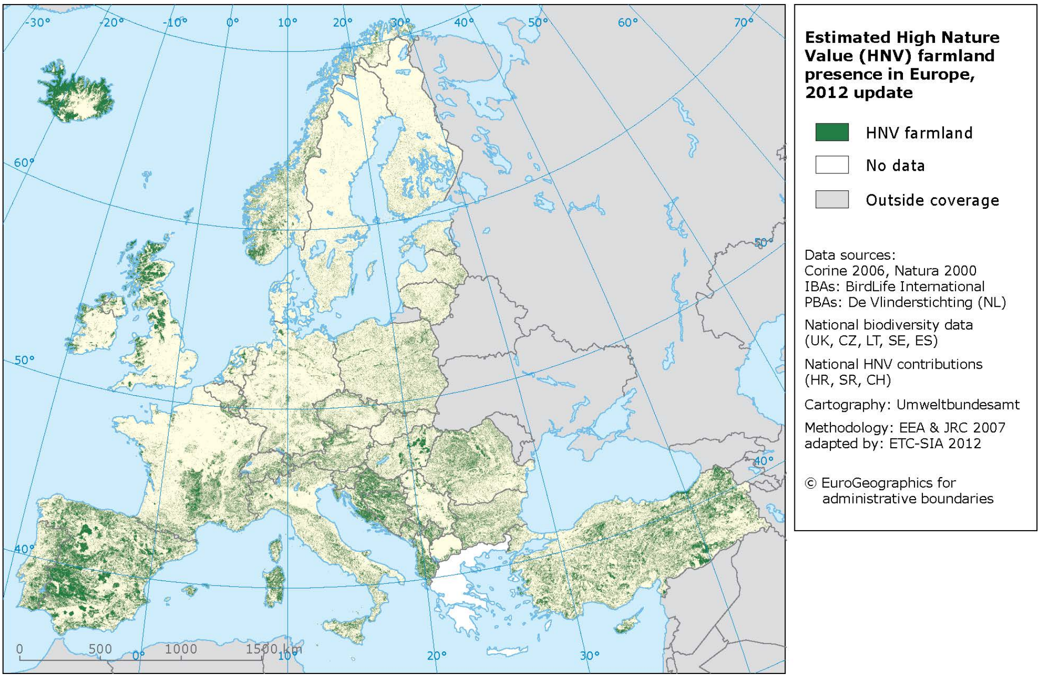

Figure 1: Presencia estimada de tierras agrícolas de alto valor natural en Europa (European Environment Agency, 2015).

Los paisajes dominados por sistemas agrícolas tradicionales generalmente se encuentran en zonas marginales, donde las características biofísicas limitan la productividad de los cultivos (por ejemplo, suelos pobres, laderas con pendientes pronunciadas, escasas precipitaciones o elevada altitud) (Keenleyside et al., 2014). Estos paisajes suelen mantener una alta cobertura de hábitats seminaturales (SNH) y una gran diversidad de usos del suelo (por ejemplo, diferentes cultivos, barbechos, pastos y elementos del paisaje como bordes de cultivos, muros de piedra o setos), creando mosaicos complejos que albergan una gran biodiversidad de especies sinantrópicas tan valiosa como la biodiversidad silvestre (Keenleyside et al., 2014; Phillips, 1998; Plieninger et al., 2006; Plieninger y Bieling, 2013). Sin embargo, los paisajes agrícolas tradicionales son bastante vulnerables, ya que dependen de niveles intermedios de perturbación humana, estando amenazados tanto por el abandono como por la intensificación (Baldock et al., 1994; Keenleyside et al., 2014; Plieninger et al., 2006). Por ejemplo, en el periodo comprendido entre 1973 y 1992, 245.000 ha de tierras de cultivo de baja intensidad fueron abandonadas y rápidamente colonizadas por arbustos en Portugal, mientras que 1.400.000 ha se convirtieron en campos de regadío altamente intensificados en España, dos de los países con una mayor cobertura de sistemas agrícolas tradicionales (Bignal y Mccracken, 1996; Keenleyside et al., 2014). Esta dualidad, con el abandono de la agricultura tradicional localizada en zonas más marginales y la intensificación de la situada en suelos más fértiles, representa la principal amenaza para la persistencia de paisajes agrícolas tradicionales de excepcional valor desde el punto de vista de la conservación (Fischer et al., 2012; Grass et al., 2021; Plieninger y Bieling, 2013).

La región mediterránea presenta una gran parte de las tierras agrícolas de alto valor natural europeas y cuenta con la mayor diversidad de sistemas agrícolas tradicionales (Baldock et al., 1994). Entre ellos, los cultivos permanentes (principalmente olivares, pero también viñedos, almendros y frutales) destacan por su estabilidad, complejidad y la biodiversidad que albergan (Horak et al., 2013; Keenleyside et al., 2014; Nielsen et al., 2011; Potts et al., 2006; Rosas-Ramos et al., 2020a). Estos cultivos permanentes, y en particular el olivar (considerado el cultivo arbóreo más tradicional de la cuenca mediterránea), han sido especialmente intensificados y los sistemas de baja intensidad restantes han quedado relegados a zonas marginales donde corren el riesgo de ser abandonados (Bignal y Mccracken, 1996; Kizos y Koulouri, 2006; Martínez-Sastre et al., 2017; Wolpert et al., 2020).

2. Intensificación agrícola: características, consecuencias y alternativas

Desde la Segunda Guerra Mundial, se ha producido una rápida expansión e intensificación de la agricultura en todo el mundo, impulsada por la necesidad de satisfacer la creciente demanda de alimentos y otros bienes derivados de los cultivos (Ratnadass, 2020; Sandhu et al., 2010), así como por la disponibilidad de nueva maquinaria y de pesticidas, herbicidas y fertilizantes de origen sintético (Raven y Wagner, 2021). Este método de producción agrícola difiere de sus predecesores en su mayor grado de mecanización, mayores tamaños de parcela y predominio de los monocultivos, uso de variedades de semillas optimizadas y dependencia de pesticidas, herbicidas y fertilizantes de origen sintético (Johnston et al., 2011; Raven y Wagner, 2021).

En Europa, la intensificación agrícola se está produciendo a expensas de los sistemas tradicionales (Fig. 2), sustituyendo los paisajes heterogéneos caracterizados por la presencia de abundantes recursos alimenticios y refugios con los que la biodiversidad asociada ha evolucionado durante siglos, por paisajes simplificados y homogéneos con una superficie mínima sin cultivar y donde los artrópodos, las plantas y otros organismos se encuentran con escasos recursos y con las amenazas derivadas de los agroquímicos (Batáry et al., 2015; Benton et al., 2003; Cardoso et al., 2020; Tscharntke et al., 2005). Como resultado, la intensificación agrícola tiene graves consecuencias para la conservación de la biodiversidad y, de hecho, se considera la principal causa de la pérdida de biodiversidad a nivel mundial (Feber et al., 2015; Tscharntke et al., 2005) y del grave declive de las poblaciones de artrópodos (Raven y Wagner, 2021; Seibold et al., 2019). Además, la simplificación del paisaje y los bajos niveles de biodiversidad asociados a la agricultura intensiva perjudican a los servicios ecosistémicos, como el control natural de plagas (Bianchi et al., 2006; Estrada-Carmona et al., 2022; Rusch et al., 2016) y la polinización (Estrada-Carmona et al., 2022; Kremen et al., 2002; Potts et al., 2010), convirtiendo los cultivos intensivos en ecosistemas vulnerables cuyo mantenimiento depende de una elevada inversión en su manejo (Rusch et al., 2016; Swift y Anderson, 1994).

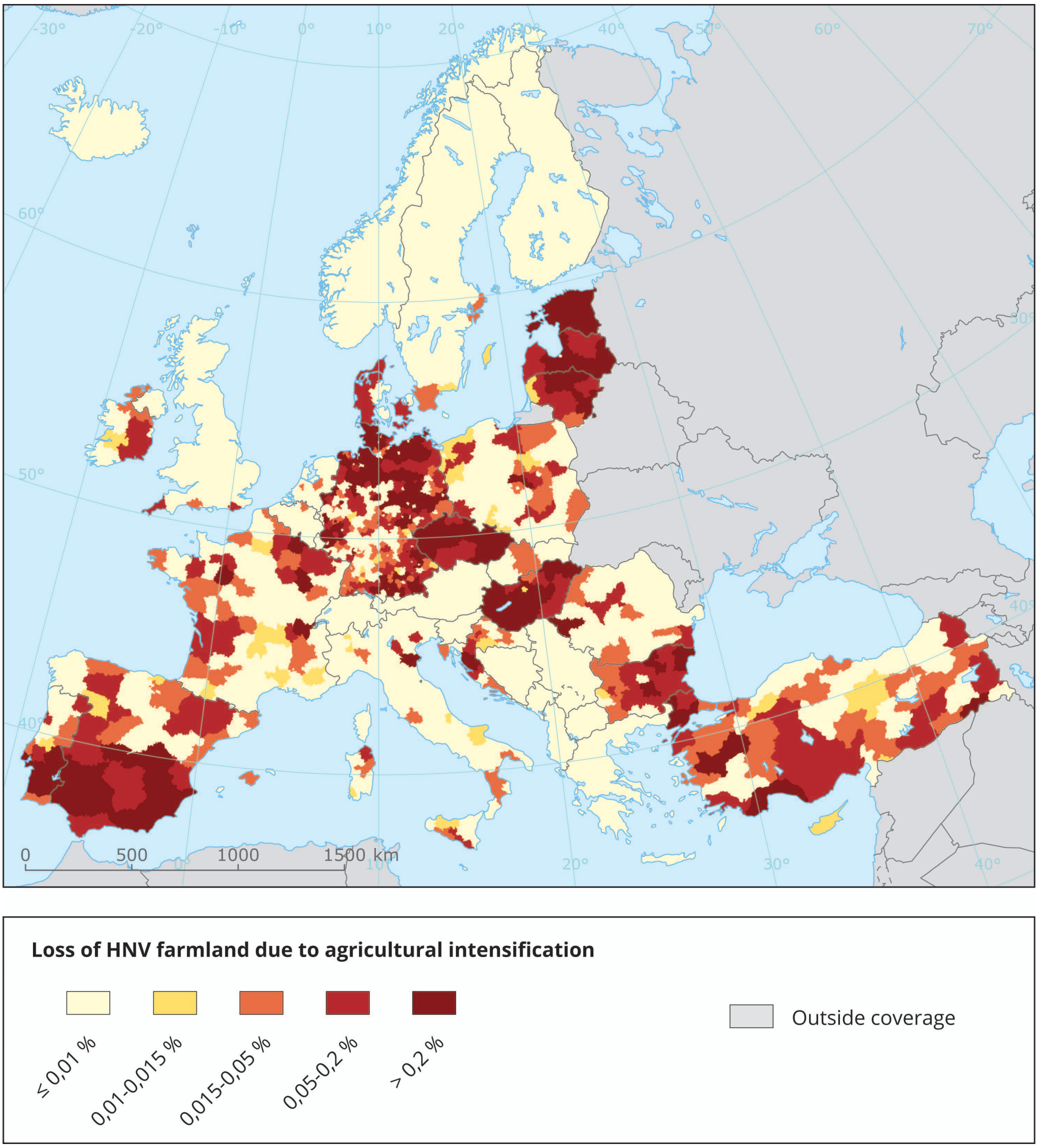

Figure 2: Pérdida de tierras agrícolas de alto valor natural debida la intensificación agrícola (European Environment Agency, 2019).

La preocupación por estos efectos negativos sobre la biodiversidad y los servicios ecosistémicos ha llevado al desarrollo de alternativas a la agricultura intensiva, entre las que destaca la agricultura ecológica (Rahmann, 2011). Este método de producción agrícola elimina o evita casi por completo el uso de pesticidas, herbicidas y fertilizantes sintéticos (Tuck et al., 2014) y promueve prácticas consideradas beneficiosas para el ecosistema, como la rotación de cultivos, el uso de semillas autóctonas, y la integración de la ganadería en los sistemas agrícolas (Emeana et al., 2018; Macfadyen et al., 2009).

Cada vez hay más evidencias de que, en comparación con la agricultura intensiva, la agricultura ecológica conlleva importantes beneficios para la biodiversidad, incrementando la riqueza y abundancia de especies a escala local en aproximadamente un 34 % y un 50 %, respectivamente (Bengtsson et al., 2005; Hole et al., 2005; Tscharntke et al., 2021). Grupos como las plantas y las abejas son los que más se benefician de la agricultura ecológica, mientras que otros artrópodos y las aves se ven favorecidos en menor medida (Seufert y Ramankutty, 2017). Además, los efectos positivos de la agricultura ecológica también varían según el contexto paisajístico, siendo generalmente mayores en paisajes simplificados que presentan una elevada cobertura de cultivos intensivos (Seufert y Ramankutty, 2017); y según el tipo de cultivo, con más beneficios proporcionados en los cultivos de cereales que en los de hortalizas y frutales (Bruggisser et al., 2010; Macfadyen et al., 2009; Tuck et al., 2014). La agricultura ecológica no es la única medida de extensificación para contrarrestar las consecuencias negativas de la agricultura intensiva: reducir el tamaño de las parcelas, la diversificación de cultivos o el mantenimiento de parches de hábitats seminaturales son otras opciones de manejo que pueden ser incluso más beneficiosas para la biodiversidad que la aplicación de la agricultura ecológica (Batáry et al., 2017; Tscharntke et al., 2021).

3. Abandono agrícola: consecuencias para la biodiversidad

La superficie total dedicada a la agricultura ha disminuido ligeramente en los últimos 20 años, pero esta disminución no ha sucedido por igual en todo el mundo, siendo Europa la región que ha perdido el mayor porcentaje de tierras agrícolas (5 %) (FAO, 2022). Esto significa que, en Europa, más de 18,5 millones de hectáreas agrícolas han perdido esta función, principalmente debido al abandono (FAOSTAT, 2022; Pereira y Navarro, 2015). Este proceso está impulsado fundamentalmente por factores socioeconómicos, como la migración del campo a la ciudad en busca de mejores oportunidades (Benayas et al., 2007).

El abandono de la agricultura puede verse como una oportunidad para la restauración de la naturaleza (conocido por el término en inglés *rewilding*, que se define como la "gestión pasiva de la sucesión ecológica con el objetivo de restaurar los procesos naturales del ecosistema y reducir el control humano de los paisajes" (Gillson et al., 2011; Pereira y Navarro, 2015)) o como una amenaza para la rica biodiversidad que se encuentra asociada a los sistemas agrícolas tradicionales (Fischer et al., 2012; Plieninger y Bieling, 2013). Algunos estudios han encontrado resultados positivos del abandono agrícola. Por ejemplo, la recuperación de los bosques, a través de la sucesión de la vegetación, puede dar lugar a un mayor secuestro de carbono, una mayor provisión de recursos madereros, la recuperación del suelo y una mayor disponibilidad de nutrientes (Benayas et al., 2007; Pointereau et al., 2008; Pugh et al., 2019). Otros muestran impactos negativos como la erosión del suelo, el aumento del riesgo de incendios forestales y la reducción de la disponibilidad de agua (Benayas et al., 2007; Bentley y Coomes, 2020; Moreira y Russo, 2007; Stanchi et al., 2012).

Se han realizado varias revisiones y metaanálisis con el objetivo de comprender las consecuencias del abandono de la agricultura sobre la biodiversidad. Sin embargo, la principal conclusión es que no existe una única respuesta a esta pregunta, ya que estas consecuencias parecen depender de la región, los taxones, la escala, el clima y el contexto local considerados (Plieninger et al., 2014; Queiroz et al., 2014; Quintas-Soriano et al., 2022). En una revisión global, Benayas et al. (2007) encontraron 77 estudios que observaron efectos negativos y 39 que encontraron efectos positivos sobre la biodiversidad. Queiroz et al. (2014) descubrieron que el 65 % de los estudios que evaluaban los efectos del abandono agrícola sobre la biodiversidad en Europa reportaron efectos negativos y solo el 6 % efectos positivos, con grandes diferencias entre taxones. En una revisión centrada en la región mediterránea, Plieninger et al. (2014) encontraron ligeros incrementos en la riqueza y abundancia de plantas y animales tras el abandono, aunque sus resultados fueron muy heterogéneos, y observaron de una tendencia generalmente negativa tras periodos de abandono de 50 años o más. Katayama et al. (2019) centraron su revisión en cultivos permanentes (huertos y viñedos), incluyendo 12 estudios que compararon los niveles de biodiversidad entre agroecosistemas convencionales y abandonados (principalmente cultivos de manzano), encontrando efectos generalmente positivos en la diversidad alfa, beta y gamma. La última y más reciente de estas revisiones fue realizada por Quintas-Soriano et al. (2022) en la región mediterránea y, aunque este trabajo presentaba un enfoque más amplio, sobre los efectos del abandono en las contribuciones de la naturaleza a las personas, también consideraba los efectos del abandono agrícola en la biodiversidad y encontraron consecuencias mayoritariamente negativas (aunque el 80 % de los estudios que consideraron se centraban en plantas y aves).

Resulta evidente que es necesaria más investigación para desentrañar los efectos del abandono agrícola sobre la biodiversidad en general, y los artrópodos en particular, especialmente en agroecosistemas poco representados como los cultivos permanentes tradicionales (Kajtoch, 2017; Quintas-Soriano et al., 2022).

4. Contexto paisajístico: el papel de los hábitats seminaturales

Los agroecosistemas, ya sean tradicionales o intensivos, no están aislados de los hábitats circundantes, sino que se ven afectados por ellos. La biodiversidad que albergan, así como las consecuencias de las prácticas de manejo o de medidas agroambientales como la agricultura ecológica, dependen del contexto paisajístico (Concepción et al., 2012; Tscharntke et al., 2012). El contexto paisajístico puede definirse a partir de dos características principales: la composición y la configuración del paisaje (Fig. 3) (Duelli, 1997; Fahrig et al., 2011; Martin et al., 2019). La composición del paisaje se refiere a la disponibilidad y las cantidades relativas de diferentes usos del suelo, como pueden ser pastizales, cultivos permanentes, tierras arables, bosques o hábitats seminaturales (Martin et al., 2016). Por otro lado, la configuración del paisaje se centra en la disposición espacial de los diferentes hábitats, así como en la forma de cada parche, proporcionando información sobre la densidad de los ecotonos entre los tipos de hábitat y su grado de interpenetración (Fahrig et al., 2011; Martin et al., 2016). Existen numerosos parámetros para medir la configuración del paisaje, entre los que destacan la densidad o longitud de los bordes y el tamaño medio de los parches (Fahrig et al., 2015; Martin et al., 2016).

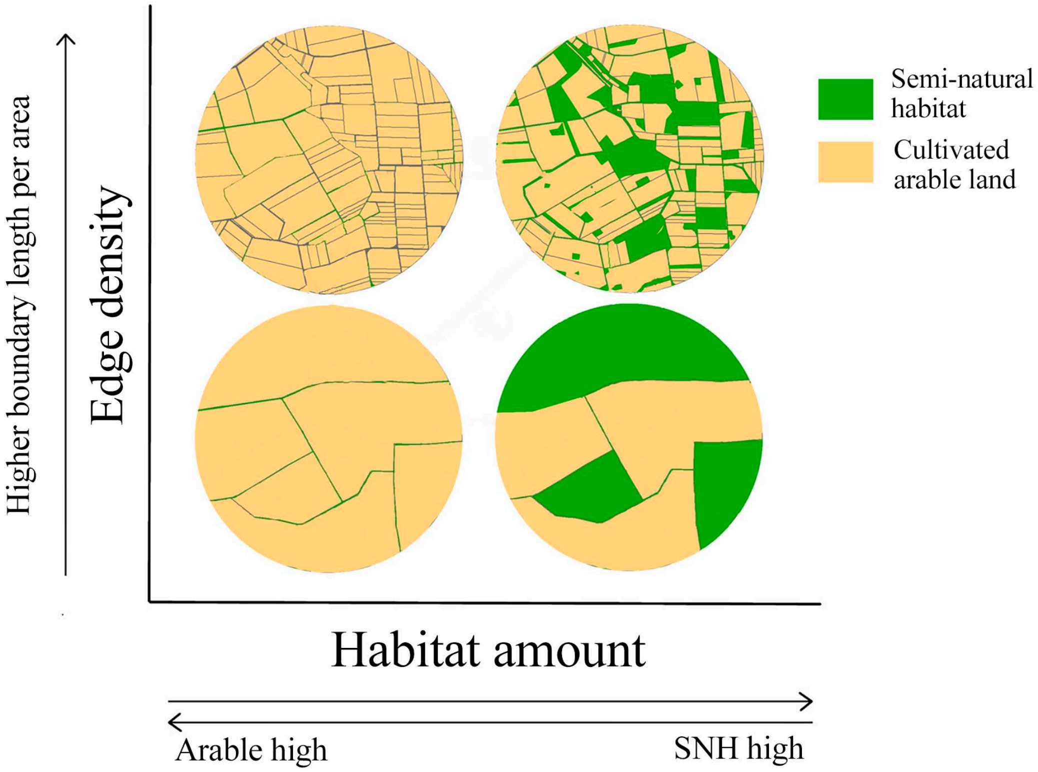

Figure 3: Representación conceptual de las diferencias en composición y configuración del paisaje (modificado a partir de Martin et al. (2019)). Se representan cuatro paisajes agrícolas teóricos con diferente composición paisajística (cantidad de hábitat) y configuración (densidad de borde).

Los efectos de la composición y configuración del paisaje sobre la biodiversidad son variados y específicos para cada taxón (Bottero et al., 2023). Sin embargo, en general se puede asumir que los paisajes que presentan varios tipos de hábitats diferentes son capaces de sustentar una diversidad de especies superior a la de aquellos paisajes dominados por uno o dos tipos de usos del suelo, ya que distintos hábitats pueden favorecer a especies diferentes (Bianchi et al., 2006; Sirami et al., 2019). Además, el aumento de la heterogeneidad configuracional (es decir, parches más pequeños y mayor densidad de bordes) favorece la riqueza y abundancia de múltiples taxones (Fahrig et al., 2011; Sirami et al., 2019).

Las respuestas de la biodiversidad a la composición y configuración del paisaje también dependen de la escala considerada, ya que especies distintas tienden a responder al contexto paisajístico a diferentes escalas (Holland et al., 2004; Martin, 2018; Martin y

Fahrig, 2012). Distintas variables ambientales pueden afectar a una respuesta determinada de una especie a diferentes escalas espaciales (Coffey y Fahrig, 2012; McGarigal et al., 2016; Patenaude et al., 2015). Asimismo, la escala del efecto de una determinada variable ambiental parece depender del tipo de respuesta (por ejemplo, que la abundancia de una especie responda a la composición del paisaje a una escala diferente que la presencia o fecundidad de esa especie) (Martin, 2018). Sin embargo, el principal predictor de la escala espacial a la que responde una especie suele ser su capacidad de dispersión (a mayor distancia de dispersión o área de campeo, mayor escala de respuesta (Jackson y Fahrig, 2012; Miguet et al., 2016)), aunque esta relación podría no ser tan directa como se pensaba (Arroyo-Rodríguez et al., 2023). Por lo tanto, es importante evaluar las respuestas de la biodiversidad a la composición y configuración del paisaje a diferentes escalas espaciales (Arroyo-Rodríguez et al., 2023; Jackson y Fahrig, 2015).

La mayoría de los estudios que evalúan los efectos de la composición paisajística sobre la biodiversidad en paisajes agrícolas se han centrado en la superficie de hábitats seminaturales (SNH) como indicador de la complejidad del paisaje (p. ej., Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Gkisakis et al., 2016; Marja et al., 2022; Rusch et al., 2016). Los SNH, definidos como "cualquier hábitat dentro o fuera del cultivo que contenga una comunidad de especies vegetales no cultivadas" (Holland et al., 2017) son esenciales para el mantenimiento de la biodiversidad en paisajes agrícolas (Estrada-Carmona et al., 2022; Gámez-Virués et al., 2015; Marja et al., 2022; Tscharntke et al., 2021), donde hasta el 65 % de las especies animales dependen de la presencia de estos hábitats (Duelli y Obrist, 2003). Varios estudios han demostrado una disminución de la diversidad de especies con la pérdida de SNH o con el aumento de la distancia a estos hábitats (por ejemplo, Batáry et al., 2011; Garibaldi et al., 2011). Los hábitats seminaturales proporcionan una amplia gama de microhábitats y condiciones microclimáticas, recursos alternativos (por ejemplo, recursos de forrajeo, presas y hospedadores y recursos de nidificación), refugio y lugares de hibernación para artrópodos beneficiosos y otros grupos (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Duelli y Obrist, 2003; Estrada-Carmona et al., 2022; Hevia et al., 2021; Kennedy et al., 2013; Marino y Landis, 1996; Maurer et al., 2022; Tscharntke et al., 2021; Zhu et al., 2023). Además, los SNH suelen tener una vegetación estructuralmente más compleja, una variable importante para diferentes grupos de artrópodos (por ejemplo, parasitoides (Bartual et al., 2019; Finke y Denno, 2002; Meyhofer y Hindayana, 2000) o arañas (Benhadi-Marín et al., 2020; Rosas-Ramos et al., 2019, 2018; Uetz et al., 1999)) y otros taxones (por ejemplo, aves (Kajtoch, 2017)).

Los paisajes más complejos (es decir, aquellos con una mayor cobertura de SNH) albergan una mayor diversidad de especies, contrarrestando la homogeneización biótica, y promueven la estabilidad de las dinámicas poblacionales a través de una mayor resiliencia y capacidad para recuperarse de las perturbaciones (Bengtsson et al., 2003; Estrada-Carmona et al., 2022; Feit et al., 2021; Gámez-Virués et al., 2015; Oliver et al., 2010; Tscharntke et al., 2012). Además, la complejidad del paisaje puede mediar en las respuestas de la biodiversidad al manejo a escala local, como propone la *hipótesis de la complejidad intermedia del paisaje* (Concepción et al., 2012; Tscharntke et al., 2012). Esta hipótesis sostiene que "la eficacia de las medidas de conservación a escala local es moderada por el paisaje, siendo mayor en los paisajes estructuralmente sencillos que en los extremadamente simplificados o muy complejos" (Tscharntke et al., 2012); lo que significa que tanto en los paisajes intensificados (<1% de hábitat no cultivado) como en los complejos (>20% de hábitat no cultivado), solo cabe esperar pequeñas respuestas positivas a las medidas de extensificación a escala local (como la agricultura ecológica o el abandono) debido a la escasez de reservas de especies en el paisaje y a la elevada inmigración procedente de los hábitats seminaturales, respectivamente, y que solo los paisajes simples, con niveles intermedios de complejidad, responden positivamente a estas medidas. Por lo tanto, considerar el contexto paisajístico es fundamental en los estudios que evalúan los efectos del manejo o del cambio de uso del suelo sobre la biodiversidad asociada a los paisajes agrícolas (Beaumelle et al., 2021; Karp et al., 2018; Tscharntke et al., 2012).

5. Biodiversidad de artrópodos en agroecosistemas

El término biodiversidad engloba a la variedad de organismos vivos, a las diferencias genéticas entre ellos, a las comunidades y ecosistemas en los que se encuentran y a los procesos ecológicos y evolutivos que los mantienen en funcionamiento y en constante cambio y adaptación (Noss y Cooperrider, 1994). En los ecosistemas agrícolas, la biodiversidad depende de varios factores, entre los que destacan cuatro: la diversidad de la vegetación dentro y alrededor del agroecosistema; la presencia de los distintos cultivos dentro del agroecosistema; la intensidad del manejo y el grado de aislamiento del agroecosistema con respecto a la vegetación natural (Altieri y Nicholls, 2004; Southwood y Way, 1970).

Tanto la biodiversidad planificada de los agroecosistemas (es decir, las especies cultivadas o ganaderas incluidas intencionadamente por el agricultor) como la biodiversidad asociada (las especies que colonizan los cultivos procedentes de zonas adyacentes y que prosperan en ellos en función de su estructura y tipo de manejo) intervienen en el funcionamiento del ecosistema y proporcionan importantes servicios ecosistémicos (Altieri y Nicholls, 2004), que se definen como los beneficios que el ser humano obtiene de los ecosistemas (Millennium Ecosystem Assessment, 2005).

Los artrópodos constituyen uno de los principales componentes de la biodiversidad asociada a los agroecosistemas. Este grupo extremadamente diverso y abundante tiene importantes implicaciones para la productividad agrícola, ya que incluye algunos de los principales proveedores de servicios ecosistémicos fundamentales, como la polinización, el control natural de plagas y la descomposición (Isaacs et al., 2009; McCravy, 2018; Noriega et al., 2018). Sin embargo, los artrópodos también pueden causar graves daños, ya que muchos de sus grupos constituyen plagas agrícolas capaces de causar impactos significativos en la producción (Vansynghel et al., 2022), además de otros efectos negativos mediados por este grupo, como la depredación de enemigos naturales y polinizadores y el daño o transmisión de patógenos a las plantas (Barbercheck y Wallace, 2021; Pereira et al., 2004; Way y Khoo, 1992).

5.1 Bactrocera oleae y sus enemigos naturales

Bactrocera oleae (Rossi, 1790) (Diptera: Tephritidae), la mosca del olivo, constituye la principal plaga de los olivares a nivel global (Ortega et al., 2016). En la cuenca mediterránea, que concentra el 98 % del cultivo mundial del olivo (Bueno y Jones, 2002), esta plaga provoca pérdidas de hasta el 40 % de la producción (Pereira et al., 2004) o, en algunos casos, de casi el 100 % (Boccaccio y Petacchi, 2009), además de una reducción de la calidad del fruto, tanto para aceituna de mesa como para aceite (Nardi et al., 2005).

Generalmente, los adultos de *B. oleae* emergen a principios de primavera, se reproducen, se dispersan y depositan sus huevos en el interior de las aceitunas en torno a julio (Marchini et al., 2017). Durante este periodo son especialmente vulnerables a depredadores generalistas como arañas (Picchi et al., 2017a) y aves (Bigler et al., 1986). Las larvas emergen de los huevos a los 2-3 días (Marchini et al., 2017) y se desarrollan alimentándose del mesocarpo de la aceituna, periodo durante el que son particularmente susceptibles al ataque de parasitoides (Boccaccio y Petacchi, 2009; Ortega et al., 2016). Desde el verano hasta mediados de otoño, las larvas completan el ciclo en el interior de las aceitunas, emergiendo los adultos en 10-15 días (Marchini et al., 2017; Pereira et al., 2004); mientras que, a partir de mediados de otoño, las larvas de tercer estadio abandonan las aceitunas y pupan en la capa superficial del suelo (~ 3 cm) (Dimou et al., 2003), permaneciendo quiescentes hasta la primavera (Delrio y Lentini, 2016). En el suelo, las pupas son vulnerables frente a depredadores edáficos generalistas, especialmente carábidos, estafilínidos, arañas y hormigas (Dinis et al., 2016). En la región mediterránea, la mosca del olivo puede completar entre 3 y 5 ciclos al año (Preu et al., 2020).

Los escarabajos de las familias Carabidae y Staphylinidae son depredadores generalistas abundantes en los agroecosistemas, que proporcionan un valioso servicio de control biológico al reducir las poblaciones de varios artrópodos que constituyen plagas (Albertini et al., 2017; MacLeod et al., 2004). Las hormigas, el grupo de artrópodos edáficos más abundante en los olivares, también pueden actuar como agentes de control de plagas, además de participar en otros procesos ecosistémicos y servir como bioindicadores (Campos et al., 2011; Peck et al., 1998; Santos et al., 2007); aunque también pueden causar daños, por ejemplo, a través de la depredación de enemigos naturales (Pereira et al., 2004).

Además de por la depredación y parasitismo por parte de enemigos naturales, las poblaciones de *B. oleae* pueden verse afectadas por otros factores, de forma directa o indirecta, como el clima, el contexto paisajístico y las prácticas de manejo de los cultivos (Delrio y Lentini, 2016; Ortega et al., 2018). Por ejemplo, Picchi et al. (2017b) demostraron que la agricultura ecológica puede causar una disminución de las pupas de *B. oleae*, debido a una mayor presencia de enemigos naturales en comparación con las parcelas manejadas de forma convencional.

5.2 Arañas

Las arañas son (con algunas excepciones) depredadores generalistas abundantes y ubicuos en los ecosistemas terrestres, donde constituyen una parte importante de todos los invertebrados depredadores (Wise, 1993). Las arañas son un grupo diverso de artrópodos, con algo más de 51 000 especies (World Spider Catalog, 2023), que atacan principalmente a insectos, pero también a una amplia gama de otros artrópodos, incluidas otras arañas, pudiendo afectar a la densidad de presas y a las dinámicas de la estructura de la comunidad (Wise, 1993). Además, son uno de los grupos de depredadores más abundante en los agroecosistemas, donde pueden reducir significativamente las poblaciones de insectos que constituyen plagas (Benamú et al., 2017; Marc et al., 1999; Michalko et al., 2019; Nyffeler y Sunderland, 2003).

Las arañas presentan una serie de diferentes estrategias para la captura de sus presas, tipos de tela, preferencia por distintas presas o periodos de actividad, que permiten su clasificación en gremios ("grupo de especies que explotan la misma clase de recursos ambientales de manera similar" (Root, 1973)) (Cardoso et al., 2011; Uetz et al., 1999). Esto tiene importantes implicaciones para el papel de las arañas en los ecosistemas naturales y agrícolas, ya que especies sintópicas de gremios distintos pueden mostrar una gran variabilidad de presas y explotar diferentes recursos, complementándose entre sí (Nyffeler et al., 1989; Sunderland y Samu, 2000; Uetz et al., 1999). Los principales gremios de arañas, propuestos por Uetz et al. (1999) y posteriormente modificados por Cardoso et al. (2011), son: cazadoras de las hojas, cazadoras del suelo, cazadoras por acoso, cazadoras al acecho, constructoras de telas en sábana, constructoras de telas orbiculares y constructoras de telas espaciales.

Las arañas se ven afectadas por las características del hábitat a escala local (Barton et al., 2017; Theron et al., 2020), siendo particularmente sensibles a la fisonomía del ambiente (por ejemplo, la complejidad de la arquitectura o la diversidad de la vegetación) (Dennis et al., 2015; Gómez et al., 2016; Spears y MacMahon, 2012; Uetz et al., 1999; Wise, 1993) y a la disponibilidad de presas (Halaj et al., 1998; Markó et al., 2009; Spears y MacMahon, 2012). En los agroecosistemas, las arañas se ven afectadas por las medidas de manejo a escala local y por el contexto paisajístico. Por ejemplo, las arañas se ven favorecidas por el manejo ecológico (Bengtsson et al., 2005; Cárdenas et al., 2015; Kolb et al., 2020; Rosas-Ramos et al., 2020b; pero véase Bruggisser et al., 2010) y las infraestructuras ecológicas complejas (Cárdenas et al., 2015; Rosas-Ramos et al., 2019, 2018), y afectadas negativamente por la aplicación de pesticidas (por ejemplo, Picchi et al., 2017a). Además, varios estudios han observado una mayor diversidad de arañas en paisajes complejos o de configuración heterogénea (Bianchi et al., 2006; Kolb et al., 2020; Mestre et al., 2018; Rischen et al., 2023; Schmidt y Tscharntke, 2005; Shackelford et al., 2013; pero véase Picchi et al., 2017a).

5.3 Himenópteros parasitoides

Los parasitoides son insectos cuyas larvas se desarrollan alimentándose del cuerpo de otros artrópodos, normalmente insectos, a los que terminan matando. Se diferencian de los depredadores en que sólo necesitan un único hospedador para alcanzar el estado adulto, y de los parásitos en que el hospedador siempre muere (Godfray, 1994). Existen parasitoides en muchos órdenes de insectos, que en número decreciente de especies son los siguientes: Hymenoptera, Diptera, Coleoptera, Neuroptera, Lepidoptera, Strepsiptera y Trichoptera (Godfray, 1994; Heraty, 2017). Los himenópteros parasitoides comprenden alrededor del 75 % de todas las especies de parasitoides, con aproximadamente 80 000 especies descritas (Belshaw et al., 2003; Huber, 2017). Sin embargo, los himenópteros parasitoides son uno de los grupos de insectos menos conocido y el número estimado de especies existentes oscila entre 176 000 y 6 millones, aunque las estimaciones más probables varían entre 630 000 y 1.6 millones de especies (Godfray, 1994; Heraty, 2017; LaSalle y Gauld, 1991).

Teniendo en cuenta cómo interactúan con su hospedador, los parasitoides pueden dividirse en varias categorías, útiles para describir las principales estrategias conocidas (Godfray, 1994; Nastasi et al., 2023). Atendiendo a su rango de hospedadores, los parasitoides se consideran polífagos cuando pueden atacar a una amplia variedad de hospedadores no relacionados (de diferentes familias u órdenes), oligófagos cuando se limitan a unos pocos hospedadores estrechamente relacionados, y monófagos si parasitan a una sola especie de hospedador. Los parasitoides pueden ser ectoparasitoides o endoparasitoides, si se desarrollan externamente o dentro del cuerpo de sus hospedadores, respectivamente. Los parasitoides idiobiontes paralizan a sus hospedadores y detienen su desarrollo, mientras que los parasitoides koinobiontes no interrumpen el desarrollo de sus hospedadores. Dependiendo del número de individuos que se desarrollen en un único hospedador pueden clasificarse, a grandes rasgos, como solitarios (un solo huevo por hospedador) o gregarios (varias larvas se desarrollan dentro de cada hospedador), aunque existen interacciones más complejas, incluyendo el hiperparasitismo (parasitoides que utilizan a otros parasitoides como hospedadores) (Godfray, 1994; Nastasi et al., 2023). Los parasitoides de insectos holometábolos pueden clasificarse a su vez en función de la fase a la que atacan, diferenciando entre parasitoides de huevos, larvas, pupas y adultos. Algunos parasitoides koinobiontes ponen sus huevos en una fase del hospedador, pero emergen de otra, por ejemplo, parasitoides huevo-larva o parasitoides larva-pupa (Godfray, 1994).

Los hospedadores de los parasitoides son casi exclusivamente insectos, aunque algunas especies atacan a arañas, ácaros o incluso ciempiés (Godfray, 1994; Nastasi et al., 2023). Los parasitoides tienen un papel fundamental en la regulación natural de las poblaciones de hospedadores y, por tanto, en el funcionamiento y estabilidad de los ecosistemas terrestres, donde participan en numerosas interacciones tróficas (LaSalle y Gauld, 1993, 1991; Shaw y Hochberg, 2001). Además, su capacidad para regular poblaciones de insectos fitófagos los convierte en uno de los principales grupos responsables del control natural de plagas (servicio ecosistémico valorado en más de 20.000 millones de dólares anuales solo en EEUU), siendo ampliamente utilizados en programas de control biológico (Hajek y Eilenberg, 2018; Henri y Van Veen, 2011; LaSalle y Gauld, 1993; Pennisi, 2010).

Varias características hacen de los himenópteros parasitoides un grupo particularmente propenso a la extinción: pertenecen a un nivel trófico alto, siendo particularmente sensibles a las perturbaciones ambientales; pueden tener poblaciones crónicamente pequeñas y a menudo dependen de recursos poco fiables, por ejemplo, cuando regulan eficazmente a hospedadores con bajas densidades poblacionales (LaSalle y Gauld, 1993, 1991; Shaw y Hochberg, 2001). A pesar de su importancia y de su elevado riesgo de extinción, los parasitoides son generalmente ignorados en las estrategias de conservación de insectos (Shaw y Hochberg, 2001).

En los paisajes agrícolas, los parasitoides son particularmente vulnerables a las prácticas de manejo intensivas (por ejemplo, el uso de pesticidas), pero se benefician de la presencia de recursos alimenticios (néctar, polen y melaza) y hospedadores, incluidas las plagas de los cultivos (Bianchi et al., 2006; Cronin y Reeve, 2005; Kishinevsky et al., 2017; Mates et al., 2012; Shaw, 2006). Varios estudios han observado una mayor diversidad de parasitoides en paisajes complejos con una elevada cobertura de SNH y una alta conectividad entre parches, ya que los parasitoides se benefician de los hábitats estructuralmente más complejos, los recursos de refugio y alimentación, los lugares de hibernación y los hospedadores alternativos que proporcionan los SNH (Bianchi et al., 2006; Boccaccio y Petacchi, 2009; Chaplin-Kramer et al., 2011; Holland et al., 2016; Marino y Landis, 1996; Marja et al., 2022; Martin et al., 2019).

5.4 Abejas

Las abejas son un grupo diverso de insectos polinizadores que cuenta con más de 20 000 especies en todo el mundo (Danforth et al., 2019). Son los principales polinizadores de plantas silvestres y cultivadas y, como tales, desempeñan un papel fundamental en el mantenimiento de la biodiversidad y los procesos ecosistémicos, ya que alrededor del 90% de las angiospermas y una proporción significativa de las gimnospermas dependen de la polinización animal (Ollerton, 2017; Ollerton et al., 2011; Potts et al., 2016, 2010). De todas las especies de abejas, solo 50 son manejadas en la actualidad, 12 de ellas específicamente para la polinización de cultivos (principalmente, la abeja de la miel europea *Apis mellifera* Linnaeus 1758); sin embargo, las abejas silvestres y las manejadas contribuyen de forma similar a la polinización de cultivos, valorada en unos 3 000 $/ha, siendo esenciales para la seguridad alimentaria (Kleijn et al., 2015; Klein et al., 2018; Potts et al., 2016). A pesar de su importancia, tan solo alrededor del 2% de las especies de abejas silvestres contribuye significativamente a la polinización de los cultivos, ya que la mayoría de las especies restantes son incapaces de sobrevivir en paisajes agrícolas intensificados (Kleijn et al., 2015). Numerosos estudios han mostrado una disminución significativa de la diversidad y abundancia de abejas silvestres, lo que podría limitar los servicios de polinización (Ollerton et al., 2011; Potts et al., 2010; Zattara y Aizen, 2021). Los cambios en el uso del suelo y la intensidad del manejo, el cambio climático, el uso de pesticidas y organismos modificados genéticamente, el manejo de los polinizadores, los patógenos y las especies invasoras se han identificado como las principales causas del declive de las abejas (Potts et al., 2016).

La mayor parte de las abejas manejadas son sociales (es decir, tienen una división reproductiva del trabajo según la cual solo algunas hembras (las reinas) se reproducen, mientras que otras (las obreras) recolectan polen y néctar, construyen y protegen el nido y ayudan a criar a la descendencia de la reina). Sin embargo, las abejas silvestres son, en su mayoría, solitarias (> 75%); solo un 13% son cleptoparásitas (parásitas de nidos) y un 9% son sociales (con un amplio rango de niveles de sociabilidad) (Danforth et al., 2019). Cada abeja solitaria tiene la capacidad de reproducirse, construye y mantiene su propio nido y recolecta los recursos florales (principalmente polen y néctar) necesarios para abastecer sus celdas de cría (Danforth et al., 2019; Michener, 2007). Las abejas silvestres varían en sus comportamientos de nidificación, pudiendo presentar diversas estrategias en relación al lugar donde construyen sus nidos, el tipo de sustrato que utilizan y el material que requieren para construirlos (Danforth et al., 2019; Michener, 2007; Potts et al., 2005). Estas características permiten clasificar a las abejas silvestres (con algunas excepciones) en tres grandes gremios de nidificación: especies que excavan sus nidos en el suelo (la mayoría de las especies pertenecen a este gremio), especies que anidan en cavidades preexistentes (por ejemplo, tallos huecos de plantas, cavidades en rocas, madrigueras de insectos abandonadas, conchas de caracoles), y especies que excavan sus nidos en sustratos leñosos (Danforth et al., 2019; Michener, 2007; Potts et al., 2005). Además, las abejas varían en su grado de especialización alimentaria, pudiendo diferenciarse abejas monolécticas, que recolectan polen de una sola especie de planta; abejas oligolécticas, que recolectan polen de varias especies pertenecientes a un mismo género o familia; y abejas polilécticas, que recolectan polen de varias familias distintas (Cane y Sipes, 2006; Müller y Kuhlmann, 2008). Pueden dividirse a su vez en subcategorías en función de la amplitud de su dieta dentro de cada categoría, pudiendo cosiderarse oligolécticas o polilécticas de rango amplio o estrecho (Cane y Sipes, 2006; Müller y Kuhlmann, 2008). Otro factor que afecta a la especialización alimentaria es la longitud de la lengua, ya que las abejas de lengua larga pueden acceder a flores más profundas, de corolas largas, mientras que las de lengua corta están limitadas a flores de corolas poco profundas, con néctar y polen más expuestos (Michener, 2007). Además, las abejas son forrajeadoras de lugar central y necesitan tener acceso a todos los recursos que requieren para completar su ciclo de vida dentro de su área y periodo de vuelo (Ogilvie y Forrest, 2017; Westrich, 1996).

Dentro de los agroecosistemas, las características de las abejas y sus requerimientos determinan sus respuestas frente a las medidas de manejo a escala local y a la composición y configuración del paisaje (Hall et al., 2019; Kennedy et al., 2013; Williams et al., 2010; Williams y Kremen, 2007). Por ejemplo, varios estudios han demostrado que las abejas dependen de los recursos proporcionados por los hábitats seminaturales, viéndose favorecidas por una mayor cobertura de estos hábitats en el paisaje (Estrada-Carmona et al., 2022; Kennedy et al., 2013; Maurer et al., 2022; Roth et al., 2023) y perjudicadas al estar aisladas de ellos (Garibaldi et al., 2011; Ricketts et al., 2008); mientras que una mayor heterogeneidad en la configuración paisajística (por ejemplo, mayor densidad de borde) tiende a afectarlas positivamente (Hass et al., 2018; Holzschuh et al., 2010; Martin et al., 2019; pero véase Maurer et al., 2022).

6. Objetivos de la tesis

El objetivo principal de esta tesis es analizar las consecuencias del abandono de cultivos tradicionales permanentes bajo diferentes sistemas agrícolas y contextos paisajísticos sobre las comunidades de artrópodos beneficiosos asociadas y una importante plaga agrícola. Los objetivos específicos son:

1. Analizar el efecto del abandono de olivares tradicionales y del manejo ecológico sobre la población de *Bactrocera oleae* y sobre la composición de la comunidad de enemigos naturales, los parámetros de diversidad y las familias dominantes (Capítulo I).

2. Evaluar las diferencias de composición, riqueza y abundancia de las comunidades de arañas, abejas y parasitoides entre parcelas de cultivo tradicional de almendro abandonadas y activas en paisajes simples y complejos, analizando sus respuestas a la cobertura de hábitats seminaturales a 150 m y 500 m (Capítulo II).

3. Estudiar cómo el contexto paisajístico y la tasa de recambio pueden mediar en las respuestas de la comunidad de parasitoides, a nivel de género (composición

y parámetros de diversidad), al abandono de parcelas de almendro tradicionales y a la cobertura de usos del suelo a 150 m y 500 m (Capítulo III).

4. Investigar las respuestas taxonómicas y a nivel de gremios de las abejas al abandono de cultivos de almendro tradicionales en paisajes con porcentajes diferentes de hábitats seminaturales, así como a la composición del uso del suelo a diferentes escalas, evaluando el papel del recambio de especies en la mediación de estas respuestas (Capítulo IV).

5. Describir una nueva especie del género *Lonchidia* (Hymenoptera: Figitidae) y proporcionar una clave de determinación para separar las especies europeas (Capítulo V).

References | Referencias

Albertini, A., Pizzolotto, R., Petacchi, R., 2017. Carabid patterns in olive orchards and woody semi-natural habitats: first implications for conservation Biol Control against *Bactrocera oleae*. BioControl 62, 71–83. https://doi.org/10.1007/S10526-016-9780-X/FIGURES/5

Altieri, M.A., Nicholls, C.I., 2004. Biodiversity and Pest Management in Agroecosystems, 2nd ed. The Haworth Press, New York.

Andersen, E., Baldock, D., Bennet, H., Beaufoy, G., Bignal, E., Brouwer, F., Elbersen, B., Eiden, G., Godeschalk, F., Jones, G., McCracken, D., Nieuwenhuizen, W., van Eupen, M., Hennekes, S., Zervas, G., 2003. Developing a High Nature Value Farming area indicator. Final report. European Environment Agency, Copenhagen, Denmark.

Arroyo-Rodríguez, V., Martínez-Ruiz, M., Bezerra, J.S., Galán-Acedo, C., San-José, M., Fahrig, L., 2023. Does a Species' Mobility Determine the Scale at Which It Is Influenced by the Surrounding Landscape Pattern? Curr Landsc Ecol Rep 8, 23–33. https://doi.org/10.1007/S40823-022-00082-7

Baldock, D., Beaufoy, G., Clark, J., 1994. The Nature of Farming. Low Intensity Farming Systems in Nine European Countries. Institute for European Environmental Policy, London.

Barbercheck, M.E., Wallace, J., 2021. Weed–Insect Interactions in Annual Cropping Systems. Ann Entomol Soc Am 114, 276–291. https://doi.org/10.1093/AESA/SAAB002

Barton, P.S., Evans, M.J., Foster, C.N., Cunningham, S.A., Manning, A.D., 2017. Environmental and spatial drivers of spider diversity at contrasting microhabitats. Austral Ecol 42, 700–710. https://doi.org/10.1111/aec.12488

Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. Agric Ecosyst Environ 279, 43–52. https://doi.org/10.1016/j.agee.2019.04.009

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. Proc R Soc B: Biol Sci 278, 1894–1902. https://doi.org/10.1098/rspb.2010.1923

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv Biol 29, 1006–1016. https://doi.org/10.1111/cobi.12536

Batáry, P., Gallé, R., Riesch, F., Fischer, C., Dormann, C.F., Mußhoff, O., Császár, P., Fusaro, S., Gayer, C., Happe, A.K., Kurucz, K., Molnár, D., Rösch, V., Wietzke, A., Tscharntke, T., 2017.

The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. Nat Ecol Evol 1, 1279–1284. https://doi.org/10.1038/s41559-017-0272-x

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

Belshaw, R., Grafen, A., Quicke, D.L.J., 2003. Inferring life history from ovipositor morphology in parasitoid wasps using phylogenetic regression and discriminant analysis. Zool J Linn Soc 139, 213–228. https://doi.org/10.1046/j.1096-3642.2003.00078.x

Benamú, M.A., Lacava, M., García, L.F., Santana, M., Viera, C., 2017. Spiders Associated with Agroecosystems: Roles and Perspectives, in: Viera, C., Gonzaga, M.O. (Eds.), Behaviour and Ecology of Spiders: Contributions from the Neotropical Region. Springer International Publishing, Cham, pp. 275–302. https://doi.org/10.1007/978-3-319-65717-2_11

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: An overview of drivers and consequences. CAB Rev: Perspect Agric Vet Sci Nutr Nat Resour 2, 1–14. https://doi.org/10.1079/PAVSNNR20072057

Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: A meta-analysis. J Appl Ecol 42, 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nyström, M., 2003. Reserves, Resilience and Dynamic Landscapes. Ambio 32, 389–396. https://doi.org/10.1579/0044-7447-32.6.389

Benhadi-Marín, J., Pereira, J.A., Sousa, J.P., Santos, S.A.P., 2020. Distribution of the spider community in the olive grove agroecosystem (Portugal): potential bioindicators. Agric For Entomol 22, 10–19. https://doi.org/10.1111/afe.12352

Bentley, L., Coomes, D.A., 2020. Partial river flow recovery with forest age is rare in the decades following establishment. Glob Chang Biol 26, 1458–1473. https://doi.org/10.1111/GCB.14954

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends Ecol Evol 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

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

Bigler, F., Neuenschwander, P., Delucchi, V., Michelakis, S., 1986. Natural enemies of preimaginal stages of *Dacus oleae* Gmel. (Dipt., Tephritidae) in Western Crete. II. Impact on olive fly populations. Boll Lab Entomol Agrar Portici 43, 79–96.

Bignal, E.M., Mccracken, D.I., 1996. Low-Intensity Farming Systems in the Conservation of the Countryside. J Appl Ecol 33, 413–424.

Boccaccio, L., Petacchi, R., 2009. Landscape effects on the complex of *Bactrocera oleae* parasitoids and implications for conservation Biol Control. BioControl 54, 607–616. https://doi.org/10.1007/s10526-009-9214-0

Bottero, I., Dominik, C., Schweiger, O., Albrecht, M., Attridge, E., Brown, M.J.F., Cini, E., Costa, C., De la Rúa, P., de Miranda, J.R., Di Prisco, G., Dzul Uuh, D., Hodge, S., Ivarsson, K., Knauer, A.C., Klein, A.-M., Mänd, M., Martínez-López, V., Medrzycki, P., Pereira-Peixoto, H., Potts, S., Raimets, R., Rundlöf, M., Schwarz, J.M., Senapathi, D., Tamburini, G., Talaván, E.T., Stout, J.C., 2023. Impact of landscape configuration and composition on pollinator communities across different European biogeographic regions. Front Ecol Evol 11, 309. https://doi.org/10.3389/FEVO.2023.1128228

Bruggisser, O.T., Schmidt-Entling, M.H., Bacher, S., 2010. Effects of vineyard management on biodiversity at three trophic levels. Biol Conserv 143, 1521–1528. https://doi.org/10.1016/j.biocon.2010.03.034

Bueno, A.M., Jones, O., 2002. Alternative methods for controlling the olive fly, *Bactrocera oleae*, involving semiochemicals. IOBC wprs Bulletin 25, 147–156.

Campos, M., Fernández, L., Ruano, F., Cotes, B., Cárdenas, M., Castro, J., 2011. Short term response of ants to the removal of ground cover in organic olive orchards. Eur J Entomol 108, 417–423. https://doi.org/10.14411/eje.2011.053

Cane, J., Sipes, S., 2006. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty, in: Waser, N., Ollerton, J. (Eds.), Plant-Pollinator Interactions from Specialization to Generalization. IL: University of Chicago Press, Chicago, pp. 99–122.

Cardenas, M., Pascual, F., Campos, M., Pekar, S., 2015. The Spider Assemblage of Olive Groves Under Three Management Systems. Environ Entomol 44, 509–518. https://doi.org/10.1093/ee/nvv030

Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kwak, M.L., Mammola, S., Ari Noriega, J., Orfinger, A.B., Pedraza, F., Pryke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C., Samways, M.J., 2020. Scientists' warning to humanity on insect extinctions. Biol Conserv 242, 108426. https://doi.org/10.1016/J.BIOCON.2020.108426

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global Patterns of Guild Composition and Functional Diversity of Spiders. PLoS One 6, e21710. https://doi.org/10.1371/journal.pone.0021710

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol Lett 14, 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Coffey, H.M.P., Fahrig, L., 2012. Relative effects of vehicle pollution, moisture and colonization sources on urban lichens. J Appl Ecol 49, 1467–1474. https://doi.org/10.1111/J.1365-2664.2012.02208.X

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J Appl Ecol 49, 695–705. https://doi.org/10.1111/j.1365-2664.2012.02131.x

Cronin, J.T., Reeve, J.D., 2005. Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. Proc R Soc B: Biol Sci 272, 2225–2235. https://doi.org/10.1098/rspb.2005.3286

Danforth, B.N., Minckley, R.L., Neff, J.L., 2019. The solitary bees: biology, evolution, conservation. Princeton University Press, Princeton.

Delrio, G., Lentini, A., 2016. Dinamica e fattori di regolazione delle popolazioni della mosca delle olive. Atti Accademia Nazionale Italiana di Entomologia 64, 55–62.

Dennis, P., Skartveit, J., Kunaver, A., McCracken, D.I., 2015. The response of spider (Araneae) assemblages to structural heterogeneity and prey abundance in sub-montane vegetation modified by conservation grazing. Glob Ecol Conserv 3, 715–728. https://doi.org/10.1016/j.gecco.2015.03.007

Dimou, I., Koutsikopoulos, C., Economopoulos, A.P., Lykakis, J., 2003. Depth of pupation of the wild olive fruit fly, *Bactrocera* (*Dacus*) *oleae* (Gmel.) (Dipt., Tephritidae), as affected by soil abiotic factors. J Appl Entomol 127, 12–17. https://doi.org/10.1046/J.1439-0418.2003.00686.X

Dinis, A.M., Pereira, J.A., Pimenta, M.C., Oliveira, J., Benhadi-Marín, J., Santos, S.A.P., 2016. Suppression of *Bactrocera oleae* (Diptera: Tephritidae) pupae by soil arthropods in the olive grove. J Appl Entomol 140, 677–687. https://doi.org/10.1111/jen.12291

Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: An approach at two different scales. Agric Ecosyst Environ 62, 81–91. https://doi.org/https://doi.org/10.1016/S0167-8809(96)01143-7

Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of semi-natural habitat islands. Basic Appl Ecol 4, 129–138. https://doi.org/10.1078/1439-1791-00140

Emeana, E.M., Trenchard, L., Dehnen-Schmutz, K., Shaikh, S., 2018. Evaluating the role of public agricultural extension and advisory services in promoting agro-ecology transition in Southeast Nigeria. Agroecol Sustain Food Syst 43, 123–144. https://doi.org/10.1080/21683565.2018.1509410

Estrada-Carmona, N., Sánchez, A.C., Remans, R., Jones, S.K., 2022. Complex agricultural landscapes host more biodiversity than simple ones: A global meta-analysis. Proc Natl Acad Sci USA 119, e2203385119. https://doi.org/10.1073/pnas.2203385119

European Environment Agency, 2019. Loss of HNV farmland due to agricultural intensification per NUTS3 [WWW Document]. URL https://www.eea.europa.eu/data-and-maps/figures/loss-of-hnv-farmland-due-1 (accessed 4.28.23).

European Environment Agency, 2015. Estimated High Nature (HNV) presence in Europe [WWW Document]. URL https://www.eea.europa.eu/data-and-maps/figures/estimated-high-nature-hnv-presence (accessed 4.28.23).

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14, 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K.F., Mitchell, S., Tischendorf, L., 2015. Farmlands with smaller crop fields have higher within-field biodiversity. Agric Ecosyst Environ 200, 219–234. https://doi.org/10.1016/j.agee.2014.11.018

FAO, 2022. World Food and Agriculture – Statistical Yearbook 2022, World Food and Agriculture – Statistical Yearbook 2022. FAO, Rome. https://doi.org/10.4060/CC2211EN

FAOSTAT, 2022. FAOSTAT - Food and agriculture data [WWW Document]. URL https://www.fao.org/faostat/es/#data/RL/visualize (accessed 4.30.23).

Feber, R.E., Johnson, P.J., Bell, J.R., Chamberlain, D.E., Firbank, L.G., Fuller, R.J., Manley, W., Mathews, F., Norton, L.R., Townsend, M., Macdonald, D.W., 2015. Organic farming:

Biodiversity impacts can depend on dispersal characteristics and landscape context. PLoS One 10, e0135921. https://doi.org/10.1371/journal.pone.0135921

Feit, B., Blüthgen, N., Daouti, E., Straub, C., Traugott, M., Jonsson, M., 2021. Landscape complexity promotes resilience of biological pest control to climate change. Proc R Soc B: Biol Sci 288, 20210547. https://doi.org/10.1098/RSPB.2021.0547

Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. Ecology 83, 643–652. https://doi.org/10.1890/0012-9658(2002)083[0643:IPDICS]2.0.CO;2

Fischer, J., Hartel, T., Kuemmerle, T., 2012. Conservation policy in traditional farming landscapes. Conserv Lett 5, 167–175. https://doi.org/10.1111/j.1755-263X.2012.00227.x

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., Klein, A.M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tscharntke, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat Commun 6, 8568 https://doi.org/10.1038/ncomms9568

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol Lett 14, 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Gillson, L., Ladle, R.J., Araújo, M.B., 2011. Baselines, patterns and process., in: Ladle, R.J., Whittaker, R.J. (Eds.), Conservation Biogeography. Wiley-Blackwell, Oxford, pp. 31–44.

Gkisakis, V., Volakakis, N., Kollaros, D., Bàrberi, P., Kabourakis, E.M., 2016. Soil arthropod community in the olive agroecosystem: Determined by environment and farming practices in different management systems and agroecological zones. Agric Ecosyst Environ 218, 178–189. https://doi.org/10.1016/j.agee.2015.11.026

Godfray, H.C.J., 1994. Parasitoids. Behavioral and Evolutionary Ecology. Princeton University Press, New Jersey. https://doi.org/10.2307/J.CTVS32RMP

Gómez, J.E., Lohmiller, J., Joern, A., 2016. Importance of vegetation structure to the assembly of an aerial web-building spider community in North American open grassland. J Arachnol 44, 28. https://doi.org/10.1636/P14-58.1

Grass, I., Batáry, P., Tscharntke, T., 2021. Combining land-sparing and land-sharing in European landscapes, in: Advances in Ecological Research. Academic Press Inc., pp. 251–303. https://doi.org/10.1016/bs.aecr.2020.09.002

Hajek, A.E., Eilenberg, J., 2018. Natural Enemies: An Introduction to Biological Control, 2nd ed. Cambridge University Press, Cambridge, UK.

Halaj, J., Ross, D.W., Moldenke, A.R., 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. J Arachnol 26, 203–220. https://doi.org/10.2307/3706159

Hall, M.A., Nimmo, D.G., Cunningham, S.A., Walker, K., Bennett, A.F., 2019. The response of wild bees to tree cover and rural land use is mediated by species' traits. Biol Conserv 231, 1–12. https://doi.org/10.1016/j.biocon.2018.12.032

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Baillod, A.B., Sirami, C., Fahrig, L., Martin, J.L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Bure, F., Georges, R., Giralt, D., Marcos-García, M., Ricarte, A., Siriwardena, G., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc R Soc B: Biol Sci 285, 20172242. https://doi.org/10.1098/rspb.2017.2242

Henri, D.C., Van Veen, F.J.F., 2011. Body Size, Life History and the Structure of Host-Parasitoid Networks, in: Advances in Ecological Research. Academic Press Inc., pp. 135–180. https://doi.org/10.1016/B978-0-12-386475-8.00004-6

Heraty, J., 2017. Parasitoid Biodiversity and Insect Pest Management, in: Foottit, R.G., Adler, P.H. (Eds.), Insect Biodiversity. John Wiley & Sons, Oxford, pp. 603–625. https://doi.org/10.1002/9781118945568.CH19

Hevia, V., Carmona, C.P., Azcárate, F.M., Heredia, R., González, J.A., 2021. Role of floral strips and semi-natural habitats as enhancers of wild bee functional diversity in intensive agricultural landscapes. Agric Ecosyst Environ 319, 107544. https://doi.org/10.1016/j.agee.2021.107544

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P. V., Evans, A.D., 2005. Does organic farming benefit biodiversity? Biol Conserv 122, 113–130. https://doi.org/10.1016/j.biocon.2004.07.018

Holland, J.D., Bert, D.G., Fahrig, L., 2004. Determining the Spatial Scale of Species' Response to Habitat. Bioscience 54, 227–233.

Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation Biol Control:

a review of European studies. Pest Manag Sci 72, 1638–1651. https://doi.org/10.1002/ps.4318

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support Biol Control, pollination and soil conservation in Europe. A review. Agron Sustain Dev 37, 31. https://doi.org/10.1007/s13593-017-0434-x

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J Anim Ecol 79, 491–500. https://doi.org/10.1111/j.1365-2656.2009.01642.x

Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D., Zasadil, P., 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. Agric Ecosyst Environ 178, 71–77. https://doi.org/10.1016/j.agee.2013.06.020

Huber, J.T., 2017. Biodiversity of Hymenoptera, in: Foottit, R.G., Adler, P.H. (Eds.), Insect Biodiversity: Science and Society. John Wiley & Sons, Ltd, Oxford, pp. 419–461. https://doi.org/10.1002/9781118945568.CH12

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., Landis, D., 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front Ecol Environ 7, 196–203. https://doi.org/10.1890/080035

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24, 52–63. https://doi.org/10.1111/geb.12233

Jackson, H.B., Fahrig, L., 2012. What size is a biologically relevant landscape? Landsc Ecol 27, 929–941. https://doi.org/10.1007/s10980-012-9757-9

Johnston, M., Licker, R., Foley, J., Holloway, T., Mueller, N.D., Barford, C., Kucharik, C., 2011. Closing the gap: Global potential for increasing biofuel production through agricultural intensification. Environ Res Lett 6, 034028. https://doi.org/10.1088/1748-9326/6/3/034028

Kajtoch, Ł., 2017. The importance of traditional orchards for breeding birds: The preliminary study on Central European example. Acta Oecol 78, 53–60. https://doi.org/10.1016/j.actao.2016.12.010

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tscharntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J.M., Bianchi, F.J.J.A., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-López, B., Carrière, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Ćetković, A., Henri, D.C., Chabert, A., Costamagna, A.C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseth, A.S., Inclán, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plećaš, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N.P., Schneider, G., Schüepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc Natl Acad Sci USA 115, E7863–E7870. https://doi.org/10.1073/pnas.1800042115

Katayama, N., Bouam, I., Koshida, C., Baba, Y.G., 2019. Biodiversity and yield under different land-use types in orchard/vineyard landscapes: A meta-analysis. Biol Conserv 229, 125-133. https://doi.org/10.1016/j.biocon.2018.11.020

Keenleyside, C., Beaufoy, G., Tucker, G., Jones, G., 2014. High Nature Value farming throughout EU-27 and its financial support under the CAP. Institute for European Environmental Policy (IEEP), London. https://doi.org/10.2779/91086

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol Lett 16, 584–599. https://doi.org/10.1111/ele.12082

Kishinevsky, M., Keasar, T., Harari, A.R., Chiel, E., 2017. A comparison of naturally growing vegetation vs. border-planted companion plants for sustaining parasitoids in pomegranate orchards. Agric Ecosyst Environ 246, 117–123. https://doi.org/10.1016/j.agee.2017.05.034

Kizos, T., Koulouri, M., 2006. Agricultural landscape dynamics in the Mediterranean: Lesvos (Greece) case study using evidence from the last three centuries. Environ Sci Policy 9, 330–342. https://doi.org/10.1016/j.envsci.2006.02.002

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat Commun 6, 7414. https://doi.org/10.1038/ncomms8414

Klein, A.M., Boreux, V., Fornoff, F., Mupepele, A.C., Pufal, G., 2018. Relevance of wild and managed bees for human well-being. Curr Opin Insect Sci 26, 82-88. https://doi.org/10.1016/j.cois.2018.02.011

Kolb, S., Uzman, D., Leyer, I., Reineke, A., Entling, M.H., 2020. Differential effects of semi-natural habitats and organic management on spiders in viticultural landscapes. Agric Ecosyst Environ 287, 106695. https://doi.org/10.1016/j.agee.2019.106695

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci USA 99, 16812–16816. https://doi.org/10.1073/PNAS.262413599/SUPPL_FILE/4135TABLE5.HTML

LaSalle, J., Gauld, I.D. (Eds.), 1993. Hymenoptera and Biodiversity. C.A.B. International, Wallingford, Oxon, UK.

LaSalle, J., Gauld, I.D., 1991. Parasitic Hymenoptera and the biodiversity crisis. Redia 74, 315–334.

Macfadyen, S., Gibson, R., Raso, L., Sint, D., Traugott, M., Memmott, J., 2009. Parasitoid control of aphids in organic and conventional farming systems. Agric Ecosyst Environ 133, 14–18. https://doi.org/10.1016/j.agee.2009.04.012

MacLeod, A., Wratten, S.D., Sotherton, N.W., Thomas, M.B., 2004. 'Beetle banks' as refuges for beneficial arthropods in farmland: long-term changes in predator communities and habitat. Agric For Entomol 6, 147–154. https://doi.org/10.1111/J.1461-9563.2004.00215.X

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agric Ecosyst Environ 74, 229–273. https://doi.org/10.1016/S0167-8809(99)00038-9

Marchini, D., Petacchi, R., Marchi, S., 2017. *Bactrocera oleae* reproductive biology: New evidence on wintering wild populations in olive groves of Tuscany (Italy). Bull Insectology 70, 121–128.

Marino, P.C., Landis, D.A., 1996. Effect of Landscape Structure on Parasitoid Diversity and Parasitism in Agroecosystems. Ecol Appl 6, 276–284. https://doi.org/10.2307/2269571

Marja, R., Tscharntke, T., Batáry, P., 2022. Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis. Agric Ecosyst Environ 326, 107822. https://doi.org/10.1016/j.agee.2021.107822

Markó, V., Keresztes, B., Fountain, M.T., Cross, J. V., 2009. Prey availability, pesticides and the abundance of orchard spider communities. Biol Control 48, 115–124. https://doi.org/10.1016/j.biocontrol.2008.10.002

Martin, A.E., 2018. The Spatial Scale of a Species' Response to the Landscape Context Depends on which Biological Response You Measure. Curr Landsc Ecol Rep 3, 23–33. https://doi.org/10.1007/s40823-018-0030-z

Martin, A.E., Fahrig, L., 2012. Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol Appl 22, 2277–2292. https://doi.org/10.1890/11-2224.1

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M. V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A.C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol Lett 22, 1083-1094. https://doi.org/10.1111/ele.13265

Martin, E.A., Seo, B., Park, C.R., Reineking, B., Steffan-Dewenter, I., 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecol Appl 26, 448–462. https://doi.org/10.1890/15-0856

Martínez-Sastre, R., Ravera, F., González, J.A., López Santiago, C., Bidegain, I., Munda, G., 2017. Mediterranean landscapes under change: Combining social multicriteria evaluation and the ecosystem services framework for land use planning. Land use policy 67, 472–486. https://doi.org/10.1016/J.LANDUSEPOL.2017.06.001

Mates, S.G., Perfecto, I., Badgley, C., 2012. Parasitoid wasp diversity in apple orchards along a pest-management gradient. Agric Ecosyst Environ 156, 82–88. https://doi.org/10.1016/j.agee.2012.04.016

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., Albrecht, M., 2022. Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. J Appl Ecol 59, 2604-2615. https://doi.org/10.1111/1365-2664.14260

McCravy, K.W., 2018. A Review of Sampling and Monitoring Methods for Beneficial Arthropods in Agroecosystems. Insects 9, 170. https://doi.org/10.3390/INSECTS9040170

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol 31, 1161–1175. https://doi.org/10.1007/S10980-016-0374-X/FIGURES/3

Mestre, L., Schirmel, J., Hetz, J., Kolb, S., Pfister, S.C., Amato, M., Sutter, L., Jeanneret, P., Albrecht, M., Entling, M.H., 2018. Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. Agric Ecosyst Environ 267, 141–146. https://doi.org/10.1016/j.agee.2018.08.018

Meyhofer, R., Hindayana, D., 2000. Effects of intraguild predation on aphid parasitoid survival. Entomol Exp Appl 97, 115–122. https://doi.org/10.1046/j.1570-7458.2000.00722.x

Michalko, R., Pekár, S., Dul'a, M., Entling, M.H., 2019. Global patterns in the biocontrol efficacy of spiders: A meta-analysis. Glob Ecol Biogeogr 28, 1366–1378. https://doi.org/10.1111/geb.12927

Michener, C.D., 2007. The Bees of the World, 2nd ed. The Johns Hopkins University Press, Baltimore.

Miguet, P., Jackson, H.B., Jackson, N.D., Martin, A.E., Fahrig, L., 2016. What determines the spatial extent of landscape effects on species? Landsc Ecol 31, 1177–1194. https://doi.org/10.1007/s10980-015-0314-1

Millennium Ecosystem Assessment, 2005. Ecosystems and human well-being. Island press, Washington DC.

Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. Landsc Ecol 22, 1461–1476. https://doi.org/10.1007/S10980-007-9125-3/FIGURES/7

Müller, A., Kuhlmann, M., 2008. Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. Biol J Linn Soc 95, 719–733. https://doi.org/10.1111/j.1095-8312.2008.01113.x

Nardi, F., Carapelli, A., Dallai, R., Roderick, G.K., Frati, F., 2005. Population structure and colonization history of the olive fly, *Bactrocera oleae* (Diptera, Tephritidae). Mol Ecol 14, 2729–2738. https://doi.org/10.1111/J.1365-294X.2005.02610.X

Nastasi, L.F., Kresslein, R.L., Fowler, K.O., Flores, S.R.F., 2023. Biodiversity & Classification of Wasps, First edition. ed. WaspID Course.

Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S.G., Roberts, S.P.M., Settele, J., Szentgyörgyi, H., Vaissière, B.E., Vaitis, M., Woyciechowski, M., Bazos, I., Biesmeijer, J.C., Bommarco, R., Kunin, W.E., Tscheulin, T., Lamborn, E., Petanidou, T., 2011. Assessing bee species richness in two Mediterranean communities: Importance of habitat type and sampling techniques. Ecol Res 26, 969–983. https://doi.org/10.1007/s11284-011-0852-1

Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J.I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D.A., Moretti, M., Potts, S.G., Slade, E.M., Stout, J.C., Ulyshen, M.D., Wackers, F.L., Woodcock, B.A., Santos, A.M.C., 2018. Research trends in ecosystem services provided by insects. Basic Appl Ecol 26, 8–23. https://doi.org/10.1016/J.BAAE.2017.09.006

Noss, R.F., and Cooperrider, A.Y., 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington D.C.

Nyffeler, M., Dean, D.A., Sterling, W.L., 1989. Prey Selection and Predatory Importance of Orb-Weaving Spiders (Araneae: Araneidae, Uloboridae) in Texas Cotton. Environ Entomol 18, 373–380. https://doi.org/10.1093/EE/18.3.373

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

Ogilvie, J.E., Forrest, J.R., 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. Curr Opin Insect Sci 21, 75-82. https://doi.org/10.1016/j.cois.2017.05.015

Oliver, T., Roy, D.B., Hill, J.K., Brereton, T., Thomas, C.D., 2010. Heterogeneous landscapes promote population stability. Ecol Lett 13, 473–484. https://doi.org/10.1111/J.1461-0248.2010.01441.X

Ollerton, J., 2017. Pollinator Diversity: Distribution, Ecological Function, and Conservation. Annu Rev Ecol Evol Syst 48, 353–76. https://doi.org/10.1146/annurev-ecolsys-110316

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Ortega, M., Pascual, S., Rescia, A.J., 2016. Spatial structure of olive groves and scrublands affects *Bactrocera oleae* abundance: a multi-scale analysis. Basic Appl Ecol 17, 696–705. https://doi.org/10.1016/j.baae.2016.06.001

Ortega, M., Sánchez-Ramos, I., González-Núñez, M., Pascual, S., 2018. Time course study of *Bactrocera oleae* (Diptera: Tephritidae) pupae predation in soil: the effect of landscape structure and soil condition. Agric For Entomol 20, 201–207. https://doi.org/10.1111/afe.12245

Patenaude, T., Smith, A.C., Fahrig, L., 2015. Disentangling the effects of wetland cover and urban development on quality of remaining wetlands. Urban Ecosyst 18, 663–684. https://doi.org/10.1007/S11252-015-0440-1/FIGURES/12

Peck, S.L., Mcquaid, B., Campbell, C.L., 1998. Using Ant Species (Hymenoptera: Formicidae) as a Biological Indicator of Agroecosystem Condition. Environ Entomol 27, 1102–1110. https://doi.org/10.1093/EE/27.5.1102

Pennisi, E., 2010. The Little Wasp That Could. Science 327, 260–262. https://doi.org/10.1126/science.327.5963.260

Pereira, H.M., Navarro, L.M., 2015. Rewilding European Landscapes. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-12039-3

Pereira, J.A., Alves, M.R., Casal, S., Oliveira, M.B.P.P., 2004. Effect of olive fruit fly infestation on the quality of olive oil from cultivars cobrançosa, madural and verdeal transmontana. Ital J Food Sci 16, 355–365.

Phillips, A., 1998. The nature of cultural landscapes — a nature conservation perspective. Landsc Res 23, 21–38. https://doi.org/10.1080/01426399808706523

Picchi, Malayka S., Entling, M., Petacchi, R., 2017a. Effects of semi-natural habitats on spiders in olive groves and their potential role against *Bactrocera oleae* (Rossi) (Diptera: Tephritidae). IOBC/WPRS Bulletin 121, 105–109.

Picchi, M.S., Marchi, S., Albertini, A., Petacchi, R., 2017b. Organic management of olive orchards increases the predation rate of overwintering pupae of *Bactrocera oleae* (Diptera: Tephritidae). Biol Control 108, 9–15. https://doi.org/10.1016/j.biocontrol.2017.02.002

Plieninger, T., Bieling, C., 2013. Resilience-Based Perspectives to Guiding High-Nature-Value Farmland through Socioeconomic Change. Ecol Soc 18, 20. https://doi.org/10.5751/ES-05877-180420

Plieninger, T., Höchtl, F., Spek, T., 2006. Traditional land-use and nature conservation in European rural landscapes. Environ Sci Policy 9, 317–321. https://doi.org/10.1016/j.envsci.2006.03.001

Plieninger, T., Hui, C., Gaertner, M., Huntsinger, L., 2014. The Impact of Land Abandonment on Species Richness and Abundance in the Mediterranean Basin: A Meta-Analysis. PLoS One 9, e98355. https://doi.org/10.1371/journal.pone.0098355

Pointereau, P., Coulon, F., Girard, P., Lambotte, M., Stuczynski, T., Sánchez-Ortega, V., Del Rio, A., 2008. Analysis of Farmland Abandonment and the Extent and Location of Agricultural Areas that are Actually Abandoned or are in Risk to be Abandoned. Institute of Environment and Sustainability. Joint Research Centre, European Commission, Luxemburg.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol Evol 25, 345-353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L. V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588

Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., Willmer, P., 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biol Conserv 129, 519–529. https://doi.org/10.1016/j.biocon.2005.11.019

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., Willmer, P., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol Entomol 30, 78–85. https://doi.org/10.1111/j.0307-6946.2005.00662.x

Preu, M., Frieß, J.L., Breckling, B., Schröder, W., 2020. Case Study 1: Olive Fruit Fly (*Bactrocera oleae*), in: von Gleich, A., Schröder, W. (Eds.), Gene Drives at Tipping Points. Springer International Publishing, Cham, pp. 79–101. https://doi.org/https://doi.org/10.1007/978-3-030-38934-5_4

Pugh, T.A.M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., Calle, L., 2019. Role of forest regrowth in global carbon sink dynamics. Proc Natl Acad Sci USA 116, 4382–4387. https://doi.org/10.1073/PNAS.1810512116/SUPPL_FILE/PNAS.1810512116.SD02.TXT

Queiroz, C., Beilin, R., Folke, C., Lindborg, R., 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. Front Ecol Environ 12, 288–296. https://doi.org/10.1890/120348

Quintas-Soriano, C., Buerkert, A., Plieninger, T., 2022. Effects of land abandonment on nature contributions to people and good quality of life components in the Mediterranean region: A review. Land use policy 116, 106053. https://doi.org/10.1016/j.landusepol.2022.106053

Rahmann, G., 2011. Biodiversity and Organic farming. What do we know? vTI Agric For Res 3, 189–208.

Ratnadass, A., 2020. Crop Protection for Agricultural Intensification Systems in Sub-Saharan Africa, in: Lichtfouse, E. (Ed.), Sustainable Agriculture Reviews 39. Springer International Publishing, Cham, pp. 1–34. https://doi.org/10.1007/978-3-030-38881-2_1

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proc Natl Acad Sci USA 118, 1–6. https://doi.org/10.1073/PNAS.2002548117

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol Lett 11, 499–515. https://doi.org/10.1111/J.1461-0248.2008.01157.X

Rischen, T., Kaffenberger, M., Plath, E., Wolff, J., Fischer, K., 2023. Configurational landscape heterogeneity: Crop-fallow boundaries enhance the taxonomic diversity of carabid beetles and spiders. Agric Ecosyst Environ 341, 108194. https://doi.org/10.1016/j.agee.2022.108194

Root, R.B., 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica oleracea*). Ecol Monogr 43, 95–124. https://doi.org/10.2307/1942161

Rosas-Ramos, N., Baños-Picón, L., Tobajas, E., de Paz, V., Tormos, J., Asís, J.D., 2018. Value of ecological infrastructure diversity in the maintenance of spider assemblages: A case study of

Mediterranean vineyard agroecosystems. Agric Ecosyst Environ 265, 244–253. https://doi.org/10.1016/j.agee.2018.06.026

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2020a. Natural enemies and pollinators in traditional cherry orchards: Functionally important taxa respond differently to farming system. Agric Ecosyst Environ 295, 106920. https://doi.org/10.1016/j.agee.2020.106920

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2020b. Farming system shapes traits and composition of spider assemblages in Mediterranean cherry orchards. PeerJ 8, e8856. https://doi.org/10.7717/peerj.8856

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2019. The complementarity between ecological infrastructure types benefits natural enemies and pollinators in a Mediterranean vineyard agroecosystem. Ann Appl Biol 175, 193–201. https://doi.org/10.1111/aab.12529

Roth, T., Coll, M., Mandelik, Y., 2023. The Role of Uncultivated Habitats in Supporting Wild Bee Communities in Mediterranean Agricultural Landscapes. Diversity 15, 294. https://doi.org/10.3390/d15020294

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W.W., Winqvist, C., Woltz, M., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agric Ecosyst Environ 221, 198–204. https://doi.org/10.1016/j.agee.2016.01.039

Sandhu, H.S., Wratten, S.D., Cullen, R., 2010. Organic agriculture and ecosystem services. Environ Sci Policy 13, 1–7. https://doi.org/10.1016/J.ENVSCI.2009.11.002

Santos, S.A.P., Cabanas, J.E., Pereira, J.A., 2007. Abundance and diversity of soil arthropods in olive grove ecosystem (Portugal): Effect of pitfall trap type. Eur J Soil Biol 43, 77–83. https://doi.org/10.1016/J.EJSOBI.2006.10.001

Schmidt, M.H., Tscharntke, T., 2005. Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. J Biogeogr 32, 467–473. https://doi.org/10.1111/j.1365-2699.2004.01244.x

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.D., Vogt, J., Wöllauer, S., Weisser, W.W. 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3

Seufert, V., Ramankutty, N., 2017. Many shades of gray—the context-dependent performance of organic agriculture. Sci Adv 3, e1602638. https://doi.org/10.1126/SCIADV.1602638/SUPPL_FILE/1602638_SM.PDF

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol Rev 88, 1002–1021. https://doi.org/10.1111/brv.12040

Shaw, M.R., 2006. Habitat considerations for parasitic wasps (Hymenoptera). J Insect Conserv 10, 117–127. https://doi.org/10.1007/s10841-006-6288-1

Shaw, M.R., Hochberg, M.E., 2001. The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. J Insect Conserv 5, 253–263.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-Garcia, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tscharntke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc Natl Acad Sci USA 116, 16442–16447. https://doi.org/10.1073/pnas.1906419116

Southwood, T.R.E., Way, M.J., 1970. Ecological background to pest management, in: Rabb, R.L., Guthrie, F.E. (Eds.), Concepts of Pest Management. North Carolina State University, Raleigh, pp. 7–13.

Spears, L.R., MacMahon, J.A., 2012. An experimental study of spiders in a shrub-steppe ecosystem: the effects of prey availability and shrub architecture. J Arachnol 40, 218–227. https://doi.org/10.1636/P11-87.1

Stanchi, S., Freppaz, M., Zanini, E., 2012. The influence of Alpine soil properties on shallow movement hazards, investigated through factor analysis. Nat Hazards Earth Syst Sci 12, 1845–1854. https://doi.org/10.5194/NHESS-12-1845-2012

Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. Entomol Exp Appl 95, 1–13. https://doi.org/10.1046/j.1570-7458.2000.00635.x

Swift, M.J., Anderson, J.M., 1994. Biodiversity and Ecosystem Function in Agricultural Systems, in: Schulze, E.-D., Mooney, H.A. (Eds.), Biodiversity and Ecosystem Function. Springer, Berlin, pp. 15–41. https://doi.org/10.1007/978-3-642-58001-7_2

Theron, K.J., Gaigher, R., Pryke, J.S., Samways, M.J., 2020. High quality remnant patches in a complex agricultural landscape sustain high spider diversity. Biol Conserv 243, 108480. https://doi.org/10.1016/j.biocon.2020.108480

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends Ecol Evol 36, 919–930. https://doi.org/10.1016/j.tree.2021.06.010

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol Lett 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. J Appl Ecol 51, 746–755. https://doi.org/10.1111/1365-2664.12219

Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild Structure of Spiders in Major Crops. J Arachnol 27, 270–280.

Vansynghel, J., Ocampo-Ariza, C., Maas, B., Martin, E.A., Thomas, E., Hanf-Dressler, T., Schumacher, N.C., Ulloque-Samatelo, C., Yovera, F.F., Tscharntke, T., Steffan-Dewenter, I., 2022. Quantifying services and disservices provided by insects and vertebrates in cacao agroforestry landscapes. Proc R Soc B: Biol Sci 289, 20221309. https://doi.org/10.1098/RSPB.2022.1309

Way, M.J., Khoo, K.C., 1992. Role of Ants in Pest Management. Annu Rev Entomol 37, 479–503. https://doi.org/10.1146/ANNUREV.EN.37.010192.002403

Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats., in: Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P., Williams, I.H. (Eds.), The Conservation of Bees. Academic Press, London, UK, pp. 1–16.

Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biol Conserv 143, 2280–2291. https://doi.org/10.1016/j.biocon.2010.03.024

Williams, N.M., Kremen, C., 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecol Appl 17, 910–921. https://doi.org/10.1890/06-0269

Wise, D.H., 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511623431

Wolpert, F., Quintas-Soriano, C., Plieninger, T., 2020. Exploring land-use histories of tree-crop landscapes: a cross-site comparison in the Mediterranean Basin. Sustain Sci 15, 1267–1283. https://doi.org/10.1007/s11625-020-00806-w

World Spider Catalog, 2023. NMBE - World Spider Catalog [WWW Document]. URL https://wsc.nmbe.ch/ (accessed 5.2.23).

Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. One Earth 4, 114–123. https://doi.org/10.1016/j.oneear.2020.12.005

Zhu, Y., Chen, J., Zou, Y., Huang, X., Jiang, T., Wyckhuys, K.A.G., van der Werf, W., Xiao, H., 2023. Response of the rice stem borer *Chilo suppressalis* (Walker) and its parasitoid assemblage to landscape composition. Agric Ecosyst Environ 343, 108259. https://doi.org/10.1016/j.agee.2022.108259

Chapter I

EFFECT OF ORGANIC FARMING AND AGRICULTURAL ABANDONMENT ON BENEFICIAL ARTHROPOD COMMUNITIES ASSOCIATED WITH OLIVE GROVES IN WESTERN SPAIN: IMPLICATIONS FOR *BACTROCERA OLEAE* MANAGEMENT

EFECTOS DE LA AGRICULTURA ECOLÓGICA Y EL ABANDONO SOBRE LAS COMUNIDADES DE ARTRÓPODOS BENEFICIOSOS ASOCIADAS A OLIVARES DEL OESTE DE ESPAÑA: IMPLICACIONES PARA EL MANEJO DE BACTROCERA OLEAE

Effect of organic farming and agricultural abandonment on beneficial arthropod communities associated with olive groves in western Spain: implications for *Bactrocera oleae* management

Efectos de la agricultura ecológica y el abandono sobre las comunidades de artrópodos beneficiosos asociadas a olivares del oeste de España: implicaciones para el manejo de Bactrocera oleae

de Paz, V., Tobajas, E., Rosas-Ramos, N., Tormos, J., Asís, J.D., Baños-Picón, L.

Adapted from: de Paz et al. (2022) Insects, 13, 48, https://doi.org/10.3390/insects13010048

Resumen

El abandono y la intensificación agrícola se encuentran entre los principales cambios en el uso del suelo en Europa. Paralelamente a estos procesos, se han desarrollado diferentes estrategias para contrarrestar los efectos negativos derivados de la intensificación agrícola, entre las que se encuentra la agricultura ecológica. En este contexto, nos propusimos determinar cómo el manejo ecológico y el abandono de tierras de cultivo afectan a *Bactrocera oleae* y a sus principales grupos de enemigos naturales: himenópteros parasitoides, arañas, hormigas, carábidos y estafilínidos. Entre mayo y octubre de 2018, se realizaron cuatro muestreos en nueve olivares (tres bajo manejo ecológico, tres bajo manejo tradicional y tres abandonados), en una zona rural en la frontera entre España y Portugal (Salamanca, oeste de España). Nuestros resultados sugieren que existen diferencias en la composición de la comunidad de enemigos naturales entre los olivares abandonados y ecológicos, con niveles ligeramente superiores de riqueza y abundancia en los abandonados. No encontramos diferencias entre los olivares ecológicos y los tradicionales. Los olivares trabajados mantienen una comunidad de enemigos naturales diferente, pero igualmente rica y diversa que los olivares abandonados, los cuales son más complejos estructuralmente y no actúan como reservorio de *B. oleae* en nuestra zona de estudio. Ambos sistemas podrían estar proporcionando hábitats complementarios; sin embargo, un incremento del abandono podría conllevar una reducción de la heterogeneidad a escala de paisaje y, en consecuencia, una pérdida de biodiversidad.

Abstract

Agricultural abandonment and intensification are among the main land-use changes in Europe. Along with these processes, different proposals have been developed to counteract the negative effects derived from agricultural intensification, including organic management. In this context, we aimed to determine how organic management and farmland abandonment affect *Bactrocera oleae* and its main groups of natural enemies: hymenopteran parasitoids, spiders, ants, carabids, and staphylinids. Between May and October 2018, four samplings were carried out in nine olive groves (three under organic management, three under traditional management, and three abandoned) in a rural area on the border between Spain and Portugal (Salamanca, Western Spain). Our results suggested differences between the natural enemy community composition of abandoned and organic groves, with slightly higher levels of richness and abundance in abandoned groves. We found no differences between organic and traditional groves. The managed olive groves sustained a different natural enemy community but were similarly rich and diverse compared with the more complex abandoned groves, with the latter not acting as a reservoir of *B. oleae* in our study area. Both systems may provide complementary habitats; however, further abandonment could cause a reduction in heterogeneity at the landscape scale and, consequently, a biodiversity loss.

Keywords: abandonment; organic farming; traditional olive groves; Bactrocera oleae; parasitoids; spiders; staphylinids

1. Introduction

Land-use change is the main driver of biodiversity loss worldwide, with the expansion and intensification of agriculture—characterized by an increased input of synthetic pesticides, herbicides, and fertilizers—being the prime cause of insect population declines (Díaz et al., 2019; Raven and Wagner, 2021; Tilman et al., 2002). Biodiversity loss can negatively affect arthropod-mediated ecosystem services, such as pest control by natural enemies (Dainese et al., 2019; Lichtenberg et al., 2017). To mitigate the negative effects of agricultural intensification, different strategies have been developed, including organic management, in which synthetic pesticides, herbicides, and inorganic fertilizers are avoided (Tuck et al., 2014). Although there has been considerable controversy regarding the ability of organic management to support greater biodiversity, it has been consistently demonstrated that organic farming increases the richness and abundance of arthropods and other groups (Bengtsson et al., 2005; Lichtenberg et al., 2017; Tuck et al., 2014). However, the positive effect of organic farming is highly dependent on the taxon and crop evaluated, and it is greater in annual crops and intensified landscapes (Bengtsson et al., 2005; Tuck et al., 2014). Therefore, the landscape context modulates local biodiversity responses to organic farming, as predicted by the *intermediate landscape complexity hypothesis* (Concepción et al., 2012). This hypothesis states that in both cleared (<1% of non-crop habitat) and complex landscapes (>20% of non-crop habitat), only small positive responses to local agri-environmental management (such as organic farming) can be expected because of poor species pools and high immigration from semi-natural habitats, respectively, and that only simple landscapes, with intermediate levels of complexity, respond positively to agri-environmental schemes (Tscharntke et al., 2012) . Moreover, increased biodiversity in organic farming may not happen in permanent crops, such as fruit orchards or vineyards, that present low disturbance levels, and the further reduction in the disturbance intensity of organic farming might not result in greater biodiversity (Bruggisser et al., 2010). This is explained by the *intermediate disturbance hypothesis*, which predicts higher diversity levels at intermediate levels of disturbance, with both slightly and highly disturbed systems harboring less biodiversity (Connell, 1978).

While agricultural intensification usually takes place on fertile soils, in marginal areas with traditional non-intensive farming systems, there is an ongoing process of farmland abandonment (Cramer et al., 2008). The consequences of the abandonment of traditional crops vary depending on the geographical region, scale, and taxa (Benayas et al., 2007). In Europe, traditional farming systems have existed for centuries and constitute high-nature-value systems (Baldock et al., 1993), characterized by a low input of pesticides and synthetic fertilizers, with low levels of mechanization and high associated biodiversity, which are currently threatened by land abandonment (Fischer et al., 2012;

Keenleyside et al., 2014; Queiroz et al., 2014). In fact, Queiroz et al. (2014), reviewing farmland abandonment effects on biodiversity, found that in Europe, most studies revealed negative effects. However, the majority of the studies that assessed farmland abandonment effects on arthropods were carried out in grasslands and annual crops in Central and Northern Europe.

In the Mediterranean Basin, a review by Plieninger et al. (2014) revealed slightly positive effects of farmland abandonment on biodiversity, although their results were highly heterogeneous, and only four cases related to arthropods in permanent crops were included. They also found a decline in species richness after an abandonment period of fifty or more years that, they suggest, "may indicate that exclusion processes eventually follow colonization processes in many of the case studies". Actually, many studies found higher biodiversity levels in the early stages of farmland abandonment, which tend to decrease as plant succession progresses (Cremene et al., 2005; Fartmann et al., 2012; Nardi and Marini, 2021; Öckinger et al., 2006). In the early stages of farmland abandonment, plant diversity reaches its maximum, with herbaceous plants and scrubs coexisting, which results in habitats with high vegetation complexity (Bonet and G. Pausas, 2004; Cremene et al., 2005). Vegetation complexity, measured as structural and chemical complexity, enhances arthropod abundance and diversity by providing more microhabitats and resources, as well as diverse plant volatiles (Öckinger et al., 2006; Randlkofer et al., 2010). In the late stages of farmland abandonment, scrub and tree species of the surrounding vegetation become dominant, excluding open-habitat species, and reduce heterogeneity at a landscape scale, resulting in reduced biodiversity levels (Benayas et al., 2007).

More work is needed to disentangle the effects of farmland abandonment on arthropod communities, especially in permanent crops, which are underrepresented in the bibliogra phy, as well as in the Mediterranean Basin considering that it is one of the world's diversity hotspots (Myers et al., 2000) and also an area where land abandonment is prevalent (Weissteiner et al., 2011). In this region, landscapes have been shaped by humans for millennia, creating different cultural landscapes that form the identity of the Mediterranean (Blondel et al., 2010). Such is the case of olive (*Olea europaea* L.)-dominated landscapes, where olive cultivation has been taking place since the Roman

Age (Loumou and Giourga, 2003). Within the Mediterranean region, Spain, with a production of almost 1.8 million tons of olive oil and 10 million tons of olives, is the largest producer (FAOSTAT, 2021). Olive grove yields can be affected by a variety of pests, with the olive fruit fly, *Bactrocera oleae* (Rossi, 1790), being the most relevant (Daane and Johnson, 2010). *Bactrocera oleae* is attacked by a variety of natural enemies and it produces between three and five generations per year in the Mediterranean area, starting in early spring (Marchini et al., 2017; Ordano et al., 2015). The adult flies oviposit in olives, where the larvae are vulnerable to hymenopteran parasitoids, and after completing their development, the larvae leave the fruits to pupate in the ground, where they are again exposed to generalist predators, mainly spiders, carabids and staphylinids, and ants (Albertini et al., 2018; Ortega et al., 2016).

Despite the importance of the olive groves in the Mediterranean region and specifically in Spain, studies that evaluated the effect of the abandonment of olive groves on the associated arthropod biodiversity are scarce (but see Potts et al. (2006) for bees, Solomou et al. (2019) for isopods, and Sánchez-Fernández et al. (2020) for butterflies), and to our knowledge, no studies have evaluated the effect of olive grove abandonment on *B. oleae* and the arthropod groups that include its most important natural enemies, especially in traditional landscapes with different management regimes. In this context, we set out to determine (i) the possible effect of organic management and farmland abandonment on *B. oleae* and the structure and composition of the natural enemy community in traditional olive groves in a complex landscape; (ii) the differences in richness, abundance, and diversity of natural enemies between organic and abandoned olive groves; and (iii) the response of the dominant natural enemy families and *B. oleae* to olive grove abandonment. Considering the *intermediate disturbance hypothesis* and the *intermediate landscape complexity hypothesis*, we hypothesized that *B. oleae* and the natural enemy community will barely differ between traditional olive groves (with intermediate levels of perturbation) and organic olive groves (with slightly lower levels of perturbation). Nevertheless, the natural enemy community structure and composition would be expected to differ between managed and abandoned groves, with the latter harboring a richer and more abundant natural enemy community. We also hypothesized that managed groves will host more *B. oleae* individuals.

2. Materials and Methods

2.1. Study Area

The study was carried out in the municipality of Ahigal de los Aceiteros (Salamanca, Western Spain) (40°52′ N, 6°44′ W). The location of this region, at the Portuguese border, with small villages and limited infrastructure, has led to a continuous process of isolation, depopulation, and farmland abandonment. Conversely, a significant number of the managed plots are transitioning to organic agriculture, with some of them having been organic certified since 2014. Therefore, the agricultural landscape of this region is practically devoid of synthetic pesticides and fertilizers, and structurally, it is a mosaic formed by the combination of managed plots (in many cases with the absence of mechanization and low investment) and abandoned plots in various stages of plant succession, interspersed with fragments of natural vegetation. These remnants of natural vegetation typical of Mediterranean sclerophyllous scrub are formed mainly by *Cytisus* shrublands (*Cytisus multiflorus* (L'Hér.) Sweet, *Cytisus scoparius* (L.) Link), rock rose (*Cistus ladanifer* L.), French lavender (*Lavandula pedunculata* (Mill.) Cav.), and thymes (*Thymus mastichina* (L.) L., *Thymus zygis* subsp. *zygis* Loefl. ex L.). There are also areas of Mediterranean forest, mainly composed of holm oaks (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) and oaks (*Quercus pyrenaica* Willd.), although they coexist with European nettle trees (*Celtis australis* L.) and junipers (*Juniperus oxycedrus* L.), which have great ecological value and persist mainly because of the difficulty of cultivating on the steep slopes of the area, which has considerably limited agricultural practices.

The study area comprises 435 ha, its altitude ranging between 405 and 662 m a.s.l. It is located in the transition zone between landscape units 84 (gorges and valleys on the Portuguese border) and 49 (peneplains of Zamora and Salamanca, as well as the foothill of the Montes de León) (Sanz et al., 2003), within the territory of the Arribes del Duero Natural Park (Fig. 1). The climate is mild, generally warm, and temperate, with an average annual rainfall of 541 mm and an average annual temperature of 13.7 °C. The predominant soil types are cambisol and leptosol. The study area is bordered by two small streams and in its southwest region by the Águeda River, which runs through a deep canyon. The landscape is dominated by olive groves and, to a lesser extent, by vineyards and almond orchards under a traditional farming system without the application of pesticides and synthetic fertilizers. Olive cultivation is the base of the economic activity within the municipality, with the production and commercialization of extra virgin olive oil and extra virgin organic olive oil as derivative products from different varieties such as *Zorzal de Arribes* (endemic to Arribes del Duero), *Manzanilla Cacerena*, and *Picual*, among others.

Figure 1: Location of the study area in Salamanca (Western Spain) and the location of the nine olive groves sampled within the study area. Traditional olive groves: yellow squares, organic groves: red triangles, and abandoned groves: blue circles.

2.2. Sampling design

We selected nine olive groves: three organic certified, three traditional, and three abandoned (mean area: 12 822.2 ± 4 237.3 m^2, mean distance to the nearest grove: 564.4 ± 120.4 m). The organic olive groves obtained their certification in 2014; therefore, synthetic pesticides and fertilizers have not been used in these groves at least since 2011. In the traditional category, we included orchards under traditional management that did not have an organic certification but where synthetic pesticides and fertilizers have not been used for at least 10 years, according to the owners. We included them in our study to check for differences between organic-certified orchards and traditional orchards that follow an organic-like type of management but that have not been officially certified as organic and where an occasional and infrequent application of synthetic pesticides or fertilizers could still be performed. Ground cover vegetation was controlled in both systems by mowing once or twice a year, all groves are rainfed, and they have an average production of 12 kilos of olives per tree. Finally, all abandoned groves had been abandoned for at least 15 years.

Sampling was performed from May to October 2018 every seven to eight weeks, starting with the flowering period (early May) and finishing just before the olive harvest (late October), attending to the period of highest arthropod abundance (Ruano et al., 2004) and following the *B. oleae* life cycle (Picchi et al., 2016). Each sampling took place over six consecutive days, randomly assigning the order in which the groves were sampled. Weather conditions were kept as uniform as possible between the sampling periods, avoiding rainy and windy days.

To capture edaphic fauna (spiders, carabids, staphylinids, and ants) six uncovered pitfall traps (9 cm diameter, 12.3 cm depth) were placed in each grove, three under the olive tree canopy and three between rows (54 in total). The traps were filled to a third with a mixture of 70% alcohol and antifreeze (10% ethylene glycol) in a 3:2 ratio (600 mL of alcohol and 400 mL of antifreeze per liter). The traps were also placed 20 m apart from each other and the groves' edges to reduce trap-to-trap interference and edge effects, and remained in the field for 72 h. To collect hymenopteran parasitoids and vegetation spiders, we randomly selected four trees in each olive grove and vacuumed each tree and the surrounding vegetation in a 2 m × 2 m quadrant for three minutes using a gardener's leaf-blower (Garland GAS 550 G) (Avinent and Llacer, 1995) modified as a suction machine. For the capture of *B. oleae* specimens, we placed 10 chromatic sticky traps (25 cm × 10 cm) (Koppert Biological Systems—Horiver) in each grove. The traps were hung from the lower branches of the olive trees (at a height of 1.5–2 m above the ground), arranged with a south-facing orientation and separated by a minimum of 10 m from each other, and remained active for 72 h (Fig. 2). All the collected specimens were sorted in the laboratory and identified at the family level. This higher taxa approach (e.g., family taxonomic resolution) was found to be a reliable approach for revealing species richness and compositional patterns (de Oliveira et al., 2020).

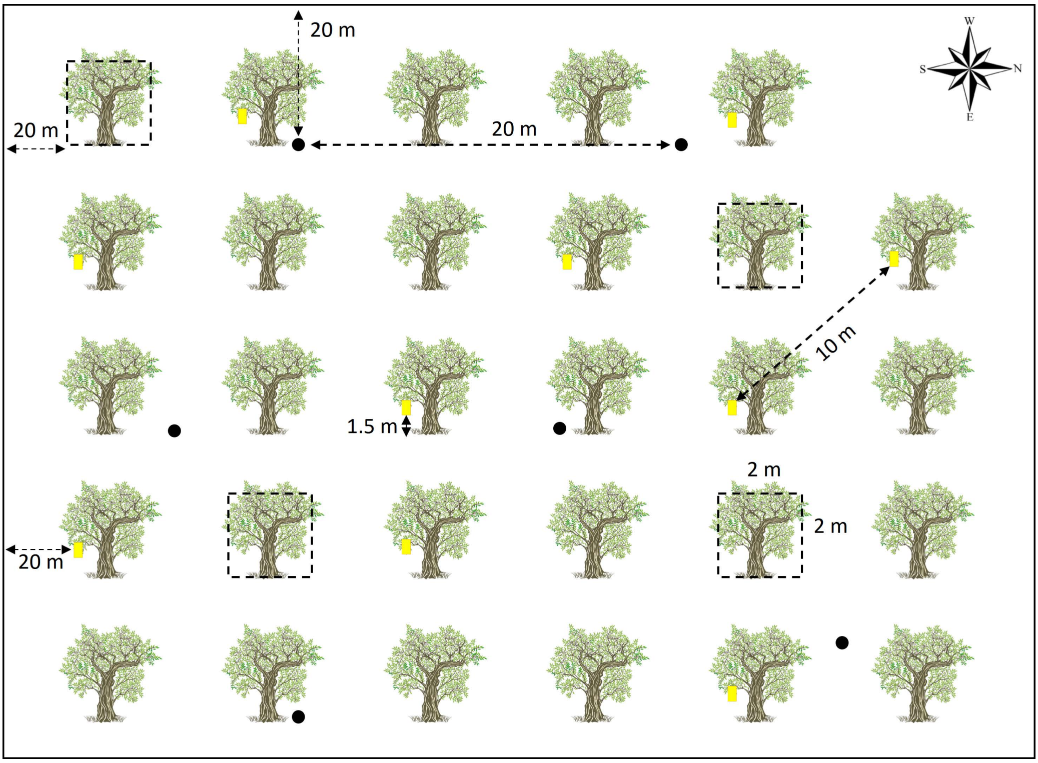

Figure 2: Sampling design. Black circles: pitfall traps; yellow rectangles: sticky traps; empty squares: 2 m × 2 m vacuuming quadrants. Dashed arrows represent the minimum distance between traps or the grove's edge.

2.3. Statistical Analyses

Prior to performing the analyses, we assessed the completeness of the sampling methods for each group (spiders, parasitoids, and natural enemy community (spiders, parasitoids, staphylinids, carabids, and ants)) using the non-parametric Chao1 estimator (Colwell, 2009). Both methods exhibited high levels of completeness (pitfall traps: 92% of the 12 estimated parasitoid families, 96% of the 25 estimated spider families, and 93% of the 41 estimated natural enemy families; vacuuming: 96% of the 23 estimated parasitoid families, 84% of the 19 estimated spider families, and 80% of the 51 estimated natural enemy families).

The effects of the *system* type (organic certified, traditional, and abandoned) on the natural enemy, spider, and parasitoid communities were analyzed with PERMANOVA (*system* and *sampling month* as fixed factors, with 9 999 permutations, and "permutation of residuals under a reduced model" as the permutation method) and MDS (multidimensional scaling). Similarity matrices were calculated using Bray–Curtis coefficients with the abundances square-root transformed to reduce the weight of the most dominant families. Considering that the PERMANOVA results (Table 1) revealed no significant differences between the organic-certified and traditional plots, we excluded the latter in the rest of the analyses and focused on studying the differences between organic and abandoned groves.

To test for spatial autocorrelation between the study sites, we performed a Mantel correlogram based on a similarity matrix (Bray–Curtis) and the geographical coordinates of the study sites (Borcard et al., 2018). The results revealed a significant spatial autocorrelation for the parasitoids and for the spider families Gnaphosidae and Linyphiidae. There-fore, we added spatial correlation structures to these models and compared their AICs to select the best model (Zuur et al., 2009). We also checked for temporal correlation using the auto-correlation function (ACF), and when we detected significant temporal patterns, we added a correlation structure for a short time series and a variance structure that al-lowed for different variances for each level of the variable *sampling month* to our models and compared the AICs (Zuur et al., 2009).

We used linear least-squares models, linear mixed models, generalized linear models, and generalized linear mixed models to test the effect of the *system* (organic certified or abandoned), the *sampling month* and the interaction (when significant) (as fixed factors), and the *site* as a random factor (when applicable) on the family richness, abundance, and Shannon's index values for the natural enemies, spiders, and parasitoids and for the abundance of the most dominant families of the whole natural enemy community (>60 individuals, 17 out of 52 families). The residuals of each model were checked to ensure normality, independence, and homoscedasticity. Additionally, a factorial correspondence analysis (FCA) was carried out to represent the association between these families and the two types of olive groves (abandoned and organic).

To analyze the possible effect of the system (organic certified, traditional, and abandoned) on the populations of *B. oleae*, we applied a generalized linear mixed-effects model (GLMM), with the variables *system*, the *sampling month*, and their interaction as fixed factors, and the *site* as a random factor. Since we did not detect any *B. oleae* adults in the two summer sampling periods, we excluded them from the analysis, as the high number of zeros could be a source of error in the analysis. Then, we performed the analysis only with the data from the first and last sampling periods (May and October, respectively).

For the analyses, the statistical packages PRIMER v6 (PERMANOVA, MDS) (PRIMER-E Ltd., Plymouth, UK) (Clarke and Gorley, 2006), R 3.6.2 (linear least-squares models, linear mixed models, generalized linear models, generalized linear mixed models, and zero-inflated models) (R Core Team, 2016), and XlStat 2014 (factorial correspondence analysis) (Addinsoft, 2014) were used.

Table 1. Results of the PERMANOVA for the variables *system* and *sampling month* (full model results and pairwise comparisons among the three systems).

Response Variable	**Explanatory Variables**	**d.f.**	**Pseudo-F**	***p*-value**
Natural enemies	*System*	2	2.312	<0.001
	Sampling month	3	8.911	<0.001
Spiders	*System*	2	3.052	<0.001
	Sampling month	3	6.204	<0.001
Parasitoids	*System*	2	0.793	0.702
	Sampling month	3	5.329	<0.001
Pairwise Comparisons			**Pseudo-t**	***p*-value**
Natural enemies	Abandoned, organic		1.747	<0.001
	Abandoned, traditional		1.731	<0.001
	Organic, traditional		0.923	0.630
Spiders	Abandoned, organic		2.098	<0.001
	Abandoned, traditional		2.034	<0.001
	Organic, traditional		0.741	0.807
Parasitoids	Abandoned, organic		0.689	0.835
	Abandoned, traditional		1.025	0.428
	Organic, traditional		0.948	0.543

3. Results

A total of 13,300 arthropods belonging to the focal groups were collected—1730 spiders (26 families), 2125 parasitoids (22 families), 27 carabids, 255 staphylinids, 8483 ants and, and 680 *B. oleae* individuals.

The PERMANOVA revealed a significant effect of the *system* on the natural enemy and spider communities (pseudo-F = 2.312, p = 0.0001 and pseudo-F = 3.052, p = 0.0001, respectively) but none for the parasitoid community (pseudo-F = 0.7927, p = 0.702); these differences occurred only between the managed and abandoned systems but not between the organic and traditional plots (Table 1). These results were also noticeable in the MDS, where, for the natural enemy and spider communities, the abandoned groves were clearly separated from the managed groves, which was not the case for the parasitoid community (Fig. 3).

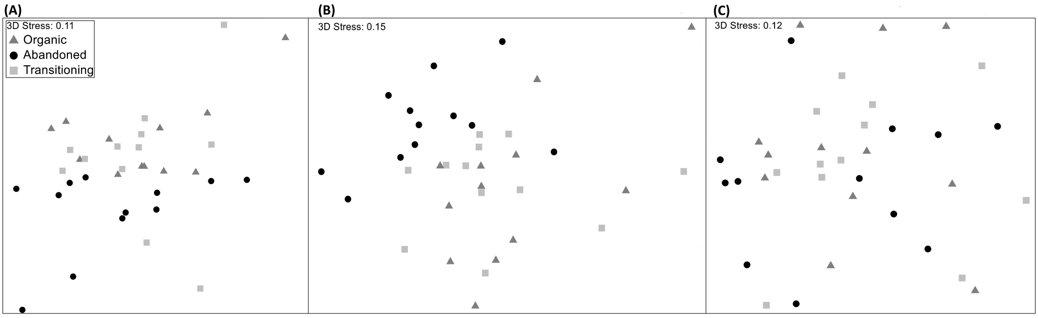

Figure 3: MDS of the natural enemy (A), spider (B), and parasitoid (C) communities sampled (Bray–Curtis index, square-root transformed abundances). Triangles: organic groves; circles: abandoned groves; squares: traditional groves.

When considering the whole natural enemy community, we did not find differ-ences in richness, abundance, or diversity between organic and abandoned groves (Ta-ble 2). Nevertheless, the models showed that spiders were significantly affected by the system, with the abandoned plots harboring richer and more abundant communities, although we also found a marginally significantly higher spider diversity in the organic groves toward the end of the sampling period. Parasitoids were partly affected by the system, showing no differences in richness or abundance, but their diversity was significantly higher in the abandoned plots. This difference decreased throughout the sampling period, and at the end of the season, organic plots harbored a higher parasitoid diversity (Table 2), showing a trend similar to that of the spiders.

Table 2: Results of the different models for the richness, abundance, and diversity (Shannon index (H)) of natural enemies, spiders, and parasitoids. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, and *** < 0.001) for the intercept and the explanatory variable *system*, as well as the interaction between the variables *system* and the *sampling month* (when significant), are provided. The complete results, including the explanatory variable *sampling month*, are given in Table S1.

Response Variable	**Explanatory Variable**	**Value/Estimate**	**Std. Error**	***t*-Value/*z*-Value**	***p*-value**	*****
Natural enemy family richness [a]	Intercept	20.667	1.208	17.114	<0.001	***
	System (organic)	−0.667	1.080	−0.617	0.544	ns
Natural enemy abundance [a]	Intercept	247.081	33.023	7.482	<0.001	***
	System (organic)	4.506	31.315	0.144	0.887	ns
Natural enemy diversity (H) [a]	Intercept	1.557	0.159	9.789	<0.001	***
	System (organic)	−0.155	0.142	−1.087	0.291	ns
Spider family richness (square root) [a]	Intercept	2.838	0.094	30.134	<0.001	***
	System (organic)	−0.157	0.072	−2.161	0.044	*
Spider abundance [b]	Intercept	3.200	0.126	25.352	<0.001	***
	System (organic)	−0.346	0.136	−2.555	0.011	*
Spider diversity (H) [a]	Intercept	1.913	0.140	13.675	<0.001	***
	System (organic)	0.075	0.183	0.409	0.689	ns
	Sampling month (June): *system* (organic)	−0.135	0.258	−0.524	0.608	ns
	Sampling month (August): *system* (organic)	0.423	0.205	2.059	0.056	•
	Sampling month (October): *system* (organic)	0.467	0.247	1.894	0.077	•
Parasitoid family richness [c]	Intercept	2.368	0.107	22.136	<0.001	***
	System (organic)	−0.034	0.099	−0.347	0.732	ns
Parasitoid abundance [d]	Intercept	48.917	8.685	5.632	<0.001	***
	System (organic)	−5.833	10.328	−0.565	0.602	ns
Parasitoid diversity [a]	Intercept	2.144	0.130	16.445	<0.001	***
	System (organic)	−0.473	0.184	−2.568	0.021	*
	Sampling month (June): *system* (organic)	0.421	0.200	2.103	0.052	•
	Sampling month (August): *system* (organic)	0.108	0.277	0.389	0.702	ns
	Sampling month (October): *system* (organic)	0.701	0.303	2.317	0.034	*

[a] GLS; [b] GLMM with a Poisson distribution; [c] quasi-GLM model; [d] LME.

The results of the linear models applied to the most abundant families showed different responses to the variable *system* across taxa. Nevertheless, we found a general tendency of natural enemy families to associate with abandoned groves (nine out of seventeen), with only four families being more abundant in the organic groves (Gnaphosidae, Linyphiidae, Philodromidae, and Staphylinidae) (Table 3). Four families were not associated with either type of *system* (Formicidae, Pteromalidae, Salticidae, and Scelionidae). These results were consistent with those of the correspondence analysis

(Fig. 4), except for four families. Mymaridae and Encyrtidae were more abundant in the abandoned groves according to the models, but they were not associated with these groves in the correspondence analysis; the contrary applied to the family Pteromalidae, which was associated with the abandoned groves in the correspondence analysis but not according to the generalized linear mixed model. The results of the model for the family Philodromidae revealed a significantly higher abundance in the organic groves that was not supported by the correspondence analysis (Fig. 4). In the case of the main olive pest, *B. oleae*, the managed groves harbored significantly higher abundance than the abandoned groves in October (Table 3). In May, the *B. oleae* abundance was too low to detect differences between systems (105 versus 575 individuals in October). We did not capture any adults during the summer sampling.

Table 3: Results of the different linear models for the abundance of the most dominant families. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variable *system*, as well as the interaction between the variables *system* and the *sampling month* (when significant), are provided. No results are shown for Formicidae because the variable *system* did not remain in the optimal model. The complete results, including the explanatory variable *sampling month*, are given in Table S2.

Response Variable	Explanatory Variable	Value/Estimate	Std. Error	*t*-Value/*z*-Value	*p*-value	*
Araneidae abundance [a]	Intercept	1.680	0.244	6.875	<0.001	***
	System (organic)	−1.069	0.244	−4.376	<0.001	***
Gnaphosidae abundance [a]	Intercept	0.784	0.491	1.597	0.110	ns
	System (organic)	0.584	0.650	0.899	0.369	ns
	Sampling month (June): *system* (organic)	−0.657	0.557	−1.179	0.238	ns
	Sampling month (August): *system* (organic)	0.208	0.601	0.346	0.730	ns
	Sampling month (October): *system* (organic)	1.594	0.865	1.843	0.065	•
Linyphiidae abundance [a]	Intercept	0.654	0.474	1.379	0.168	ns
	System (organic)	0.758	0.599	1.266	0.205	ns
	Sampling month (June): *system* (organic)	1.391	0.608	2.287	0.022	*
	Sampling month (August): *system* (organic)	−5.11E-05	0.625	0.000	0.999	ns
	Sampling month (October): *system* (organic)	−0.074	0.688	−0.108	0.914	ns
Oxyopidae abundance [a]	Intercept	0.834	0.388	2.152	0.031	*
	System (organic)	−1.946	1.068	−1.823	0.068	•
	Sampling month (June): *system* (organic)	−0.251	1.500	−0.168	0.867	ns
	Sampling month (August): *system* (organic)	−1.571	0.538	−2.92	0.004	**

	Sampling month (October): *system* (organic)	−2.683	0.624	−4.301	<0.001	***
Philodromidae abundance (square root) ^{b}	Intercept	0.334	0.378	0.884	0.388	ns
	System (organic)	0.576	0.114	5.058	<0.001	***
Salticidae abundance ^{b}	Intercept	2.000	0.645	3.098	0.006	**
	System (organic)	−0.667	0.577	−1.155	0.263	ns
Theridiidae abundance ^{a}	Intercept	0.245	0.466	0.525	0.600	ns
	System (organic)	−1.287	0.310	−4.15	<0.001	***
Thomisidae abundance ^{a}	Intercept	0.835	0.390	2.141	0.032	*
	System (organic)	−0.002	0.550	−0.004	0.997	ns
	Sampling month (June): *system* (organic)	0.167	0.673	0.248	0.804	ns
	Sampling month (August): *system* (organic)	−1.447	0.770	−1.879	0.060	•
	Sampling month (October): *system* (organic)	−0.442	0.683	−0.646	0.518	ns
Braconidae abundance (square root) ^{b}	Intercept	2.943	0.529	5.567	<0.001	***
	System (organic)	−2.000	0.748	−2.675	0.017	*
	Sampling month (June): *system* (organic)	1.576	0.835	1.889	0.077	•
	Sampling month (August): *system* (organic)	1.805	0.857	2.105	0.051	•
	Sampling month (October): *system* (organic)	2.667	0.933	2.858	0.011	*
Encyrtidae abundance ^{a}	Intercept	1.194	0.334	3.576	<0.001	***
	System (organic)	−1.625	0.789	−2.061	0.039	*
	Sampling month (June): *system* (organic)	2.197	0.837	2.625	0.007	**
	Sampling month (August): *system* (organic)	−0.056	0.876	−0.064	0.949	ns
	Sampling month (October): *system* (organic)	3.091	0.848	3.644	<0.001	***
Eulophidae abundance ^{a}	Intercept	1.814	0.200	9.058	<0.001	***
	System (organic)	−0.321	0.173	−1.853	0.064	•
Mymaridae abundance ^{b}	Intercept	1.843	0.197	9.337	<0.001	***
	System (organic)	−0.530	0.175	−3.034	0.007	**
Pteromalidae abundance ^{a}	Intercept	0.668	0.530	1.259	0.208	ns
	System (organic)	−0.372	0.664	−0.561	0.575	ns
Scelionidae abundance ^{a}	Intercept	2.557	0.133	19.257	<0.001	***
	System (organic)	0.169	0.120	1.401	0.161	ns
Trichogrammatidae abundance ^{b}	Intercept	1.426	0.233	6.126	<0.001	***
	System (organic)	−0.600	0.228	−2.634	0.016	*
Staphylinidae abundance ^{a}	Intercept	1.936	0.353	5.479	<0.001	***
	System (organic)	1.405	0.469	2.998	0.003	**
Bactrocera oleae abundance ^{a}	Intercept	1.662	0.566	2.938	0.003	**
	System (traditional)	0.346	0.788	0.439	0.660	ns
	System (organic)	0.859	0.775	1.108	0.268	ns
	Sampling month (October): *system* (traditional)	1.820	0.302	6.027	<0.001	***
	Sampling month (October): *system* (organic)	1.531	0.263	5.817	<0.001	***

^{a} GLMM with a Poisson distribution; ^{b} GLS.

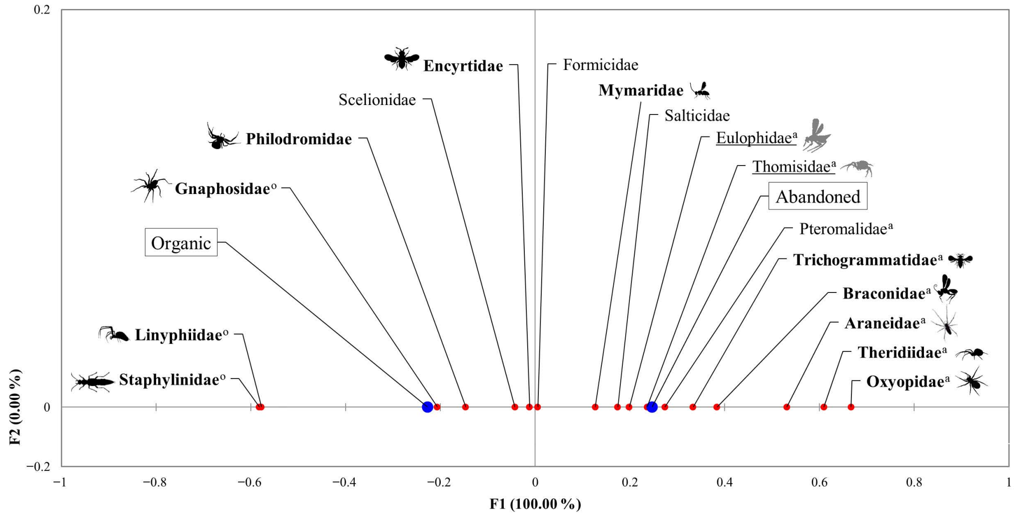

Figure 4: Factorial correspondence analysis was performed on the abundance of the most relevant families of natural enemies on each type of *system* (organic and abandoned). Families in bold with black drawings were those significantly affected by the variable *system*, whereas underlined families with grey drawings were marginally affected by this variable, according to the results obtained from the linear models fitted on the abundances of the most dominant families. Red dot: principal coordinate value for each family in the first axis of the FCA; blue dot: principal coordinate value for each farming system in the first axis of the FCA. ^{o} Significant association with the organic groves in the correspondence analysis; ^{a} significant association with the abandoned groves in the correspondence analysis.

4. Discussion

In accordance with our hypothesis, the structure of the natural enemy community differed between the abandoned and organic olive groves, except when considering parasitoid wasps alone. Parasitoid wasps were the most mobile group in the study, and they tend to be more affected by variables at a landscape scale (Bianchi et al., 2006; Cronin and Reeve, 2005; Puech et al., 2014). They were most likely moving along patches adjacent to the groves in the matrix, using the multiple resources in abandoned groves and semi-natural habitats for foraging, refuge, and alternative hosts (Alignier et al., 2014), and spilling over to managed groves, mostly searching for hosts (Tscharntke et al., 2005). In agreement with our hypothesis, we found no differences between organic and traditional groves. The landscape complexity of our study area would explain the lack of effect of the farming system (according to the *intermediate landscape complexity hypothesis*) (Tscharntke et al., 2012), where local extensification measures, such as organic farming, are expected to have little effect on species richness (Concepción et al., 2012). Moreover, Bruggisser et al. (2010) suggested that "the biodiversity benefits of organic farming in annual cropping systems may not hold for perennial crops, particularly if the use of pesticides is minimal," based on the *intermediate disturbance hypothesis* (Connell, 1978). Nevertheless, the similarity be-tween organic and traditional groves also indicated that traditional agriculture, with a very occasional input of synthetic pesticides and fertilizers, may be able to maintain similar levels of natural enemy diversity as organic agriculture. Therefore, our results, in agreement with those of other studies, highlighted traditional agriculture as high-nature-value farming systems that supported high biodiversity in agricultural landscapes (Cooper et al., 2007; Horak et al., 2013). As we expected, the main olive pest, namely, *B. oleae*, was associated with the managed groves. In the abandoned groves, given the lack of management (especially pruning), olive trees produced less fruit; therefore, olive availability for *B. oleae* oviposition was scarce, and few adults developed in unmanaged habitats. In fact, olive production was so low that the *B. oleae* adults that we found in the abandoned groves may have dispersed from the managed groves. The abandoned groves would not act as reservoirs of *B. oleae*; they may even be sink habitats (i.e., re-source-poor habitats where the death rate exceeds the birth rate and the populations are maintained, in the long term, by immigration (Pulliam, 1988)) because of the higher rate of natural enemies, functioning similarly to trap crops, which attract pests and induce a higher rate of pest mortality (e.g., through reduced larval survival or suppression by natural enemies) (Badenes-Perez et al., 2004; Fanadzo et al., 2018).

Surprisingly, we did not find differences in richness, abundance, or diversity for the whole natural enemy community between organic and abandoned olive groves, even though the structure of the communities tended to diverge. Both organic and abandoned groves would provide valuable and diverse microhabitats that harbor different natural enemy communities but be similarly rich and diverse given their high niche availability (Fischer et al., 2012; Kajtoch, 2017). Abandoned groves, with an intermediate structure between the more open habitat of managed groves, and the closer one of the Mediterranean shrubland and forest, with structurally dense vegetation, maintain diverse communities that are different from managed groves and probably also from the natural habitats that surround them (see Nardi and Marini (2021) for an example with spiders in

European grasslands). Consequently, abandoned groves may increase landscape complexity, as well as microhabitat and resource availability, in agreement with other studies in different eco-systems (e.g., Kajtoch (2017) for fruit orchards and Nardi and Marini (2021) for grasslands; see Plieninger et al. (2014) for a review).

Focusing on the most important groups of natural enemies considered in this study, namely, spiders and parasitoids, we found that the abandoned groves harbored richer and more abundant spider communities and higher parasitoid diversity. The structurally more complex vegetation of abandoned groves provided a wider range of microhabitats and especially more resources for feeding and refuge, which may have favored these groups. Several studies have shown that spiders are constrained by different habitat features at a local scale (e.g., Barton et al., 2017; Theron et al., 2020), favoring habitats with more com-plex vegetation architecture (Benhadi-Marín et al., 2020; Rosas-Ramos et al., 2019, 2018; Uetz et al., 1999) and increased prey availability (Markó et al., 2009; Spears and MacMahon, 2012). Therefore, the characteristics of the abandoned groves allowed them to sustain richer and more abundant spider communities. Concerning parasitoid wasps, the abandoned groves had a higher habitat complexity, which was found to enhance natural enemies in olive groves, but with little effects in parasitoid abundance (Álvarez et al., 2019). Not only do these groves provide more resources (i.e., floral resources, overwintering sites, alternative hosts) that favor parasitoids (Rusch et al., 2010) but also this may reduce negative interactions (such as intraguild predation, competition, or hyperparasitism) (Finke and Denno, 2002; Meyhofer and Hindayana, 2000), which result in a more even community with higher diversity values.

Regarding community changes throughout the season, we detected a change of trend in the diversity observed in the two systems, with the organic groves harboring a higher diversity of both spiders and parasitoids than the abandoned groves toward the end of the sampling period. In the studied areas, farmers managed the natural vegetation cover in productive groves through conservation till-age (i.e., a form of non-intensive tillage that leaves at least 30% of the previous cover's residue on the surface (Stinner and House, 1990)) in July. It was shown that rapid perturbations, such as tillage, predominantly affect dominant species (Arnoldi et al., 2018), reducing competition over hosts/prey and other resources. Therefore, the organic groves harbored a slightly higher richness of spiders and parasitoids in October, which, when combined with the lower abundance found in this month, resulted in a significantly higher diversity. In fact, conservation tillage was shown to favor predators and parasitoids in simple and complex landscapes (Tamburini et al., 2016) and to increase predator diversity and evenness (Rowen et al., 2020). Our results are in accordance with those of previous studies that highlight that mild disturbances of traditional agroecosystems can favor biodiversity (Cooper et al., 2007; Cremene et al., 2005; Fartmann et al., 2012; Horak et al., 2013; Kajtoch, 2017).

According to our expectations, the abandoned groves achieved a higher abundance of the most dominant families of natural enemies in general but with clear differences between taxa. Five out of seven parasitoid families were more abundant in the abandoned groves, with none associating with the organic groves. Parasitoids belong to a high trophic level, and they are especially sensitive to environmental change and agricultural disturbances (Kruess and Tscharntke, 1994; Mates et al., 2012); thus, we would have expected to find differences in the community composition or shifts in richness or abundance between these two systems. A possible explanation is that an evaluation at the family level may not provide sufficient resolution to detect these differences (Bennett and Gratton, 2012). However, when studying the dominant families separately, we do see a clear association of these families with the abandoned olive groves, again emphasizing their higher abundance of food and shelter resources that would favor parasitoids (Rusch et al., 2010), and also their heightened chemical complexity, which may attract a greater diversity of parasitoids (Aartsma et al., 2017; Randlkofer et al., 2010).

For the spiders, we found mixed results across families. The families Araneidae and Theridiidae (space and orb-web weavers, respectively (Cardoso et al., 2011; Uetz et al., 1999)) and Oxyopidae and Thomisidae (active hunters and ambush hunters, respectively, mostly on the vegetation, with the latter especially on flowers (Cardoso et al., 2011; Uetz et al., 1999)) are more abundant in the abandoned groves. As previously mentioned, these families probably favored the higher plant structural complexity of the abandoned groves, which provided more anchoring points for the webs of theridids and araneids and foraging, as well as refuge resources for oxyopids and thomisids, along with a variety of locations for ambushing prey for the latter (Rosas-Ramos et al., 2018; Spears and MacMahon, 2012; Uetz et al., 1999). On the other hand, the families Gnaphosidae, Linyphiidae, and Philodromidae are more abundant in the organic groves. Gnaphosids are ground hunters, which favor open habitats, such as those of the organic groves (Cardenas et al., 2012; Rosas-Ramos et al., 2020, 2019). Philodromids are active hunters either on the ground or the vegetation, and linyphiids include sheet-web weavers and also active hunters, both groups with ground and vegetation species. These two families may be more abundant in the organic groves because of less competition with species from other families that need more structurally complex habitats to flourish. Another possible explanation is that organic groves have filtered some ground-dwelling species of these families that occur mainly in open habitats (Bellmann, 2011; Rosas-Ramos et al., 2018) and that are dominating the spider community in these groves.

Staphylinids were more abundant in the organic groves, in contrast with the results of Baloj and Markó (2007a, 2007b), who found more abundant staphylinid communities in abandoned apple orchards and vineyards than in productive fields (conventional and IPM and conventional and organic, respectively). This result may indicate that the community composition of staphylinids in our study area was dominated by generalist and open-habitat species that favored the agricultural management of the organic groves (Honěk et al., 2012).

Four families were not associated with either system. In the case of scelionids and pteromalids, some species may favor the organic groves, masking the possible differences between organic and abandoned groves (e.g., parasitoids of ground beetles, which are more abundant in the organic groves, or parasitoids of olive pests). We also did not find any differences in ant abundance. Since we did not sort them into species or functional groups, we cannot assess the structure of the ant community. Based on the few studies that compare ant diversity in abandoned and managed agricultural fields (Altieri and Schmidt (1984) in orchards and Gómez et al. (2003) in cereal fields), we can hypothesize that abandoned groves may harbor a different, more diverse ant community because of their higher niche and different resource availability, with organic groves harboring fewer species, but they are exploiting the resources successfully, resulting in similar abundance levels. Finally, the family Salticidae includes some species adapted to hunting on the ground, while others hunt on the vegetation (Cardoso et al., 2011); thus, open-habitat species may be more abundant in organic groves, and the more complex vegetation of abandoned groves may sustain more individuals of species that hunt on the vegetation, although they tend to prefer widely spaced over dense structures (Robinson, 1981).

Although arthropod interannual population variability may result in biased conclusions McCain et al., 2016), short-term studies provide valuable results that are useful for making local comparisons (Rivers-Moore and Samways, 1996), and most studies conducted with arthropods in agroecosystems have one-year sampling periods. In any case, our results should be interpreted with caution due to their dependence on spatial and temporal context.

5. Conclusions

Our study provided the first evidence of the effects of olive grove abandonment on *B. oleae* and different groups of natural enemies in traditional agroecosystems and contributed to increasing the knowledge of these effects on woody crops, which are clearly underrepresented in the literature, even when considering the limitations de-rived by the fact that our sampling period was restricted to one year. The studied traditional olive groves may be able to sustain a different natural enemy community (but equally rich and diverse) than that of the more structurally complex abandoned groves, emphasizing the role that traditional olive groves have in conserving biodiversity in agricultural landscapes. Abandoned groves could constitute landscape elements of high importance that provide a wide variety of microhabitats and resources that are exploited by natural enemies but not by the olive fruit fly and, therefore, may not act as reservoirs for this pest in our study area. The presence of both systems, traditional and abandoned groves, at a landscape scale provides complimentary habitats that promote diverse communities of some beneficial groups, such as spiders. However, some management measures should be carried out in the abandoned groves to halt plant succession, preventing them from becoming Mediterranean scrubland or forest, similar to the one surrounding them, which would result in the loss of landscape-scale heterogeneity and biodiversity. A greater priority is to stop the abandonment of traditional olive groves that are still in use. The high biodiversity of these groves depends on their traditional management, and further abandonment would translate not only into the loss of the aesthetic and cultural values associated with these agroecosystems but also the possibly irretrievable loss of the biodiversity that they harbor. For this reason, the measures aimed at reducing the depopulation of rural areas, where these traditional systems occur, are especially important to stop the abandonment process. Organic agriculture—with the associated increase in the price of olive oil, which results in higher profits for farmers—and agricultural tourism are measures that were shown to be very effective in halting this process in our study area. More studies are needed to disentangle the effects of olive grove abandonment on the associated arthropod communities, especially in different regions and with longer sampling periods.

Acknowledgments

The authors wish to thank the farmers for allowing access to their groves, specifically Loli Sánchez, for her help in finding and accessing the groves, and the Servicio Territorial de Medio Ambiente de Castilla y León for providing the necessary permits to carry out the samplings. We also wish to thank Sara Vicente Alonso for her help with all the fieldwork. We appreciate the comments and suggestions of three anonymous reviewers that have greatly increased the quality of the manuscript.

References

Aartsma, Y., Bianchi, F.J.J.A., Werf, W., Poelman, E.H., Dicke, M., 2017. Herbivore-induced plant volatiles and tritrophic interactions across spatial scales. New Phytol 216, 1054–1063. https://doi.org/10.1111/nph.14475

Addinsoft, 2014. XLSTAT 2014: Data analysis and statistical solution for Microsoft excel.

Albertini, A., Marchi, S., Ratti, C., Burgio, G., Petacchi, R., Magagnoli, S., 2018. *Bactrocera oleae* pupae predation by *Ocypus olens* detected by molecular gut content analysis. BioControl 63, 227–239. https://doi.org/10.1007/s10526-017-9860-6

Alignier, A., Raymond, L., Deconchat, M., Menozzi, P., Monteil, C., Sarthou, J.P., Vialatte, A., Ouin, A., 2014. The effect of semi-natural habitats on aphids and their natural enemies across spatial and temporal scales. Biol Control 77, 76–82. https://doi.org/10.1016/j.biocontrol.2014.06.006

Altieri, M.A., Schmidt, L.L., 1984. Abundance patterns and foraging activity of ant communities in abandoned, organic and commercial apple orchards in Northern California. Agric Ecosyst Environ 11, 341–352. https://doi.org/10.1016/0167-8809(84)90006-9

Álvarez, H.A., Morente, M., Oi, F.S., Rodríguez, E., Campos, M., Ruano, F., 2019. Semi-natural habitat complexity affects abundance and movement of natural enemies in organic olive orchards. Agric Ecosyst Environ 285, 106618. https://doi.org/10.1016/j.agee.2019.106618

Arnoldi, J.-F., Bideault, A., Loreau, M., Haegeman, B., 2018. How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. J Theor Biol 436, 79–92. https://doi.org/10.1016/j.jtbi.2017.10.003

Avinent, L., Llacer, G., 1995. Adaptación de un aspirador de jardín para la captura de insectos. Bol Sanid Veg Plagas 21, 329–335.

Badenes-Perez, F.R., Shelton, A.M., Nault, B.A., 2004. Evaluating Trap Crops for Diamondback Moth, *Plutella xylostella* (Lepidoptera: Plutellidae). J Econ Entomol 97, 1365–1372. https://doi.org/10.1093/jee/97.4.1365

Baldock, D., Beaufoy, G., Bennett, G., Clark, J., 1993. Nature Conservation and New Directions in the Common Agricultural Policy: The Potential Role of EC Policies in Maintaining Farming and Management Systems of High Nature Value in the Community. Institute for European Environmental Policy (IEEP), London.

Balog, A., Markó, V., 2007a. Species composition and community structure of the rove beetles (Coleoptera: Staphylinidae) in an experimental vineyard under different vineyard management systems. Acta Phytopathol Entomol Hung 42, 367–376. https://doi.org/10.1556/APhyt.42.2007.2.19

Balog, A., Markó, V., 2007b. Community structure of rove beetles (Coleoptera: Staphylinidae) in apple orchards under different pest management system programs in Hungary. Acta Phytopathol Entomol Hung 42, 377–385. https://doi.org/10.1556/APhyt.42.2007.2.20

Barton, P.S., Evans, M.J., Foster, C.N., Cunningham, S.A., Manning, A.D., 2017. Environmental and spatial drivers of spider diversity at contrasting microhabitats. Austral Ecol 42, 700–710. https://doi.org/10.1111/aec.12488

Bellmann, H., 2011. Nueva guía de campo de los arácnidos de Europa. Omega.

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: An overview of drivers and consequences. CAB Rev: Perspect Agric Vet Sci Nutr Nat Resour 2, 1–14. https://doi.org/10.1079/PAVSNNR20072057

Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: A meta-analysis. J Appl Ecol 42, 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x

Benhadi-Marín, J., Pereira, J.A., Sousa, J.P., Santos, S.A.P., 2020. Distribution of the spider community in the olive grove agroecosystem (Portugal): potential bioindicators. Agric For Entomol 22, 10–19. https://doi.org/10.1111/afe.12352

Bennett, A.B., Gratton, C., 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. Landsc Urban Plan 104, 26–33. https://doi.org/10.1016/j.landurbplan.2011.09.007

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

Blondel, J., Aronson, J., Bodiou, J.Y., Boeuf, G., 2010. The Mediterranean region: biological diversity in space and time, 2nd ed. Oxford University Press, New York.

Bonet, A., G. Pausas, J., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecol 174, 257–270. https://doi.org/10.1023/B:VEGE.0000049106.96330.9c

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R, Use R! 2nd ed. Springer International Publishing, New York, USA. https://doi.org/10.1007/978-3-319-71404-2

Bruggisser, O.T., Schmidt-Entling, M.H., Bacher, S., 2010. Effects of vineyard management on biodiversity at three trophic levels. Biol Conserv 143, 1521–1528. https://doi.org/10.1016/j.biocon.2010.03.034

Cardenas, M., Castro, J., Campos, M., 2012. Short-term response of soil spiders to cover-crop removal in an organic olive orchard in a mediterranean setting. J Insect Sci 12, 1–18. https://doi.org/10.1673/031.012.6101

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global Patterns of Guild Composition and Functional Diversity of Spiders. PLoS One 6, e21710. https://doi.org/10.1371/journal.pone.0021710

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual. Plymouth Marine Laboratory, Plymouth.

Colwell, R.K., 2009 EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. User's Guide and Application. [WWW Document]. URL http://purl.oclc.org/estimates (accessed on 12 September 2021).

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J Appl Ecol 49, 695–705. https://doi.org/10.1111/j.1365-2664.2012.02131.x

Connell, J.H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199, 1302–1310.

Cooper, T., Arblaster, K., Baldock, D., Farmer, M., Beaufoy, G., Jones, G., Poux, X., McCracken, D., Bignal, E., Elbersen, B., Wascher, D., Angelstam, P., Roberge, J.M., Pointereau, P., Seffer, J., Galvanek, D., 2007. Final report on the study of HNV indicators for evaluation. Institute for European Environmental Policy, London.

Cramer, V., Hobbs, R., Standish, R., 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol Evol 23, 104–112. https://doi.org/10.1016/j.tree.2007.10.005

Cremene, C., Groza, G., Rakosy, L., Schileyko, A.A., Baur, A., Erhardt, A., Baur, B., 2005. Alterations of Steppe-Like Grasslands in Eastern Europe: a Threat to Regional Biodiversity Hotspots. Conserv Biol 19, 1606–1618. https://doi.org/10.1111/j.1523-1739.2005.00084.x

Cronin, J.T., Reeve, J.D., 2005. Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. Proc R Soc B: Biol Sci 272, 2225–2235. https://doi.org/10.1098/rspb.2005.3286

Daane, K.M., Johnson, M.W., 2010. Olive Fruit Fly: Managing an Ancient Pest in Modern Times. Annu Rev Entomol 55, 151–169. https://doi.org/10.1146/annurev.ento.54.110807.090553

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D.A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tscharntke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, A.D.M., Bianchi, F.J.J.A., Boreux, V., Bretagnolle, V., Caballero-Lopez, B., Cavigliasso, P., Ćetković, A., Chacoff, N.P., Classen, A., Cusser, S., da Silva e Silva, F.D., de Groot, G.A., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipólito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A.-M., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Mallinger, R.E., Martinez Pachon, E., Martínez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M., Nilsson, L., O'Rourke, M.E., Peters, M.K., Plećaš, M., Potts, S.G., Ramos, D. de L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Sáez, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci Adv 5, eaax0121. https://doi.org/10.1126/sciadv.aax0121 de Oliveira, S.S., Ortega, J.C.G., Ribas, L.G. dos S., Lopes, V.G., Bini, L.M., 2020. Higher taxa are sufficient to represent biodiversity patterns. Ecol Indic 111, 105994. https://doi.org/10.1016/j.ecolind.2019.105994

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman K. A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury R., Shin, Y.J., Visseren-Hamakers, I.J., Willis, K.J., Zayas, C.N., 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES. IPBES, Bohn, Germany. https://doi.org/https://doi.org/10.5281/zenodo.3553579

Fanadzo, M., Dalicuba, M., Dube, E., 2018. Application of Conservation Agriculture Principles for the Management of Field Crops Pests, in: Gaba, S., Smith, B., Lichtfouse, E. (Eds.), Sustainable Agriculture Reviews 28. Springer International Publishing, Cham (Switzerland), pp. 125–152. https://doi.org/10.1007/978-94-007-5449-2

FAOSTAT, F., 2021. Food and agriculture data. 2019. [WWW Document]. URL https://www.fao.org/faostat/en/#home (accessed 7.10.21).

Fartmann, T., Krämer, B., Stelzner, F., Poniatowski, D., 2012. Orthoptera as ecological indicators for succession in steppe grassland. Ecol Indic 20, 337–344. https://doi.org/10.1016/j.ecolind.2012.03.002

Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. Ecology 83, 643–652. https://doi.org/10.1890/0012-9658(2002)083[0643:IPDICS]2.0.CO;2

Fischer, J., Hartel, T., Kuemmerle, T., 2012. Conservation policy in traditional farming landscapes. Conserv Lett 5, 167–175. https://doi.org/10.1111/j.1755-263X.2012.00227.x

Gómez, C., Casellas, D., Oliveras, J., Bas, J.M., 2003. Structure of ground-foraging ant assemblages in relation to land-use change in the northwestern Mediterranean region. Biodivers Conserv 12, 2135–2146. https://doi.org/10.1023/A:1024142415454

Honěk, A., Kocian, M., Martinková, Z., 2012. Rove beetles (Coleoptera: Staphylinidae) in an apple orchard. Plant Prot Sci 48, 116–122. https://doi.org/10.17221/2/2012-PPS

Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D., Zasadil, P., 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. Agric Ecosyst Environ 178, 71–77. https://doi.org/10.1016/j.agee.2013.06.020

Kajtoch, Ł., 2017. The importance of traditional orchards for breeding birds: The preliminary study on Central European example. Acta Oecol 78, 53–60. https://doi.org/10.1016/j.actao.2016.12.010

Keenleyside, C., Beaufoy, G., Tucker, G., Jones, G., 2014. High Nature Value farming throughout EU-27 and its financial support under the CAP. Institute for European Environmental Policy (IEEP), London. https://doi.org/10.2779/91086

Kruess, A., Tscharntke, T., 1994. Habitat Fragmentation, Species Loss, and Biological Control. Science 264, 1581–1584. https://doi.org/10.1126/science.264.5165.1581

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., 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

Loumou, A., Giourga, C., 2003. Olive groves: “The life and identity of the Mediterranean.” Agric Human Values 20, 87–95. https://doi.org/https://doi.org/10.1023/A:1022444005336

Marchini, D., Petacchi, R., Marchi, S., 2017. *Bactrocera oleae* reproductive biology: New evidence on wintering wild populations in olive groves of Tuscany (Italy). Bull Insectology 70, 121–128.

Markó, V., Keresztes, B., Fountain, M.T., Cross, J. V., 2009. Prey availability, pesticides and the abundance of orchard spider communities. Biol Control 48, 115–124. https://doi.org/10.1016/j.biocontrol.2008.10.002

Mates, S.G., Perfecto, I., Badgley, C., 2012. Parasitoid wasp diversity in apple orchards along a pest-management gradient. Agric Ecosyst Environ 156, 82–88. https://doi.org/10.1016/j.agee.2012.04.016

McCain, C., Szewczyk, T., Bracy Knight, K., 2016. Population variability complicates the accurate detection of climate change responses. Glob Chang Biol 22, 2081–2093. https://doi.org/10.1111/gcb.13211

Meyhofer, R., Hindayana, D., 2000. Effects of intraguild predation on aphid parasitoid survival. Entomol Exp Appl 97, 115–122. https://doi.org/10.1046/j.1570-7458.2000.00722.x

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501

Nardi, D., Marini, L., 2021. Role of abandoned grasslands in the conservation of spider communities across heterogeneous mountain landscapes. Agric Ecosyst Environ 319, 107526. https://doi.org/10.1016/j.agee.2021.107526

Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol Conserv 133, 291–300. https://doi.org/10.1016/j.biocon.2006.06.009

Ordano, M., Engelhard, I., Rempoulakis, P., Nemny-Lavy, E., Blum, M., Yasin, S., Lensky, I.M., Papadopoulos, N.T., Nestel, D., 2015. Olive fruit fly (*Bactrocera oleae*) population dynamics in the Eastern Mediterranean: Influence of exogenous uncertainty on a monophagous frugivorous Insect. PLoS One 10, 1–18. https://doi.org/10.1371/journal.pone.0127798

Ortega, M., Pascual, S., Rescia, A.J., 2016. Spatial structure of olive groves and scrublands affects *Bactrocera oleae* abundance: a multi-scale analysis. Basic Appl Ecol 17, 696–705. https://doi.org/10.1016/j.baae.2016.06.001

Picchi, M.S., Bocci, G., Petacchi, R., Entling, M.H., 2016. Effects of local and landscape factors on spiders and olive fruit flies. Agric Ecosyst Environ 222, 138–147. https://doi.org/10.1016/j.agee.2016.01.045

Plieninger, T., Hui, C., Gaertner, M., Huntsinger, L., 2014. The Impact of Land Abandonment on Species Richness and Abundance in the Mediterranean Basin: A Meta-Analysis. PLoS One 9, e98355. https://doi.org/10.1371/journal.pone.0098355

Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., Willmer, P., 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biol Conserv 129, 519–529. https://doi.org/10.1016/j.biocon.2005.11.019

Puech, C., Baudry, J., Joannon, A., Poggi, S., Aviron, S., 2014. Organic vs. conventional farming dichotomy: Does it make sense for natural enemies? Agric Ecosyst Environ 194, 48–57. https://doi.org/10.1016/j.agee.2014.05.002

Pulliam, H.R., 1988. Sources, Sinks, and Population Regulation. Am Nat 132, 652–661. https://doi.org/10.1086/284880

Queiroz, C., Beilin, R., Folke, C., Lindborg, R., 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. Front Ecol Environ 12, 288–296. https://doi.org/10.1890/120348

R Core Team, 2016. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria.

Randlkofer, B., Obermaier, E., Hilker, M., Meiners, T., 2010. Vegetation complexity-The influence of plant species diversity and plant structures on plant chemical complexity and arthropods. Basic Appl Ecol 11, 383–395. https://doi.org/10.1016/j.baae.2010.03.003

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proc Natl Acad Sci USA 118, 1–6. https://doi.org/10.1073/PNAS.2002548117

Robinson, J. V., 1981. The Effect of Architectural Variation in Habitat on a Spider Community: An Experimental Field Study. Ecology 62, 73–80.

Rosas-Ramos, N., Baños-Picón, L., Tobajas, E., de Paz, V., Tormos, J., Asís, J.D., 2018. Value of ecological infrastructure diversity in the maintenance of spider assemblages: A case study of Mediterranean vineyard agroecosystems. Agric Ecosyst Environ 265, 244–253. https://doi.org/10.1016/j.agee.2018.06.026

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2020. Farming system shapes traits and composition of spider assemblages in Mediterranean cherry orchards. PeerJ 8, e8856. https://doi.org/10.7717/peerj.8856

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2019. The complementarity between ecological infrastructure types benefits natural enemies and pollinators in a Mediterranean vineyard agroecosystem. Ann Appl Biol 175, 193–201. https://doi.org/10.1111/aab.12529

Rowen, E.K., Regan, K.H., Barbercheck, M.E., Tooker, J.F., 2020. Is tillage beneficial or detrimental for insect and slug management? A meta-analysis. Agric Ecosyst Environ 294, 106849. https://doi.org/10.1016/j.agee.2020.106849

Ruano, F., Lozano, C., Garcia, P., Pena, A., Tinaut, A., Pascual, F., Campos, M., 2004. Use of arthropods for the evaluation of the olive-orchard management regimes. Agric For Entomol 6, 111–120. https://doi.org/10.1111/j.1461-9555.2004.00210.x

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2010. Biological Control of Insect Pests in Agroecosystems, in: Advances in Agronomy. Elsevier Ltd, pp. 219–259. https://doi.org/10.1016/B978-0-12-385040-9.00006-2

Sánchez-Fernández, J., Vílchez-Vivanco, J., Navarro, F., Castro-RodrÍguez, J., 2020. Farming system and soil management affect butterfly diversity in sloping olive groves. Insect Conserv Divers 13, 456–469. https://doi.org/10.1111/icad.12435

Sanz, C., Mata, R., Gómez, J., Allende, F., López, N., Molina, P., Galiana, L., 2003. Atlas de los paisajes de España. Ministerio de Medio Ambiente, Madrid.

Solomou, A.D., Sfougaris, A.I., Sfenthourakis, S., 2019. Terrestrial isopods as bioindicators for environmental monitoring in olive groves and natural ecosystems. J Nat Hist 53, 1721–1735. https://doi.org/10.1080/00222933.2019.1658821

Spears, L.R., MacMahon, J.A., 2012. An experimental study of spiders in a shrub-steppe ecosystem: the effects of prey availability and shrub architecture. J Arachnol 40, 218–227. https://doi.org/10.1636/P11-87.1

Stinner, B.R., House, G.J., 1990. Arthropods and Other Invertebrates in Conservation-Tillage Agriculture. Annu Rev Entomol 35, 299–318.

Tamburini, G., De Simone, S., Sigura, M., Boscutti, F., Marini, L., 2016. Conservation tillage mitigates the negative effect of landscape simplification on biological control. J Appl Ecol 53, 233–241. https://doi.org/10.1111/1365-2664.12544

Theron, K.J., Gaigher, R., Pryke, J.S., Samways, M.J., 2020. High quality remnant patches in a complex agricultural landscape sustain high spider diversity. Biol Conserv 243, 108480. https://doi.org/10.1016/j.biocon.2020.108480

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677. https://doi.org/10.1038/nature01014

Tscharntke, T., Rand, T.A., Bianchi, F.J.J.A., 2005. The landscape context of trophic interactions: Insect spillover across the crop-noncrop interface. Ann Zool Fennici 42, 421–432.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. J Appl Ecol 51, 746–755. https://doi.org/10.1111/1365-2664.12219

Uetz, G.W., Halaj, J., Cady, A.B., 1999. Guild Structure of Spiders in Major Crops. J Arachnol 27, 270–280.

Weissteiner, C.J., Boschetti, M., Böttcher, K., Carrara, P., Bordogna, G., Brivio, P.A., 2011. Spatial explicit assessment of rural land abandonment in the Mediterranean area. Glob Planet Change 79, 20–36. https://doi.org/10.1016/j.gloplacha.2011.07.009

Zuur, A., Ieno, E.N., N, Walker., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York.

Supplementary material

Table S1. Complete results of the different models for the richness, abundance, and diversity (Shannon index (H)) of natural enemies, spiders, and parasitoids. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables s*ystem*, the *sampling month*, and their interaction (when significant) are provided. In the first column, the type of model (GLS, generalized least squares model; LME, linear mixed model; GLM, generalized linear model; GLMM, generalized linear mixed model), the transformation applied on the explanatory variable (if any), and variance structure added to the model (if any) are given.

Model	Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
GLS	Natural enemy richness	Intercept	20.667	1.208	17.114	<0.001	***
		System (Organic)	-0.667	1.080	-0.617	0.544	ns
		Sampling month (June)	2.667	1.528	1.746	0.097	•
		Sampling month (August)	0.833	1.528	0.546	0.592	ns
		Sampling month (October)	1.167	1.528	0.764	0.454	ns
GLS (varIdent (form=~1| *Sampling month*)	Natural enemy abundance	Intercept	247.081	33.023	7.482	<0.001	***
		System (Organic)	4.506	31.315	0.143	0.887	ns
		Sampling month (June)	371.000	133.427	2.781	0.012	*
		Sampling month (August)	152.833	54.330	2.813	0.011	*
		Sampling month (October)	-83.000	35.618	-2.330	0.031	*
GLS	Natural enemy diversity (H)	Intercept	1.557	0.159	9.789	<0.001	***
		System (Organic)	-0.155	0.142	-1.087	0.291	ns
		Sampling month (June)	-0.238	0.201	-1.184	0.251	ns
		Sampling month (August)	-0.072	0.201	-0.357	0.725	ns
		Sampling month (October)	0.747	0.201	3.713	0.002	**
GLS (square root) (varIdent (form=~1| *Sampling month*)	Spider richness	Intercept	2.838	0.094	30.134	<0.001	***
		System (Organic)	-0.157	0.072	-2.161	0.044	*
		Sampling month (June)	0.340	0.117	2.905	0.009	**
		Sampling month (August)	0.678	0.101	6.687	<0.001	***
		Sampling month (October)	0.499	0.132	3.773	0.001	**
GLMM Poisson	Spider abundance	Intercept	3.200	0.126	25.352	<0.001	***
		System (Organic)	-0.346	0.136	-2.555	0.011	*
		Sampling month (June)	0.822	0.106	7.73	<0.001	***
		Sampling month (August)	1.304	0.100	13.046	<0.001	***
		Sampling month (October)	0.958	0.104	9.185	< 0.001	***
GLS (varIdent (form=~1| *Sampling month*)	Spider diversity (H)	Intercept	1.913	0.140	13.675	<0.001	***
		System (Organic)	0.075	0.183	0.409	0.688	ns
		Sampling month (June)	-0.106	0.145	-0.729	0.477	ns

		Sampling month (August)	-0.123	0.174	-0.707	0.490	ns
		Sampling month (October)	-0.217	0.198	-1.096	0.289	ns
		Sampling month (June) : *System* (Organic)	-0.135	0.258	-0.524	0.608	ns
		Sampling month (August) : *System* (Organic)	0.423	0.205	2.059	0.056	•
		Sampling month (October) : *System* (Organic)	0.467	0.247	1.894	0.077	•
	Pairwise	abandoned - organic, May == 0	0.217	0.198	1.096	0.732	ns
		abandoned - organic, June == 0	0.352	0.166	2.123	0.283	ns
		abandoned - organic, August == 0	-0.206	0.055	-3.753	0.062	•
		abandoned - organic, october == 0	-0.250	0.147	-1.699	0.435	ns
Quasi-GLM	Parasitoid richness	Intercept	2.368	0.107	22.136	<0.001	***
		System (Organic)	-0.034	0.099	-0.347	0.732	ns
		Sampling month (June)	0.105	0.131	0.803	0.432	ns
		Sampling month (August)	-0.272	0.145	-1.878	0.076	•
		Sampling month (October)	-0.211	0.142	-1.484	0.154	ns
LME	Parasitoid abundance	Intercept	48.917	8.685	5.632	<0.001	***
		System (Organic)	-5.833	10.328	-0.565	0.602	ns
		Sampling month (June)	51.833	7.676	6.753	<0.001	***
		Sampling month (August)	7.833	7.676	1.021	0.324	ns
		Sampling month (October)	-4.000	7.676	-0.521	0.619	ns
GLS (varIdent (form=~1| *Sampling month*)	Parasitoid diversity	Intercept	2.144	0.130	16.445	<0.001	***
		System (Organic)	-0.473	0.184	-2.568	0.021	*
		Sampling month (June)	-0.320	0.141	-2.265	0.038	*
		Sampling month (August)	-0.826	0.196	-4.214	<0.001	***
		Sampling month (October)	-0.737	0.214	-3.442	0.003	**
		Sampling month (June) : *System* (Organic)	0.421	0.200	2.103	0.052	•
		Sampling month (August) : *System* (Organic)	0.108	0.277	0.389	0.702	ns
		Sampling month (October) : *System* (Organic)	0.701	0.303	2.317	0.034	*
	Pairwise	abandoned - organic, May == 0	0.473	0.184	2.568	0.182	ns
		abandoned - organic, June == 0	0.053	0.078	0.680	0.924	ns

		abandoned - organic, August == 0	0.366	0.207	1.768	0.403	ns
		abandoned - organic, October == 0	-0.228	0.240	-0.948	0.809	ns

Table S2. Complete results of the different models for the abundance of the most dominant families and *Bactrocera oleae*. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables *system*, the *sampling month*, and their interaction (when significant) are provided. In the first column the type of model (GLS, generalized least squares model; LME, linear mixed model; GLM, generalized linear model; GLMM, generalized linear mixed model), the transformation applied on the explanatory variable (if any), and the correlation or variance structure added to the model (if any) are given.

Model	Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
GLMM Poisson	Araneidae abundance	Intercept	1.680	0.244	6.875	<0.001	***
		System (Organic)	-1.069	0.244	-4.376	<0.001	***
		Sampling month (June)	0.310	0.280	1.107	0.268	ns
		Sampling month (August)	0.879	0.253	3.474	<0.001	***
		Sampling month (October)	0.598	0.265	2.257	0.024	*
GLMM Poisson	Gnaphosidae abundance	Intercept	0.784	0.491	1.597	0.110	ns
		System (Organic)	0.584	0.650	0.899	0.369	ns
		Sampling month (June)	0.865	0.417	2.076	0.038	*
		Sampling month (August)	0.118	0.480	0.245	0.806	ns
		Sampling month (October)	-1.386	0.782	-1.774	0.076	•
		Sampling month (June) : *System* (Organic)	-0.657	0.557	-1.179	0.238	ns
		Sampling month (August) : *System* (Organic)	0.208	0.601	0.346	0.730	ns
		Sampling month (October) : *System* (Organic)	1.594	0.865	1.843	0.065	•
	Pairwise	abandoned - organic, May == 0	-0.584	0.650	-0.899	0.774	ns
		abandoned - organic, June == 0	0.073	0.581	0.125	1	ns
		abandoned - organic, August == 0	-0.792	0.623	-1.272	0.512	ns
		abandoned - organic, October == 0	-2.178	0.880	-2.474	0.045	*
GLMM Poisson	Linyphiidae abundance	Intercept	0.654	0.474	1.379	0.168	ns
		System (Organic)	0.758	0.599	1.266	0.205	ns
		Sampling month (June)	0.288	0.535	0.538	0.590	ns
		Sampling month (August)	0.406	0.522	0.777	0.437	ns
		Sampling month (October)	0.00009	0.571	0	0.999	ns
		Sampling month (June) : *System* (Organic)	1.391	0.608	2.287	0.022	*

		Sampling month (August) : *System* (Organic)	-0.00005	0.625	0	0.999	ns
		Sampling month (October) : *System* (Organic)	-0.074	0.688	-0.108	0.914	ns
	Pairwise	abandoned - organic, May == 0	-0.758	0.599	-1.266	0.548	ns
		abandoned - organic, June == 0	-2.149	0.510	-4.216	<0.001	***
		abandoned - organic, August == 0	-0.758	0.529	-1.432	0.435	ns
		abandoned - organic, October == 0	-0.684	0.603	-1.134	0.644	ns
GLMM Poisson	Oxyopidae abundance	Intercept	0.834	0.388	2.152	0.031	*
		System (Organic)	-1.946	1.068	-1.823	0.068	•
		Sampling month (June)	2.929	0.387	7.561	<0.001	***
		Sampling month (August)	2.565	0.392	6.548	<0.001	***
		Sampling month (October)	0.255	0.518	0.492	0.623	ns
		Sampling month (June) : *System* (Organic)	-0.251	1.500	-0.168	0.867	ns
		Sampling month (August) : *System* (Organic)	-1.571	0.538	-2.920	0.004	**
		Sampling month (October) : *System* (Organic)	-2.683	0.624	-4.301	<0.001	***
	Pairwise	abandoned - organic, May == 0	-0.255	0.518	-0.492	0.979	ns
		abandoned - organic, June == 0	-0.004	1.418	-0.003	1	ns
		abandoned - organic, August == 0	1.316	0.227	5.806	<0.001	***
		abandoned - organic, October == 0	2.428	0.389	6.249	<0.001	***
GLS (square root) (varIdent (form=~1 | *Sampling month*)	Philodromidae abundance	Intercept	0.334	0.378	0.884	0.388	ns
		System (Organic)	0.576	0.114	5.058	<0.001	***
		Sampling month (June)	0.813	0.380	2.141	0.046	*
		Sampling month (August)	3.079	0.415	7.423	<0.001	***
		Sampling month (October)	2.460	0.401	6.133	<0.001	***
GLS	Salticidae abundance	Intercept	2.000	0.645	3.098	0.006	**
		System (Organic)	-0.667	0.577	-1.155	0.263	ns
		Sampling month (June)	-0.333	0.816	-0.408	0.688	ns
		Sampling month (August)	2.333	0.816	2.858	0.010	*
		Sampling month (October)	1.333	0.816	1.633	0.119	ns
GLMM Poisson	Theridiidae abundance	Intercept	0.245	0.466	0.525	0.600	ns
		System (Organic)	-1.287	0.310	-4.15	<0.001	***
		Sampling month (June)	2.028	0.475	4.274	<0.001	***
		Sampling month (August)	1.609	0.489	3.293	0.0009	***
		Sampling month (October)	1.386	0.499	2.779	0.005	**

GLMM Poisson	Thomisidae abundance	Intercept	0.835	0.390	2.141	0.032	*
		System (Organic)	-0.002	0.550	-0.004	0.997	ns
		Sampling month (June)	0.452	0.483	0.936	0.349	ns
		Sampling month (August)	0.887	0.448	1.979	0.048	*
		Sampling month (October)	0.693	0.462	1.499	0.134	ns
		Sampling month (June) : *System* (Organic)	0.167	0.673	0.248	0.804	ns
		Sampling month (August) : *System* (Organic)	-1.449	0.770	-1.879	0.060	•
		Sampling month (October) : *System* (Organic)	-0.442	0.683	-0.646	0.518	ns
	Paiwise	abandoned - organic, May == 0	0.002	0.550	0.004	1	ns
		abandoned - organic, June == 0	-0.165	0.431	-0.383	0.992	ns
		abandoned - organic, August == 0	1.449	0.571	2.537	0.044	*
		abandoned - organic, October == 0	0.444	0.447	0.992	0.786	ns
GLS (square root) (varIdent (form=~1 | *Sampling month*)	Braconidae abundance	Intercept	2.942	0.529	5.567	<0.001	***
		System (Organic)	-2.000	0.748	-2.675	0.017	*
		Sampling month (June)	-0.910	0.590	-1.541	0.143	ns
		Sampling month (August)	-1.943	0.606	-3.205	0.006	**
		Sampling month (October)	-1.894	0.660	-2.870	0.011	*
		Sampling month (June) : *System* (Organic)	1.576	0.835	1.889	0.077	•
		Sampling month (August) : *System* (Organic)	1.805	0.857	2.105	0.051	•
		Sampling month (October) : *System* (Organic)	2.667	0.933	2.858	0.011	*
	Pairwise	abandoned - organic, May == 0	2	0.748	2.675	0.164	ns
		abandoned - organic, June == 0	0.424	0.371	1.142	0.707	ns
		abandoned - organic, August == 0	0.195	0.420	0.465	0.978	ns
		abandoned - organic, October == 0	-0.667	0.559	-1.193	0.680	ns
GLMM Poisson	Encyrtidae abundance	Intercept	1.194	0.334	3.576	<0.001	***
		System (Organic)	-1.625	0.789	-2.061	0.039	*
		Sampling month (June)	0.406	0.407	0.995	0.320	ns
		Sampling month (August)	1.308	0.356	3.679	<0.001	***
		Sampling month (October)	0.00001	0.446	0	0.999	ns
		Sampling month (June) : *System* (Organic)	2.197	0.837	2.625	0.009	**
		Sampling month (August) : *System* (Organic)	-0.056	0.876	-0.064	0.949	ns

		Sampling month (October) : *System* (Organic)	3.091	0.848	3.644	<0.001	***
	Pairwise	abandoned - organic, May == 0	1.625	0.789	2.061	0.146	ns
		abandoned - organic, June == 0	-0.572	0.357	-1.601	0.366	ns
		abandoned - organic, August == 0	1.681	0.440	3.822	<0.001	***
		abandoned - organic, October == 0	-1.466	0.383	-3.829	<0.001	***
GLMM Poisson	Eulophidae abundance	Intercept	1.814	0.200	9.058	<0.001	***
		System (Organic)	-0.321	0.173	-1.853	0.064	•
		Sampling month (June)	1.44	0.196	7.329	<0.001	***
		Sampling month (August)	-0.000007	0.250	0	1	ns
		Sampling month (October)	-0.633	0.300	-2.110	0.035	*
GLS (square root) (varIdent (form=~1 | *Sampling month*)	Mymaridae abundance	Intercept	1.843	0.197	9.337	<0.001	***
		System (Organic)	-0.530	0.175	-3.034	0.007	**
		Sampling month (June)	1.802	0.246	7.315	<0.001	***
		Sampling month (August)	-1.041	0.246	-4.226	<0.001	***
		Sampling month (October)	-1.192	0.246	-4.840	<0.001	***
GLMM Poisson	Pteromalidae abundance	Intercept	0.668	0.530	1.259	0.208	ns
		System (Organic)	-0.372	0.664	-0.561	0.575	ns
		Sampling month (June)	0.431	0.352	1.224	0.221	ns
		Sampling month (August)	-1.466	0.633	-2.318	0.021	*
		Sampling month (October)	1.347	0.308	4.381	<0.001	***
GLMM Poisson	Scelionidae abundance	Intercept	2.557	0.133	19.257	<0.001	***
		System (Organic)	0.169	0.120	1.401	0.161	ns
		Sampling month (June)	0.933	0.128	7.289	<0.001	***
		Sampling month (August)	0.895	0.129	6.956	<0.001	***
		Sampling month (October)	0.046	0.152	0.303	0.762	ns
GLS (square root) (correlation = corARMA (c(0.2), p=1, q=0))	Trichogrammatidae abundance	Intercept	1.426	0.233	6.126	<0.001	***
		System (Organic)	-0.600	0.228	-2.634	0.016	*
		Sampling month (June)	1.183	0.290	4.086	<0.001	***
		Sampling month (August)	-0.518	0.284	-1.826	0.084	•
		Sampling month (October)	-0.425	0.285	-1.488	0.153	ns
GLMM Poisson	Staphylinidae abundance	Intercept	1.936	0.353	5.479	<0.001	***
		System (Organic)	1.405	0.469	2.998	0.003	**
		Sampling month (June)	-2.866	0.387	-7.416	<0.001	***
		Sampling month (August)	-3.714	0.581	-6.389	<0.001	***
		Sampling month (October)	-0.669	0.154	-4.342	<0.001	***
GLS (square	Formicidae abundance	Intercept	12.604	0.703	17.916	<0.001	***

root) (varIdent (form=~1 | *Sampling month*)		*Sampling month* (June)	8.312	2.714	3.063	0.006	**
		Sampling month (August)	3.444	1.719	2.003	0.059	•
		Sampling month (October)	-5.598	1.531	-3.656	0.002	**
GLMM Poisson	*Bactrocera oleae* abundance	Intercept	1.662	0.566	2.938	0.003	**
		System (Traditional)	0.346	0.788	0.439	0.660	ns
		System (Organic)	0.859	0.775	1.108	0.268	ns
		Sampling month (October)	0.406	0.208	1.948	0.052	•
		Month (October) : *System* (Traditional)	1.820	0.302	6.027	<0.001	***
		Month (October) : *System* (Organic)	1.531	0.263	5.817	<0.001	***

Chapter II

EFFECTS OF TRADITIONAL ORCHARD ABANDONMENT AND LANDSCAPE CONTEXT ON THE BENEFICIAL ARTHROPOD COMMUNITY IN A MEDITERRANEAN AGROECOSYSTEM

EFECTOS DEL ABANDONO DE CULTIVOS TRADICIONALES Y DEL CONTEXTO PAISAJÍSTICO SOBRE LA COMUNIDAD DE ARTRÓPODOS BENEFICIOSOS EN UN AGROECOSISTEMA MEDITERRÁNEO

Effects of traditional orchard abandonment and landscape context on the beneficial arthropod community in a Mediterranean agroecosystem

Efectos del abandono de cultivos tradicionales y del contexto paisajístico sobre la comunidad de artrópodos beneficiosos en un agroecosistema mediterráneo

de Paz, V., Asís, J.D., Holzschuh, A., Baños-Picón, L.

Adapted from de Paz et al. (2023) Insects 14, 277. https://doi.org/10.3390/insects14030277

Resumen

El abandono agrícola es uno de los principales cambios en el uso del suelo en Europa, y sus consecuencias sobre la biodiversidad dependen del contexto y de los taxones considerados. Aunque varios estudios han trabajado este tema, pocos se han centrado en cultivos tradicionales, especialmente en paisajes con diferente grado de complejidad y en un clima mediterráneo. En este contexto, nos propusimos determinar los efectos del abandono de cultivos de almendro sobre las comunidades de tres grupos de artrópodos beneficiosos, así como el papel del contexto paisajístico en la modulación de estos efectos. Entre febrero y septiembre de 2019, se realizaron cuatro muestreos en doce parcelas de almendro (tres abandonadas y tres tradicionales (parcelas activas manejadas de forma tradicional) situadas en paisajes simples, así como tres abandonadas y tres tradicionales en paisajes complejos). Las parcelas de almendro abandonadas y tradicionales albergan comunidades de artrópodos diferentes, con distintos valores de riqueza y abundancia, fuertemente condicionadas por la estacionalidad. Las parcelas abandonadas pueden favorecer a los polinizadores y enemigos naturales, proporcionando recursos alternativos en paisajes simples. Sin embargo, el papel que desempeñan estas parcelas en paisajes simples desaparece a medida que aumenta el porcentaje de hábitats seminaturales en el paisaje. Nuestros resultados muestran que la simplificación del paisaje, a través de la pérdida de hábitats seminaturales, tiene consecuencias negativas sobre la biodiversidad de artrópodos, incluso en paisajes agrícolas tradicionales con un parcelario pequeño y una gran diversidad de cultivos.

Abstract

Agricultural abandonment is one of the main land-use changes in Europe, and its consequences on biodiversity are context- and taxa-dependent. While several studies have worked on this topic, few have focused on traditional orchards, especially in different landscapes and under a Mediterranean climate. In this context, we aimed to determine the effects of almond orchard abandonment on the communities of three groups of beneficial arthropods and the role of the landscape context in modulating these effects. Between February and September 2019, four samplings were carried out in twelve almond orchards (three abandoned and three traditional (active orchards under traditional agricultural management) located in simple landscapes as well as three abandoned and three traditional in complex landscapes). Abandoned and traditional almond orchards harbor different arthropod communities and diversity metrics that are strongly conditioned by seasonality. Abandoned orchards can favor pollinators and natural enemies, providing alternative resources in simple landscapes. However, the role that abandoned orchards play in simple landscapes disappears as the percentage of semi-natural habitats in the landscape increases. Our results show that landscape simplification, through the loss of semi-natural habitats, has negative consequences on arthropod biodiversity, even in traditional farming landscapes with small fields and high crop diversity.

Keywords: abandonment; traditional almond orchard; spider; parasitoid; bee; landscape complexity

1. Introduction

Habitat loss by conversion to intensive agriculture constitutes one of the main drivers of biodiversity loss worldwide, and it has been identified as the primary cause of the decline in insect populations (Díaz et al., 2019; Raven and Wagner, 2021; Sánchez-Bayo and Wyckhuys, 2019; Tilman et al., 2002). For these reasons, the consequences of agricultural intensification (e.g., landscape simplification; farmland consolidation; the increased use of synthetic pesticides, herbicides, and fertilizers; habitat fragmentation; a reduction in crop diversity) and the possible measures to counteract them have been thoroughly investigated (Batáry et al., 2015; Bengtsson et al., 2005; Rusch et al., 2016; Tscharntke et al., 2021, 2012a).

In Europe, while intensification is still the main trend on fertile soils, agricultural abandonment is prevalent in marginal areas with poor soils; in fact, the total area dedicated to agriculture has been steadily decreasing over the last few decades (FAOSTAT, 2020; Plieninger et al., 2014). The consequences of agricultural abandonment on biodiversity are still subject to much controversy. While some studies show an opportunity for the restoration of natural ecosystems (Pereira and Navarro, 2015), others point out the loss of the rich biodiversity associated with traditional farming systems (Oppermann et al., 2012; Plieninger and Bieling, 2013; Quintas-Soriano et al., 2022). Many studies have attempted to shed light on this topic, and the rough conclusion seems to be that in Europe, agricultural abandonment reduces overall biodiversity, especially in traditional landscapes and after long periods (Benayas et al., 2007; Plieninger et al., 2014; Queiroz et al., 2014). Conversely, some studies have found increased diversity in late successional stages or an overall beneficial effect of maintaining both managed and abandoned plots in the landscape (Hussain et al., 2018; Katayama et al., 2019; Penado et al., 2022; Walcher et al., 2020, 2017; Wersebeckmann et al., 2021).

The majority of the studies on the effects of farmland abandonment have focused on grasslands or annual crops, especially in central Europe, whereas permanent crops and, in particular, traditional orchards, have received far less attention (de Paz et al., 2022; Kajtoch, 2017). As ecological theory predicts, the consequences of agricultural abandonment (i.e., a further reduction in the disturbance level) may not be the same in annual systems and permanent crops given the low disturbance levels and increased stability of the latter (Bruggisser et al., 2010). This is based on the *intermediate disturbance hypothesis*, which predicts higher diversity levels at intermediate levels of disturbance, with both poorly and highly disturbed systems harboring less biodiversity (Connell, 1978; Grime, 1973). Furthermore, the results observed in central Europe may differ in Mediterranean areas given the extreme changes that eco-systems suffer under this climate, with a strong variability in resource availability be-tween seasons (Rivas-Martínez et al., 2017). This severe seasonality can affect plant and arthropod communities and could interact with crop management changes (Rosas-Ramos et al., 2022; Zamora et al., 2007).

Studies assessing the consequences of agricultural abandonment in different landscape scenarios are even scarcer, notwithstanding that these consequences may be modulated by the landscape context, differing between simple and complex landscapes (intermed*iate landscape complexity hypothesis* (Tscharntke et al., 2012b)). Therefore, interactive effects be-tween landscape complexity (measured using the percentage of semi-natural habitats in the landscape as a proxy of complexity) and crop management practices (or their absence) at the local scale should be expected. In addition, within a landscape, habitat complexity affects biodiversity (see Langellotto and Denno (2004), and references therein). Plant diversity and vegetation architecture increase habitat complexity and have been proven to positively affect natural enemies (Chaplin-Kramer and Kremen, 2012; Holland et al., 2016; Landis et al., 2000; Langellotto and Denno, 2004) and pollinators (Kennedy et al., 2013; Maurer et al., 2022; Westrich, 1996) through a rise in niche and resource availability as well as diverse plant volatiles (Öckinger et al., 2006; Randlkofer et al., 2010).

Consequently, the importance of semi-natural habitats depends on both occurrence in the landscape and habitat features. They provide different microhabitats and resources (i.e., floral resources, shelter, alternative hosts or prey, overwintering sites) that favor natural enemies and pollinators, which can, in turn, spill over into crops (Carrié et al., 2017; Holland et al., 2017; Rusch et al., 2010; Shi et al., 2021; Tscharntke et al., 2012b, 2005). In fact, their relevance is such that Duelli and Obrist (2003) found that more than 63% of all animal species inhabiting an agriculturally managed area depended on the presence of semi-natural habitats, although this dependence seems to be stronger in annual than in permanent crops (Picchi et al., 2020; Rey et al., 2019; Shackelford et al., 2013).

Among permanent crops, traditional orchards constitute high nature value systems that, in Europe, have been managed in the same way for centuries, creating cultural landscapes with high levels of associated biodiversity that de-pend on their traditional farming practices to persist (Baldock et al., 1993; Fischer et al., 2012; Horak et al., 2013; Keenleyside et al., 2014). Almond orchards are among the best examples of high nature value systems, with the almond being an ancient crop that has been managed in the Mediterranean Basin since the Phoenicians introduced them by 300–500 BCE (Gradziel, 2017). Within the Mediterranean region, Spain is the second largest producer in the world with 416,950 tons of almonds (FAOSTAT, 2020). Traditional almond orchard yields depend on the delivery of ecosystem services by beneficial arthropods since almond trees need insect pollination to achieve fruit sets and are highly sensitive to various pests, benefiting from natural pest control (Eilers and Klein, 2009; Henselek et al., 2018; Klein et al., 2007).

Accordingly, this study focuses on three relevant groups of beneficial arthropods that interact with almond crops. Wild bees constitute one of the most important groups of pollinators, and they play a pivotal role in almond pollination (Garibaldi et al., 2013; Klein et al., 2007; Potts et al., 2016). Spiders are one of the most abundant and diverse groups of generalist predators inhabiting agroecosystems, with an important role in pest suppression, and have been found to dominate the natural enemy community in the almond tree canopy (Benhadi-Marin et al., 2011; Birkhofer et al., 2013; Michalko et al., 2019). Hymenopteran parasitoids (hereafter parasitoids) are among the most relevant groups of natural enemies, being key for the control of almond orchard pests (Legner and Gordh, 1992; Sánchez-Ramos et al., 2017; Schäckermann et al., 2015). These groups also require a variety of resources (e.g., diverse vegetation structure and prey availability for spiders, flower resources and hosts for parasitoids, flower resources and nesting sites for bees) and can, therefore, act as indicators of the availability of these resources in different habitats (Kennedy et al., 2013; Landis et al., 2000; Rosas-Ramos et al., 2018; Rusch et al., 2010; Spears and MacMahon, 2012; Westrich, 1996).

Despite the importance of almond crop production, to our knowledge, no studies have evaluated the effects of almond orchard abandonment on their associated arthropod biodiversity, especially in traditional areas under different landscape contexts and in a Mediterranean climate with strong seasonality. To contribute to filling this knowledge gap, we set out to determine the following: (1) the possible differences in community composition, abundance, and richness of spiders, parasitoids, and bees between abandoned and active orchards under traditional management (hereafter traditional orchards); (2) the role of the landscape context in which our traditional and abandoned orchards are located in modulating these effects; and (3) the response of spiders, parasitoids, and bees to land-use composition at different spatial scales (150 m and 500 m). Based on this framework of knowledge and previous research, we hypothesized that the study groups' community structure and composition will differ be-tween managed and abandoned orchards, with more mobile organisms (i.e., bees) being more influenced by the landscape context than by the system. We also expect a generally positive effect with an increase in the percentage of semi-natural habitats in the landscape regardless of the system. Furthermore, we anticipate marked seasonality effects influencing the responses to orchard systems and semi-natural habitats through changes in resource availability.

2. Materials and Methods

2.1. Study Area

The study was carried out in the municipality of La Fregeneda (Salamanca, Western Spain) (40°59′ N, 6°52′ W). The location of this region, on the border with Portugal, together with the presence of small villages and limited infrastructures, has led to progressive isolation and depopulation as well as to a growing abandonment of agricultural activities. This socioeconomic situation has been a factor shaping the landscape, resulting in a mosaic of traditionally cultivated plots (with little mechanization and minimal economic investment) and abandoned plots in various stages of plant succession, interspersed with fragments of natural vegetation. These remnants of natural vegetation typical of Mediterranean sclerophyllous scrub are formed mainly by *Cytisus* shrublands (*Cytisus multiflorus* (L'Hér.) Sweet, *C. scoparius* (L.) Link), rock-roses (*Cistus ladanifer* L.), French lavender (*Lavandula pedunculata* (Mill.) Cav.), and thymes (*Thymus mastichina* (L.) L., *Thymus zygis* subsp. *zygis* Loefl. ex L.), among others. There are also areas of Mediterranean forest, mainly composed of holm oaks (*Quercus ilex* subsp. *ballota* (Desf.) Samp.), although they coexist with European nettle trees (*Celtis australis* L.) and junipers (*Juniperus oxycedrus* L.), which have great ecological value and persist mainly because of the difficulty in cultivating on the steep slopes of the area, which has considerably limited agricultural practices.

The study area comprises 4 900 ha, its altitude ranging between 130 and 560 m a.s.l. It is located within the Arribes del Duero Natural Park and belongs to landscape unit 84, "Gorges and valleys on the Portuguese border", with a small part located in the transition zone between this and landscape unit 49, "Peneplains of Zamora and Salamanca and foothill of the Montes de León" (Sanz et al., 2003) (Fig. 1). The climate is mild, warm, and temperate, with an average annual rainfall of 626 mm and an average annual temperature of 13.7 °C. Numerous small watercourses run through the area, which is also crossed by the CL-517 along 12.8 km. The predominant soil types are eutric cambisol and lithic leptosol (ITACYL and AEMET, 2013), following the World Reference Base for Soil Resources (IUSS Working Group WRB, 2022). Attending to habitat composition and configuration, two types of landscapes can be differentiated in the study area: a complex one, with a high proportion of semi-natural habitats (mainly scrublands but also forest remnants and ungrazed grasslands) distributed in medium-to-large patches (0.5 to 20 ha), with inserted clusters of agricultural fields; and a simpler one, closer to the village, dominated by crops (mainly almond orchards, although olive groves, vineyards, cereal fields, and grazed grasslands are also present) interspersed with small-to-medium patches (0.01–1 ha) of semi-natural habitats (grasslands and scrublands that are no longer grazed, woodland hedges, road verges, and abandoned orchards that have reached late successional stages). These crops are traditionally managed without the application of synthetic pesticides or fertilizers. The orchards still active are dominated by old trees of indigenous varieties that are not significantly profitable and are owned by small producers who sell the harvested product to cooperatives in other regions, dedicating part of the production to self-consumption. However, the social and economic revitalization of this municipality depends largely on this crop since the flowering season represents its main tourist attraction.

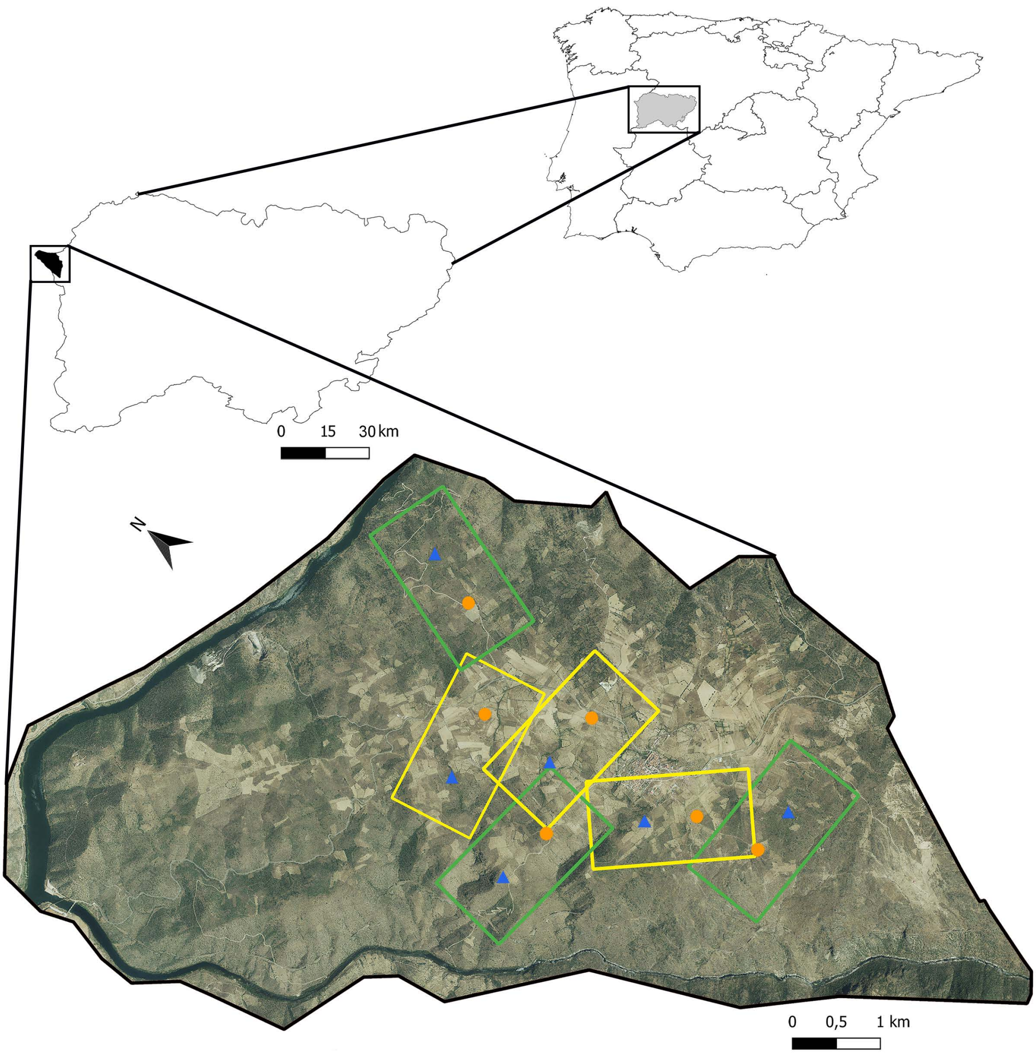

Figure 1: Location of the study area in the Salamanca province (Western Spain) and the placement of the 6 landscape windows (yellow: low level of semi-natural habitats, green: high level of semi-natural habitats) and 12 almond orchards (blue triangles: abandoned almond orchards, orange circles: traditional almond orchards).

2.2. Sampling Design

We selected six landscape windows varying in their percentage of semi-natural habitats, three of them with a low percentage of semi-natural habitats (mean 19.91 ± 11.68 %, low level of semi-natural habitats) and the other three with a high percentage of these habitats (60.19 ± 2.69 %, high level of semi-natural habitats). Each window was 1.85 km by 1 km in size—this was the minimal distance that allowed for us to select an abandoned almond orchard and an active one, under traditional agricultural management, always keeping a minimum distance of 500 m between orchards and between them and the window's edges. Landscape windows allowed for us to standardize orchard selection, ensuring that each pair of traditional and abandoned or-chards was located in the same landscape. The selected traditional orchards had a mean size of 6 530.3 ± 3 036.8 m2 and were rainfed, plowed once or twice a year to control the naturally growing vegetation, and pruned once a year; synthetic pesticides, herbicides, and fertilizers were not applied. The vegetation growing in these orchards was dominated by grasses such as *Festuca* sp., *Hordeum* sp., and *Avena* sp. and by Asteraceae; *Carduus* sp. and *Verbascum pulverulentum* Vill., among others, were also present. Selected abandoned orchards had a mean size of 6 456.9 ± 1 395.4 m^2 and a similar vegetation structure, to guarantee that all of them were in a similar successional stage, that was composed predominantly of shrubs (*Cytisus multiflorus*, *C. scoparius*, and *Lavandula pedunculata*), *Festuca* sp., and Asteraceae, among others. We also measured the land-use composition in circular sectors with 150 m and 500 m radii surrounding each orchard, with five land-use categories (artificial roads and buildings, semi-natural habitats, permanent crops, grasslands, and annual crops), using the data from the Spanish Geographic Information System for Agricultural Plots (SIGPAC).

Sampling was performed from February to September 2019 every seven-to-eight weeks, starting with the flowering period (late February) and finishing just after the almond harvest (mid-September). Each sampling period took place over six consecutive days, randomly assigning the order in which the orchards were sampled. Weather conditions were kept as uniform as possible between the sampling periods, avoiding rainy and windy days.

To capture spiders and hymenopteran parasitoids, six uncovered pitfall traps (9 cm diameter, 12.3 cm depth) were placed in each orchard, three under the almond tree canopy and three between rows (72 in total) (Cardenas et al., 2015). The traps were filled to a third with a mixture of 70% alcohol and antifreeze (10% ethylene glycol) in a 3:2 ratio (600 mL of alcohol and 400 mL of antifreeze per liter). The traps were also placed 20 m apart from each other and the groves' edges to reduce trap-to-trap interference and edge effects and they remained in the field for 72 h. To collect parasitoids and vegetation spiders, we randomly selected four trees in each almond orchard and vacuumed each tree and the surrounding vegetation in a 2 m × 2 m quadrant for three minutes using a gardener's leaf blower (Garland GAS 550 G) modified as a suction machine (Avinent and Llacer, 1995). For the capture of bees and parasitoids, we set up in each orchard two clusters of three pan traps each—one yellow, one blue, and one white. We used 500 mL plastic soup bowls painted with UV-bright yellow, white, and blue paint, and we placed them on iron poles at a 1 m height. Within each cluster, traps were placed 5 m apart. The traps were filled with water and a drop of detergent and were left in the field for 48 h (Westphal et al., 2008) (Fig. 2).

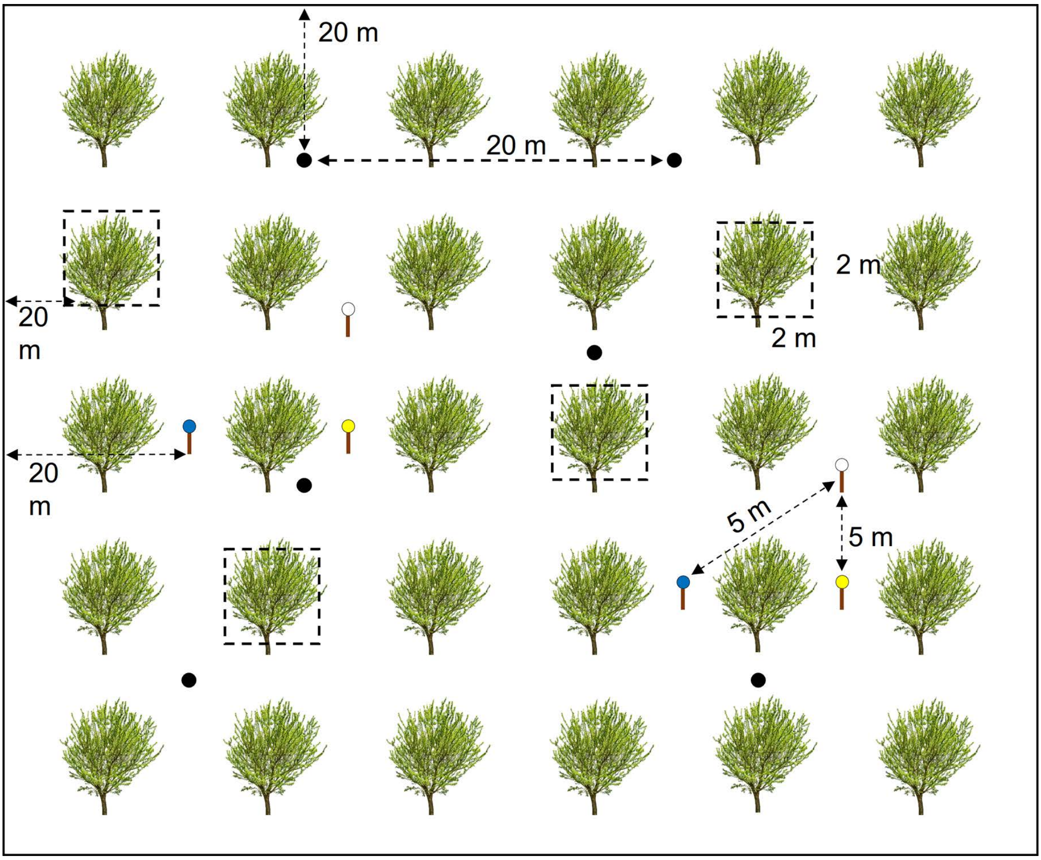

Figure 2: Sampling design. Black circles: pitfall traps; empty squares: 2 m × 2 m vacuuming quadrants; yellow, white, and blue circles: pan traps. Dashed arrows represent the minimum distance between traps or to the grove's edge.

All the collected specimens were sorted in the laboratory and identified at either the family level (spiders and parasitoids) or the genus level (bees). A higher taxa approach (e.g., family or genus taxonomic resolution) was found to be a reliable approach for revealing species richness and compositional patterns (de Oliveira et al., 2020).

2.3. Statistical Analyses

Prior to performing the analyses, we assessed the completeness of the sampling methods for each group (spiders, parasitoids, and bees) using the non-parametric Chao1 estimator (Colwell, 2013). All methods exhibited high levels of completeness (pitfall traps: 96% of the 24 estimated spider families, 93% of the 15 estimated parasitoid families; vacuuming: 83% of the 29 estimated spider families, 98% of the 24 estimated parasitoid families, 100% of the three estimated bee genera; pan traps: 96% of the 12 estimated spider families, 93% of the 21 estimated parasitoid families, 86% of the 22 estimated bee genera). We also removed the genus *Apis* (57 individuals) from the analyses to focus only on wild bees.

The effects of the *system* type (traditional vs. abandoned) and the *level of semi-natural habitats* in the landscape window (high vs. low) on the spider, parasitoid, and bee communities were analyzed with PERMANOVA (*system*, *level of semi-natural habitats*, and *sampling month* as fixed factors and *orchard* as a random factor, with 9999 permutations and "permutation of residuals under a reduced model" as the permutation method) and MDS (multidimensional scaling). Similarity matrices were calculated using the Bray–Curtis coefficients with the abundances square-root–transformed to reduce the weight of the most dominant families.

To test for spatial autocorrelation among the study orchards, we performed a Mantel correlogram based on a similarity matrix (Bray–Curtis) and the geographical data of the study orchards (Borcard et al., 2018). The results revealed a significant spatial autocorrelation for the bees and some of the spider and parasitoid families. Therefore, we added spatial correlation structures to these models and compared their AICs to select the best model (Zuur et al., 2009). We also checked for temporal correlation using the autocorrelation function (ACF), and when we detected significant temporal patterns, we added a correlation structure for short time-series and a variance structure that allows for different variances for each level of the variable *sampling month* to our models and compared the AICs (Zuur et al., 2009) (Tables S1 and S2).

Family and genus richness and abundance data were analyzed in a two-step process. First, we used linear mixed models and generalized linear mixed models to test the effect of the *system* (traditional vs. abandoned), the *level of semi-natural habitats* in the landscape window (high vs. low), the *sampling month*, and their interactions (as fixed factors) and the *orchard* (as a random factor) on the family or genus richness and abundance for the spiders, parasitoids, and bees and for the abundance of the most dominant families or genera (>100 individuals, 20 out of 73).

Second, we checked the correlation between each land-use category measured at 150 m and 500 m, and since they were all negatively correlated with the percentage of semi-natural habitats at 500 m, we decided to use only this category in our analyses. We also checked the correlation between the percentage of semi-natural habitats and the system to ensure that neither abandoned nor traditional orchards had higher or lower levels of this variable and they were not correlated at either scale. To analyze the effect of semi-natural habitats at 150 m and 500 m on the pooled data from the four sampling periods, we used the linear least squares and generalized linear models, including the variables *system* and *percentage of semi-natural habitats*, at both scales (in separate models) and their interaction as fixed factors; then, we used the family or genus richness and the abundance of spiders, parasitoids, and bees and the abundance of the dominant families or genera as dependent variables. In both cases, we used the AICs to determine at which scale each group showed a stronger response (Marrec et al., 2021).

To select the best models in all analyses, we used a standard backward selection procedure, and we checked the residuals of each model to ensure normality, independence, and homoscedasticity either graphically or with the package Dharma (Hartig, 2022).

For the analyses, the statistical packages PRIMER v6 (PERMANOVA, MDS) (PRIMER-E Ltd.) (Clarke and Gorley, 2006) and R 4.0.5 (Mantel correlogram, ACF function, correlation matrices, linear least squares models, linear mixed models, generalized linear models, generalized linear mixed models) (R Core Team, 2021) were used.

3. Results

We collected a total of 8352 arthropods belonging to the focal groups: 4480 spiders (31 families), 3161 parasitoids (23 families), and 711 bees (20 genera).

The PERMANOVA revealed a significant effect of the system on the spider community (pseudo-F = 2.114, p = 0.003), with differences in every month except May, and on the parasitoid community (pseudo-F = 2.351, p = 0.0176), differing only in May and September. For the bee community, we found only a significant effect for the level of semi-natural habitats in February, right at the almond blooming period; this effect faded away as the season progressed (Table 1). These results are also noticeable in the MDS (Fig. 3).

Table 1: Results of the PERMANOVA for the variables *system* (abandoned vs. traditional), *sampling month*, and *level of semi-natural habitats* (high vs. low) (full model results and pairwise comparisons). SNH = semi-natural habitats.

Response Variable	Explanatory Variables	d.f.	Pseudo-F	p-value
Spiders	System	1	5.761	0.001
	Sampling month	3	10.754	0.001
	System: Sampling month	3	2.114	0.003
Parasitoids	System	1	1.549	0.177
	Sampling month	3	12.696	0.001
	System: Sampling month	3	2.351	0.018
Bees	Sampling month	3	13.263	0.001
	Level of SNH	1	2.242	0.041
	Sampling month: Level of SNH	3	1.466	0.103
Pairwise comparisons			**Pseudo-t**	**p-value**
Spiders	Traditional—Abandoned, February = 0		2.102	0.002
	Traditional—Abandoned, May = 0		1.295	0.100
	Traditional—Abandoned, July = 0		1.773	0.023
	Traditional—Abandoned, September = 0		1.987	0.004
Parasitoids	Traditional—Abandoned, February = 0		0.835	0.641
	Traditional—Abandoned, May = 0		1.830	0.025
	Traditional—Abandoned, July = 0		1.221	0.171
	Traditional—Abandoned, September = 0		2.009	0.001
Bees	Low—High, February = 0		1.998	0.018
	Low—High, May = 0		1.143	0.283
	Low—High, July = 0		0.974	0.477
	Low—High, September = 0		0.653	0.664

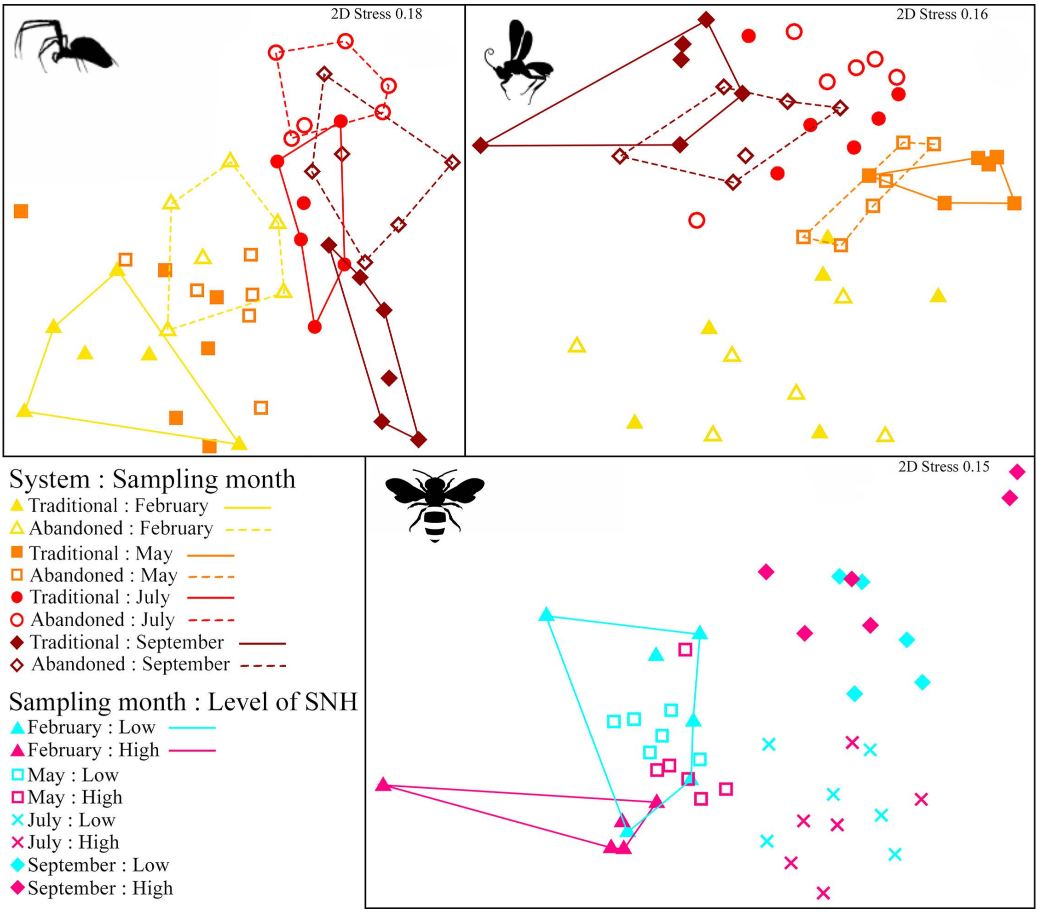

Figure 3: MDS for the spider, parasitoid, and bee communities sampled (Bray–Curtis index, square-root–transformed abundances). Polygons include the samples belonging to the same category of the variable system or level of semi-natural habitats for each sampling period. Only polygons for which significant pairwise comparisons were detected in the PERMANOVA are represented. SNH = semi-natural habitats.

The linear models not only provided different results for each group but also showed some similar general trends, especially in the response of the different groups to the percentage of semi-natural habitats at both scales.

Starting with the spiders, we found that their abundance was higher in abandoned than in traditional orchards toward the second part of the season (July and September; Fig. 4a). Spider richness was higher in the abandoned orchards during the whole season (Fig. 4c). Both spider abundance and richness peaked in July (Fig. 4a, d, Table S1). Spiders were not affected by the level of semi-natural habitats in the landscape window (1.85 km × 1 km). Spider abundance decreased in abandoned orchards and increased in traditional orchards as the percentage of semi-natural habitats at 150 m increased (Fig. 4b), and spider richness decreased as the percentage of semi-natural habitats at 150 m increased (Fig. 4e, Table S2). Regarding spider families, gnaphosids, linyphids, and lycosids were more abundant in traditional orchards (in contrast to the results for all spiders), while araneids, oxyiopids, philodromids, salticids, and theridids were more abundant in abandoned orchards, and thomisids and zodarids were not affected by the system (Table S3). Some of them were affected by the level of semi-natural habitats in the landscape window (Table S3). Most spider families responded more strongly to the percentage of semi-natural habitats at 150 m than to other scales, in most cases showing the same interaction that we found for the whole group, with abundance decreasing in abandoned orchards and increasing in tradition-al ones as the percentage of semi-natural habitats increased (Table S4).

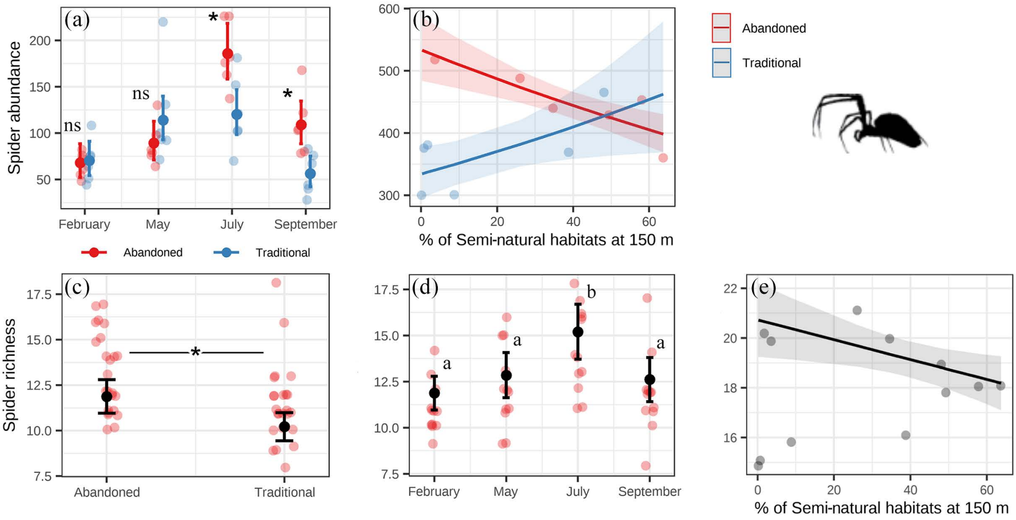

Figure 4: Results of the linear models for spider abundance (a, b) and richness (c–e). Points with error bars represent estimated means and 95% confidence intervals from the models' predictions, and dull dots represent the raw data. Significant differences ($p < 0.05$) are shown with asterisks. Differences in pairwise comparisons are shown with different letters. ns: not significant.

For the parasitoids, abundance and richness were higher in traditional than in abandoned orchards in May (when parasitoids had their peak) but were marginally higher in abandoned than in traditional orchards in September (Fig. 5a, d). Only in May was their abundance significantly higher in orchards located in landscapes with a high rather than low level of semi-natural habitats (Fig. 5b). In contrast, parasitoid abundance in traditional orchards increased as the percentage of semi-natural habitats increased at 500 m and decreased in abandoned orchards (Fig. 5c, Table S2). Parasitoid richness was not affected by the percentage of semi-natural habitats at 150 m or 500 m. The dominant parasitoid families (Braconidae, Encyrtidae, Eulophidae, Mymaridae, Platygastridae, Pteromalidae, Scelionidae) were generally more abundant in traditional orchards and landscapes with a higher level of semi-natural habitats in May (Table S3), and they showed a stronger response to the percentage of semi-natural habitats at 150 m (except for pteromalids and braconids), usually maintaining the same interaction that we found for the whole group (Table S4).

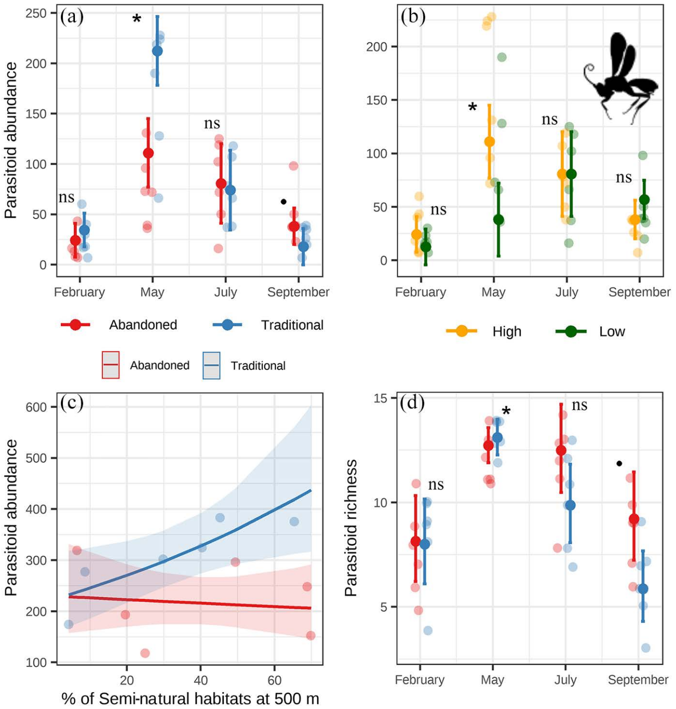

Figure 5: Results of the linear models for parasitoid abundance (a–c) and richness (d). Points with error bars represent estimated means and 95% confidence intervals from the models' predictions, and dull dots represent the raw data. Significant ($p < 0.05$) differences are shown with asterisks and marginally significant ($0.05 < p < 0.1$) differences with dots. ns: not significant.

For the bees, the highest abundance was found in February and the highest rich-ness at mid-season (Fig. 6a, c). Bee abundance in February was higher in orchards located in landscapes with a high level of semi-natural habitats (Fig. 6a). Late in the season, bee abundance was higher in orchards located in landscapes with a low per-centage of semi-natural habitats, but the number of individuals in this period was generally significantly low (Fig. 6a, Table S1). Bee abundance increased with the percentage of semi-natural habitats at 500 m (Fig. 6b), and richness decreased in abandoned orchards and increased in traditional ones as the percentage of semi-natural habitats increased at 150 m (Fig. 6d, Table S2).

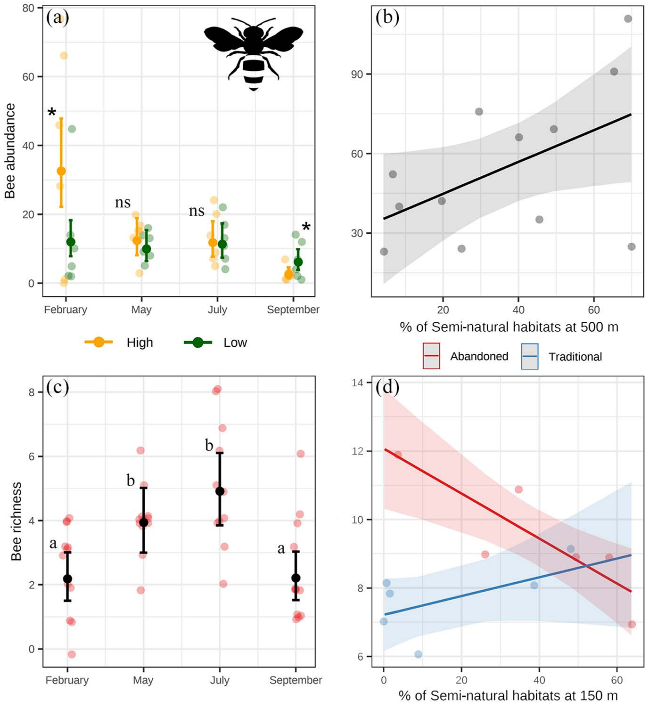

Figure 6: Results of the linear models for bee abundance (a,b) and richness (c,d). Points with error bars rep-resent estimated means and 95% confidence intervals from the models' predictions, and dull dots represent the raw data. Significant differences ($p < 0.05$) are shown with asterisks. Significant differences ($p < 0.05$) in pairwise comparisons are shown with different letters. ns: not significant.

4. Discussion

Our results showed a strong effect of the system (abandoned vs. traditional) on the community composition, abundance, and richness of spiders and parasitoids, while no effect was found for bees. Bee and parasitoid abundances also responded to the level of semi-natural habitats in the landscape window (high vs. low), but spiders were not affected by this variable. Several metrics of the studied groups behaved differently in abandoned and traditional orchards depending on the percentage of semi-natural habitats in the surrounding 150 m or 500 m sectors. The strong seasonality of the Mediterranean climate had a decisive effect on all our results.

4.1. System Effects

In agreement with our hypothesis, abandoned and traditional almond orchards showed contrasting spider and parasitoid communities. These two types of orchards differ in vegetation architecture and microhabitats and resource availability (i.e., flowers, prey, hosts, refuge); therefore, they could be harboring species with distinct requirements. The spider community was richer and more abundant in abandoned orchards, which tend to have higher habitat structural complexity and resource availability, allowing them to sustain more species and individuals (de Paz et al., 2022; Langellotto and Denno, 2004). This is consistent with numerous studies that have shown that spiders are constrained by different habitat features at a local scale (e.g., Barton et al., 2017; Theron et al., 2020), being favored in habitats with in-creased prey availability (Markó et al., 2009; Spears and MacMahon, 2012) and more complex vegetation architecture (Benhadi-Marín et al., 2020; de Paz et al., 2022; Rosas-Ramos et al., 2019, 2018). In fact, only three families were more abundant in traditional orchards: lycosids, gnaphosids, and linyphids (ground runners and sheet web weavers (Cardoso et al., 2011)), which are favored by the more open habitat of traditional orchards (Cardenas et al., 2012; de Paz et al., 2022; Rosas-Ramos et al., 2020, 2018).

Conversely, contrary to our expectations, at the beginning-middle of the season (May), parasitoid abundance and richness were higher in traditional orchards. In this period, traditional orchards have a diverse annual plant cover, more so than that of the shrub-dominated abandoned orchards; that plant cover does not dry out until early summer (late June), offering a great availability of floral resources and hosts, including almond pests, which could favor the presence and colonization of parasitoids from surrounding habitats (Gillespie et al., 2016; Landis et al., 2000; Rusch et al., 2010; Tscharntke et al., 2005).

Both parasitoid richness and abundance, as well as spider abundance, were higher in abandoned orchards exclusively in mid–late summer (July–September). Mediterranean ecosystems experience dramatic changes throughout the year, with strong disparity in resources availability between seasons and an expected reduction in plant and host accessibility during the summer drought (Rivas-Martínez et al., 2017; Rosas-Ramos et al., 2022). The consequences of this severe seasonality are exacerbated in traditional almond orchards, where the annual vegetation dries up earlier than in the shrub-dominated abandoned orchards, reducing vegetation complexity and thus hampering the diversity of resources that benefit spiders (i.e., anchoring points, prey abundance (Gómez et al., 2016; Spears and MacMahon, 2012)) and parasitoids (i.e., floral re-sources, alternative hosts, refuge (Gillespie et al., 2016; Rusch et al., 2010)).

Bee richness was almost only affected by seasonality, reflecting a high species turnover caused by the marked changes that ecosystems suffer under a Mediterranean climate (Petanidou and Lamborn (2005), and references therein). The lack of differences in bee abundance and richness between abandoned and traditional almond orchards could be explained by the successional stage of our abandoned orchards since the shrubland stage, dominated by one or two *Cystus* or *Cytisus* species, was found to provide less food resources and harbored the lowest bee abundance and richness of any successional stage of those compared in a recent study in a similar ecosystem (Penado et al., 2022). The absence of differences could also be derived from the main management practice performed in the traditional orchards (tillage), which has been found to negatively affect the ground nesting bees (such as *Andrena*, *Eucera*, *Halictus* or *Lasioglossum*) that dominate our community (Kim et al., 2006; Roulston and Goodell, 2011). In consequence, it is likely that neither abandoned nor traditional almond or-chards would provide sufficient feeding and nesting resources outside of the almond blooming period, explaining our generally low bee abundance.

4.2. Landscape Effects

Parasitoid abundance was higher in landscape windows with a high level of semi-natural habitats. Complex landscapes, with a high percentage of semi-natural habitats, have greater habitat heterogeneity than simplified agriculture-dominated landscapes, thus providing a wider variety of microhabitats, overwintering and feeding resources, and alternative hosts (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Holland et al., 2016; Tscharntke et al., 2012b). Diverse and abundant resources may result in increased parasitoid abundance in landscapes with a high percentage of semi-natural habitats (Bianchi et al., 2006, 2005; Gillespie et al., 2016; Marino and Landis, 1996; Thies et al., 2005; Thies and Tscharntke, 1999). Moreover, parasitoids, given the high trophic level, are particularly sensitive to landscape simplification since they are directly and indirectly affected by habitat loss and agricultural perturbations (Jonsson et al., 2012; Kruess and Tscharntke, 1994; Mates et al., 2012).

As we hypothesized, bees responded more strongly to the level of semi-natural habitats in the landscape window than to the system. In February, different and more abundant communities appeared in orchards located in landscapes with a high percentage of semi-natural habitats, and they also showed a general increase in abundance as the percentage of semi-natural habitats at 500 m increased. In these complex landscapes, semi-natural habitats are represented by medium-to-large patches (0.5–20 ha) of ungrazed grasslands, forest remnants, and predominantly shrublands, interspersed with clusters of agricultural fields. Semi-natural habitats provide nesting and alternative foraging resources that could limit bees, especially during the almond blooming period in February, when bee abundance peaks, since they need foraging re-sources both before and after bloom in other habitats because the blooming period might be too short even for wild bees with short life spans (Eeraerts et al., 2021; Holzschuh et al., 2010; Kennedy et al., 2013; Maurer et al., 2022; Roulston and Goodell, 2011; Westrich, 1996).

Unexpectedly, several metrics (spider abundance, parasitoid abundance, bee richness, and the abundance of the majority of the dominant families and genera) showed a similar response to the percentage of semi-natural habitats measured at 150 m or 500 m. Either abundance or richness decreased in abandoned orchards and in-creased in traditional orchards as the percentage of semi-natural habitats increased (generally at 150 m). To our knowledge, only one other study in Europe assessed the interactive effects of landscape complexity and traditional orchard abandonment on arthropod abundance or diversity, and contrary to our results, an interaction between landscape structure and management practice was not found (Steffan-Dewenter and Leschke, 2003). Given this lack of similar studies, we can only hypothesize, based on our results and ecological theory (Duelli and Obrist, 2003; Tscharntke et al., 2012b), that in areas with a low percentage of semi-natural habitats, dominated by small agricultural fields with different land uses, abandoned orchards constitute favorable patches, providing alternative resources for foraging, nesting, and refuge. Therefore, they could act as islands, providing reservoir habitats in an unfavorable matrix. Nevertheless, as the percentage of semi-natural habitats escalates, habitat het-erogeneity and resource availability increase, translating into higher complementarity and heightened arthropod movement between patches (Bianchi et al., 2006; Tscharntke et al., 2021, 2012b). Within these conditions, abandoned orchards lose relevance, and the biodiversity that they harbor de-creases.

On the other hand, in the traditional orchards located in areas with a low per-centage of semi-natural habitats, the studied groups may be limited by management practices and the scarcity of alternative resources. This trend is observed despite the high crop heterogeneity and small field size, following the general pattern of European studies where other variables such as landscape complexity are of greater relevance (Priyadarshana et al., 2021 and references therein). However, as the percentage of semi-natural habitats in-creases, these limiting capacities become available in the surrounding area, thus al-lowing the communities of the study groups to thrive and spill over from these un-managed habitats and successfully exploit the resources (especially prey or hosts and floral resources during the blooming period and spring) that traditional orchards provide (Inclán et al., 2015; Marja et al., 2022; Rischen et al., 2023; Tscharntke et al., 2012b, 2005).

5. Conclusions

Agricultural abandonment is a relevant land-use change process driven by rural depopulation which, although relevant worldwide, is particularly prevalent in Spain and many other European countries. Agri-environmental payments (EPAC) have been focused on preventing the abandonment of traditional farming systems, which is considered one of the main drivers of biodiversity loss in Europe (EEA (European Environmental Agency), 2009). Nevertheless, re-search efforts to elucidate farmland abandonment consequences on biodiversity have been unequally distributed between annual and permanent crops, the latter being scarcely investigated (Kajtoch, 2017), with only a few studies generally focused on olive groves, apple orchards, or vineyards (e.g., de Paz et al., 2022; Katayama et al., 2019; Wersebeckmann et al., 2021). To our knowledge, our work constitutes the first attempt to analyze the effects of almond orchard abandonment on arthropod biodiversity, and it suggests that both abandoned and traditional almond orchards play an important role in conserving rich and abundant arthropod communities—but only in simple landscapes.

Arthropod community composition at the field scale is driven by orchard management, with abandoned and traditional orchards harboring different communities and diversity metrics that are strongly conditioned by seasonality (defined as the climatic differences between sampling periods (e.g., temperature, rainfall and humidity) that condition the plant community and influence arthropod assemblages).

The landscape context significantly interacts with almond orchard management. In our study area, abandoned orchards located in simpler landscapes seem to assume the role of semi-natural habitats in providing alternative resources that can favor pollinators and natural enemies. Nevertheless, these abandoned orchards do not substitute semi-natural habitats since their arthropod community diversity decreases as the percentage of semi-natural habitats in the surrounding area increases. Conversely, in traditional orchards, diversity increases with landscape complexity, reflecting the relevant role of semi-natural habitats as sources for arthropod spillover into crop fields. This has important implications since it shows that landscape simplification through the loss of semi-natural habitats has negative consequences on arthropod biodiversity even in traditional farming landscapes with small fields and high crop diversity.

In certain scenarios, abandoned almond orchards could increase landscape heterogeneity and complexity by providing a different habitat for beneficial arthropods. However, traditional almond orchards harbor unique spider and parasitoid communities that, including bees, are equally as rich and abundant as (or even more abundant than) those of the more complex abandoned orchards for certain periods. The biodiversity associated with these orchards relies on their traditional management to sub-sist, and although an initial increase in complexity and biodiversity is observed after abandonment, theory and empirical studies predict a decrease in both after the vegetation succession has reached the state of the surrounding natural and semi-natural habitats (see Plieninger et al., 2014; Queiroz et al., 2014 for reviews; however, see Penado et al., 2022).

Additionally, our findings are highly dependent on seasonality, emphasizing the relevance and suitability of including this factor in studies in regions with a

Mediterranean climate since it constitutes an important driver of differences with studies in other regions.

More studies are needed with longer sampling periods and at different regions, especially including samplings in semi-natural habitats, to assess the extent to which abandoned orchards could support similar arthropod communities. Assuming the temporal and spatial limitations of our study, we consider the suitability of working at a regional scale to adapt the potential recommendations to a specific context, taking into account the importance of the seasonality and the different cultural and socioeconomic conditioning factors within each region.

From a conservation management perspective, efforts should be made to halt the abandonment progress, maintaining traditional almond orchards and conserving semi-natural habitats since both provide complementary habitats for beneficial arthropods, to protect the rich biodiversity associated with these traditional cultural landscapes.

Acknowledgments

The authors wish to thank the farmers for allowing access to their orchards and the Servicio Territorial de Medio Ambiente de Castilla y León for providing the necessary permits to carry out the samplings. We also wish to thank Sara Vicente Alonso for her help with all the fieldwork, and two anonymous reviewers, whose comments helped to improve the content of this article.

References

Avinent, L., Llacer, G., 1995. Adaptación de un aspirador de jardín para la captura de insectos. Bol Sanid Veg Plagas 21, 329–335.

Baldock, D., Beaufoy, G., Bennett, G., Clark, J., 1993. Nature Conservation and New Directions in the Common Agricultural Policy: The Potential Role of EC Policies in Maintaining Farming and Management Systems of High Nature Value in the Community. Institute for European Environmental Policy (IEEP), London.

Barton, P.S., Evans, M.J., Foster, C.N., Cunningham, S.A., Manning, A.D., 2017. Environmental and spatial drivers of spider diversity at contrasting microhabitats. Austral Ecol 42, 700–710. https://doi.org/10.1111/aec.12488

Batáry, P., Dicks, L. V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv Biol 29, 1006–1016. https://doi.org/10.1111/cobi.12536

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: An overview of drivers and consequences. CAB Rev: Perspect Agric Vet Sci Nutr Nat Resour 2, 1–14. https://doi.org/10.1079/PAVSNNR20072057

Bengtsson, J., Ahnström, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: A meta-analysis. J Appl Ecol 42, 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x

Benhadi-Marin, J., Pereira, J.A., Barrientos, J.A., Bento, A., Santos, S.A.P., 2011. Diversity of predaceous arthropods in the almond tree canopy in Northeastern Portugal: A methodological approach. Entomol Sci 14, 347–358. https://doi.org/10.1111/j.1479-8298.2011.00444.x

Benhadi-Marín, J., Pereira, J.A., Sousa, J.P., Santos, S.A.P., 2020. Distribution of the spider community in the olive grove agroecosystem (Portugal): potential bioindicators. Agric For Entomol 22, 10–19. https://doi.org/10.1111/afe.12352

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

Bianchi, F.J.J.A., Van Wingerden, W.K.R.E., Griffioen, A.J., Van Der Veen, M., Van Der Straten, M.J.J., Wegman, R.M.A., Meeuwsen, H.A.M., 2005. Landscape factors affecting the control of *Mamestra brassicae* by natural enemies in Brussels sprout. Agric Ecosyst Environ 107, 145–150. https://doi.org/10.1016/j.agee.2004.11.007

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, Rochdale, UK, pp. 220–228.

Borcard, D., Gillet, F., Legendre, P., 2018. Numerical Ecology with R, Use R! 2nd ed. Springer International Publishing, New York, USA. https://doi.org/10.1007/978-3-319-71404-2

Bruggisser, O.T., Schmidt-Entling, M.H., Bacher, S., 2010. Effects of vineyard management on biodiversity at three trophic levels. Biol Conserv 143, 1521–1528. https://doi.org/10.1016/j.biocon.2010.03.034

Cardenas, M., Castro, J., Campos, M., 2012. Short-term response of soil spiders to cover-crop removal in an organic olive orchard in a mediterranean setting. J Insect Sci 12, 1–18. https://doi.org/10.1673/031.012.6101

Cardenas, M., Pascual, F., Campos, M., Pekar, S., 2015. The Spider Assemblage of Olive Groves Under Three Management Systems. Environ Entomol 44, 509–518. https://doi.org/10.1093/ee/nvv030

Cardoso, P., Pekár, S., Jocqué, R., Coddington, J.A., 2011. Global Patterns of Guild Composition and Functional Diversity of Spiders. PLoS One 6, e21710. https://doi.org/10.1371/journal.pone.0021710

Carrié, R., Andrieu, E., Cunningham, S.A., Lentini, P.E., Loreau, M., Ouin, A., 2017. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. Ecography 40, 85–97. https://doi.org/10.1111/ecog.02632

Chaplin-Kramer, R., Kremen, C., 2012. Pest control experiments show benefits of complexity at landscape and local scales. Ecol Appl 22, 1936–1948. https://doi.org/10.1890/11-1844.1

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol Lett 14, 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual. Plymouth Marine Laboratory, Plymouth.

Colwell, R.K., 2013. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. User's Guide and Application. URL: https://www.robertkcolwell.org/pages/1407-estimates (accessed on 2.2.23).

Connell, J.H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. Science 199, 1302–1310.

de Oliveira, S.S., Ortega, J.C.G., Ribas, L.G. dos S., Lopes, V.G., Bini, L.M., 2020. Higher taxa are sufficient to represent biodiversity patterns. Ecol Indic 111, 105994. https://doi.org/10.1016/j.ecolind.2019.105994

de Paz, V., Tobajas, E., Rosas-Ramos, N., Tormos, J., Asís, J.D., Baños-Picón, L., 2022. Effect of Organic Farming and Agricultural Abandonment on Beneficial Arthropod Communities Associated with Olive Groves in Western Spain: Implications for *Bactrocera oleae* Management. Insects 13, 48. https://doi.org/10.3390/insects13010048

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman K. A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury R., Shin, Y.J., Visseren-Hamakers, I.J., Willis, K.J., Zayas, C.N., 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy

Platform on Biodiversity and Ecosystem Services, IPBES. IPBES, Bohn, Germany. https://doi.org/https://doi.org/10.5281/zenodo.3553579

Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of semi-natural habitat islands. Basic Appl Ecol 4, 129–138. https://doi.org/10.1078/1439-1791-00140

EEA (European Environmental Agency), 2009. Distribution and targeting of the CAP budget from a biodiversity perspective. Technical report No 12/2009.

Eeraerts, M., Van Den Berge, S., Proesmans, W., Verheyen, K., Smagghe, G., Meeus, I., 2021. Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes. Landsc Ecol 36, 1377–1390. https://doi.org/10.1007/s10980-021-01220-y

Eilers, E.J., Klein, A.-M., 2009. Landscape context and management effects on an important insect pest and its natural enemies in almond. Biol Control 51, 388–394. https://doi.org/10.1016/j.biocontrol.2009.07.010

FAOSTAT, 2020. Food and Agriculture. [WWW Document] URL https://www.fao.org/faostat/en/#data (accessed 9.5.22).

Fischer, J., Hartel, T., Kuemmerle, T., 2012. Conservation policy in traditional farming landscapes. Conserv Lett 5, 167–175. https://doi.org/10.1111/j.1755-263X.2012.00227.x

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science 339, 1608–1611. doi:10.1126/science.1230200

Gillespie, M.A.K., Gurr, G.M., Wratten, S.D., 2016. Beyond nectar provision: the other resource requirements of parasitoid biological control agents. Entomol Exp Appl 159, 207–221. https://doi.org/10.1111/eea.12424

Gómez, J.E., Lohmiller, J., Joern, A., 2016. Importance of vegetation structure to the assembly of an aerial web-building spider community in North American open grassland. J Arachnol 44, 28. https://doi.org/10.1636/P14-58.1

Gradziel, T.M., 2017. Almonds: botany, production and uses. CABI, Wallingford. https://doi.org/10.1079/9781780643540.0000

Grime, J.P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242, 344–347.

Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package Version 0.4.6, 2022. URL: https://CRAN.R-project.org/package=DHARMa (accessed on 2.2.23).

Henselek, Y., Eilers, E.J., Kremen, C., Hendrix, S.D., Klein, A.M., 2018. Pollination requirements of almond (*Prunus dulcis*): Combining laboratory and field experiments. J Econ Entomol 111, 1006–1013. https://doi.org/10.1093/jee/toy053

Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Manag Sci 72, 1638–1651. https://doi.org/10.1002/ps.4318

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. Agron Sustain Dev 37, 31. https://doi.org/10.1007/s13593-017-0434-x

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J Anim Ecol 79, 491–500. https://doi.org/10.1111/j.1365-2656.2009.01642.x

Horak, J., Peltanova, A., Podavkova, A., Safarova, L., Bogusch, P., Romportl, D., Zasadil, P., 2013. Biodiversity responses to land use in traditional fruit orchards of a rural agricultural landscape. Agric Ecosyst Environ 178, 71–77. https://doi.org/10.1016/j.agee.2013.06.020

Hussain, R.I., Walcher, R., Brandl, D., Jernej, I., Arnberger, A., Zaller, J.G., Frank, T., 2018. Influence of abandonment on syrphid assemblages in mountainous meadows. J Appl Entomol 142, 450–456. https://doi.org/10.1111/jen.12482

Inclán, D.J., Cerretti, P., Marini, L., 2015. Landscape composition affects parasitoid spillover. Agric Ecosyst Environ 208, 48–54. https://doi.org/10.1016/j.agee.2015.04.027

ITACYL, AEMET, 2013. Inicio - Atlas agroclimático - ITACyL Portal Web [WWW Document]. URL http://www.atlas.itacyl.es/ (accessed 2.20.23).

IUSS Working Group WRB, 2022. World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps, 4th edition. ed. International Union of Soil Sciences (IUSS), Viena, Austria.

Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. J Appl Ecol 49, 706–714. https://doi.org/10.1111/j.1365-2664.2012.02130.x

Kajtoch, Ł., 2017. The importance of traditional orchards for breeding birds: The preliminary study on Central European example. Acta Oecol 78, 53–60. https://doi.org/10.1016/j.actao.2016.12.010

Katayama, N., Bouam, I., Koshida, C., Baba, Y.G., 2019. Biodiversity and yield under different land-use types in orchard/vineyard landscapes: A meta-analysis. Biol Conserv 229, 125-133. https://doi.org/10.1016/j.biocon.2018.11.020

Keenleyside, C., Beaufoy, G., Tucker, G., Jones, G., 2014. High Nature Value farming throughout EU-27 and its financial support under the CAP. Institute for European Environmental Policy (IEEP), London. https://doi.org/10.2779/91086

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol Lett 16, 584–599. https://doi.org/10.1111/ele.12082

Kim, J., Williams, N., Kremen, C., 2006. Effects of Cultivation and Proximity to Natural Habitat on Ground-nesting Native Bees in California Sunflower Fields. J Kans Entomol Soc 79, 309–320. https://doi.org/10.2317/0507.11.1

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc R Soc B: Biol Sci 274, 303-313. https://doi.org/10.1098/rspb.2006.3721

Kruess, A., Tscharntke, T., 1994. Habitat Fragmentation, Species Loss, and Biological Control. Science 264, 1581–1584. https://doi.org/10.1126/science.264.5165.1581

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. Annu Rev Entomol 45, 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139, 1–10. https://doi.org/10.1007/s00442-004-1497-3

Legner, E.F., Gordh, G., 1992. Lower Navel Orange worm (Lepidoptera: Phycitidae) Population Densities Following Establishment of *Goniozus legneri* (Hymenoptera: Bethylidae) in California. J Econ Entomol 85, 2153–2160. https://doi.org/10.1093/jee/85.6.2153

Marino, P.C., Landis, D.A., 1996. Effect of Landscape Structure on Parasitoid Diversity and Parasitism in Agroecosystems. Ecol Appl 6, 276–284. https://doi.org/10.2307/2269571

Marja, R., Tscharntke, T., Batáry, P., 2022. Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis. Agric Ecosyst Environ 326, 107822. https://doi.org/10.1016/j.agee.2021.107822

Markó, V., Keresztes, B., Fountain, M.T., Cross, J. V., 2009. Prey availability, pesticides and the abundance of orchard spider communities. Biol Control 48, 115–124. https://doi.org/10.1016/j.biocontrol.2008.10.002

Marrec, R., Le Roux, V., Martin, L., Lenoir, J., Brunet, J., Cousins, S.A.O., De Smedt, P., Deconchat, M., Diekmann, M., Ehrmann, S., Gallet-Moron, E., Giffard, B., Liira, J., Lindgren, J., Valdes, A., Verheyen, K., Wulf, M., Decocq, G., 2021. Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands. Glob Ecol Biogeogr 30, 165–182. https://doi.org/10.1111/GEB.13208

Mates, S.G., Perfecto, I., Badgley, C., 2012. Parasitoid wasp diversity in apple orchards along a pest-management gradient. Agric Ecosyst Environ 156, 82–88. https://doi.org/10.1016/j.agee.2012.04.016

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., Albrecht, M., 2022. Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. J Appl Ecol 59, 2604-2615. https://doi.org/10.1111/1365-2664.14260

Michalko, R., Pekár, S., Dul'a, M., Entling, M.H., 2019. Global patterns in the biocontrol efficacy of spiders: A meta-analysis. Glob Ecol Biogeogr 28, 1366–1378. https://doi.org/10.1111/geb.12927

Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol Conserv 133, 291–300. https://doi.org/10.1016/j.biocon.2006.06.009

Oppermann, R., Beaufoy, G., Jones, G., 2012. High nature value farming in Europe [35 European countries - experiences and perspectives]. Ubstadt-Weiher, Germany: Verlag regionalkultur.

Penado, A., Rebelo, H., Goulson, D., Wood, T.J., Porto, M., Rotheray, E.L., Beja, P., 2022. From pastures to forests: Changes in Mediterranean wild bee communities after rural land abandonment. Insect Conserv Divers 15, 325–336. https://doi.org/10.1111/icad.12562

Pereira, H.M., Navarro, L.M., 2015. Rewilding European Landscapes. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-12039-3

Petanidou, T., Lamborn, E., 2005. A land for flowers and bees: studying pollination ecology in Mediterranean communities. Plant Biosyst 139, 279–294. https://doi.org/10.1080/11263500500333941

Picchi, M.S., Bocci, G., Petacchi, R., Entling, M.H., 2020. Taxonomic and functional differentiation of spiders in habitats in a traditional olive producing landscape in Italy. Eur J Entomol 117, 18–26. https://doi.org/10.14411/eje.2020.002

Plieninger, T., Bieling, C., 2013. Resilience-Based Perspectives to Guiding High-Nature-Value Farmland through Socioeconomic Change. Ecol Soc 18, 20. https://doi.org/10.5751/ES-05877-180420

Plieninger, T., Hui, C., Gaertner, M., Huntsinger, L., 2014. The Impact of Land Abandonment on Species Richness and Abundance in the Mediterranean Basin: A Meta-Analysis. PLoS One 9, e98355. https://doi.org/10.1371/journal.pone.0098355

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L. V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://doi.org/10.1038/nature20588

Priyadarshana, T.S., Lee, M.B., Ascher, J.S., Qiu, L., Goodale, E., 2021. Crop heterogeneity is positively associated with beneficial insect diversity in subtropical farmlands. J Appl Ecol 58, 2747–2759. https://doi.org/10.1111/1365-2664.14005

Queiroz, C., Beilin, R., Folke, C., Lindborg, R., 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. Front Ecol Environ 12, 288–296. https://doi.org/10.1890/120348

Quintas-Soriano, C., Buerkert, A., Plieninger, T., 2022. Effects of land abandonment on nature contributions to people and good quality of life components in the Mediterranean region: A review. Land use policy 116, 106053. https://doi.org/10.1016/j.landusepol.2022.106053

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randlkofer, B., Obermaier, E., Hilker, M., Meiners, T., 2010. Vegetation complexity-The influence of plant species diversity and plant structures on plant chemical complexity and arthropods. Basic Appl Ecol 11, 383–395. https://doi.org/10.1016/j.baae.2010.03.003

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proc Natl Acad Sci USA 118, 1–6. https://doi.org/10.1073/PNAS.2002548117

Rey, P.J., Manzaneda, A.J., Valera, F., Alcántara, J.M., Tarifa, R., Isla, J., Molina-Pardo, J.L., Calvo, G., Salido, T., Gutiérrez, J.E., Ruiz, C., 2019. Landscape-moderated biodiversity effects of ground herb cover in olive groves: Implications for regional biodiversity conservation. Agric Ecosyst Environ 277, 61–73. https://doi.org/10.1016/j.agee.2019.03.007

Rischen, T., Kaffenberger, M., Plath, E., Wolff, J., Fischer, K., 2023. Configurational landscape heterogeneity: Crop-fallow boundaries enhance the taxonomic diversity of carabid beetles and spiders. Agric Ecosyst Environ 341, 108194. https://doi.org/10.1016/j.agee.2022.108194

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., Rivas-Sáenz, S., 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands, in: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula. Springer International Publishing AG, Cham, Switzerland, pp. 29–80.

Rosas-Ramos, N., Asís, J.D., Tobajas, E., de Paz, V., Baños-Picón, L., 2022. Disentangling the Benefits of Organic Farming for Beetle Communities (Insecta: Coleoptera) in Traditional Fruit Orchards. Agriculture 12, 243. https://doi.org/10.3390/agriculture12020243

Rosas-Ramos, N., Baños-Picón, L., Tobajas, E., de Paz, V., Tormos, J., Asís, J.D., 2018. Value of ecological infrastructure diversity in the maintenance of spider assemblages: A case study of Mediterranean vineyard agroecosystems. Agric Ecosyst Environ 265, 244–253. https://doi.org/10.1016/j.agee.2018.06.026

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2020. Farming system shapes traits and composition of spider assemblages in Mediterranean cherry orchards. PeerJ 8, e8856. https://doi.org/10.7717/peerj.8856

Rosas-Ramos, N., Baños-Picón, L., Tormos, J., Asís, J.D., 2019. The complementarity between ecological infrastructure types benefits natural enemies and pollinators in a Mediterranean vineyard agroecosystem. Ann Appl Biol 175, 193–201. https://doi.org/10.1111/aab.12529

Roulston, T.H., Goodell, K., 2011. The Role of Resources and Risks in Regulating Wild Bee Populations. Annu Rev Entomol 56, 293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W.W., Winqvist, C., Woltz, M., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agric Ecosyst Environ 221, 198–204. https://doi.org/10.1016/j.agee.2016.01.039

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., Roger-Estrade, J., 2010. Biological Control of Insect Pests in Agroecosystems, in: Advances in Agronomy. Elsevier Ltd, pp. 219–259. https://doi.org/10.1016/B978-0-12-385040-9.00006-2

Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol Conserv 232, 8-27. https://doi.org/10.1016/j.biocon.2019.01.020

Sánchez-Ramos, I., Marcotegui, A., Pascual, S., Fernández, C.E., Cobos, G., González-Núñez, M., 2017. Compatibility of organic farming treatments against *Monosteira unicostata* with non-target arthropod fauna of almond trees canopy. Span J Agric Res 15, e1004. https://doi.org/10.5424/sjar/2017152-10515

Sanz, C., Mata, R., Gómez, J., Allende, F., López, N., Molina, P., Galiana, L., 2003. Atlas de los paisajes de España. Ministerio de Medio Ambiente, Madrid.

Schäckermann, J., Pufal, G., Mandelik, Y., Klein, A.M., 2015. Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape. Ecol Entomol 40, 12–21. https://doi.org/10.1111/een.12244

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., Sait, S.M., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol Rev 88, 1002–1021. https://doi.org/10.1111/brv.12040

Shi, X., Xiao, H., Luo, S., Hodgson, J.A., Bianchi, F.J.J.A., He, H., van der Werf, W., Zou, Y., 2021. Can landscape level semi-natural habitat compensate for pollinator biodiversity loss due to farmland consolidation? Agric Ecosyst Environ 319, 107519. https://doi.org/10.1016/j.agee.2021.107519

Spears, L.R., MacMahon, J.A., 2012. An experimental study of spiders in a shrub-steppe ecosystem: the effects of prey availability and shrub architecture. J Arachnol 40, 218–227. https://doi.org/10.1636/P11-87.1

Steffan-Dewenter, I., Leschke, K., 2003. Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. Biodivers Conserv 12, 1953–1968. https://doi.org/doi.org/10.1023/A:1024199513365

Theron, K.J., Gaigher, R., Pryke, J.S., Samways, M.J., 2020. High quality remnant patches in a complex agricultural landscape sustain high spider diversity. Biol Conserv 243, 108480. https://doi.org/10.1016/j.biocon.2020.108480

Thies, C., Roschewitz, I., Tscharntke, T., 2005. The landscape context of cereal aphid–parasitoid interactions. Proc R Soc B: Biol Sci 272, 203–210. https://doi.org/10.1098/rspb.2004.2902

Thies, C., Tscharntke, T., 1999. Landscape Structure and Biological Control in Agroecosystems. Science 285, 893–895. https://doi.org/10.1126/science.285.5429.893

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677. https://doi.org/10.1038/nature01014

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. Biol Conserv 151, 53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends Ecol Evol 36, 919–930. https://doi.org/10.1016/j.tree.2021.06.010

Tscharntke, T., Rand, T.A., Bianchi, F.J.J.A., 2005. The landscape context of trophic interactions: Insect spillover across the crop-noncrop interface. Ann Zool Fennici 42, 421–432.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Walcher, R., Hussain, R.I., Karrer, J., Bohner, A., Brandl, D., Zaller, J.G., Arnberger, A., Frank, T., 2020. Effects of management cessation on hoverflies (Diptera: Syrphidae) across Austrian and Swiss mountain meadows. Web Ecol 20, 143–152. https://doi.org/10.5194/we-20-143-2020

Walcher, R., Karrer, J., Sachslehner, L., Bohner, A., Pachinger, B., Brandl, D., Zaller, J.G., Arnberger, A., Frank, T., 2017. Diversity of bumblebees, heteropteran bugs and grasshoppers maintained by both: abandonment and extensive management of mountain meadows in three regions across the Austrian and Swiss Alps. Landsc Ecol 32, 1937–1951. https://doi.org/10.1007/s10980-017-0556-1

Wersebeckmann, V., Kolb, S., Entling, M.H., Leyer, I., 2021. Maintaining steep slope viticulture for spider diversity. Glob Ecol Conserv 29, e01727. https://doi.org/10.1016/j.gecco.2021.e01727

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeuer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol Monogr 78, 653–671. https://doi.org/10.1890/07-1292.1

Westrich, P., 1996. Habitat requirements of central European bees and the problems of partial habitats., in: Matheson, A., Buchmann, S.L., O'Toole, C., Westrich, P., Williams, I.H. (Eds.), The Conservation of Bees. Academic Press, London, UK, pp. 1–16.

Zamora, J., Verdú, J.R., Galante, E., 2007. Species richness in Mediterranean agroecosystems: Spatial and temporal analysis for biodiversity conservation. Biol Conserv 134, 113–121. https://doi.org/10.1016/j.biocon.2006.08.011

Zuur, A., Ieno, E.N., N, Walker., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York.

Supplementary material

Table S1. Complete results of the different models for the richness and abundance of spiders, parasitoids, and bees. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables s*ystem*, the *sampling month*, *level of semi-natural habitats* (SNH), and their interactions (when significant) are provided. In the first column, the type of model (LME, linear mixed model; GLMM, generalized linear mixed model), the transformation applied on the explanatory variable (if any), and the variance structure added to the model (if any) are given.

Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
Spider family richness (LME) (varIdent(form =~ 1 | Sampling month), varIdent(form=~ 1 | System))	(Intercept)	11.879	0.469	25.349	0.000	***
	System (Traditional)	-1.662	0.522	-3.185	0.010	*
	Sampling month (May)	0.971	0.612	1.587	0.122	ns
	Sampling month (July)	3.323	0.749	4.439	0.000	***
	Sampling month (September)	0.736	0.595	1.236	0.225	ns
Spider abundance (GLMM – negative binomial)	(Intercept)	4.219	0.134	31.380	<0.001	***
	System (Traditional)	0.035	0.188	0.186	0.852	ns
	Sampling month (May)	0.274	0.178	1.539	0.124	ns
	Sampling month (July)	1.006	0.157	6.386	<0.001	***
	Sampling month (September)	0.473	0.171	2.760	0.006	**
	System (Traditional) : *Sampling month* (May)	0.207	0.245	0.843	0.399	ns
	System (Traditional) : *Sampling month* (July)	-0.471	0.229	-2.056	0.040	*
	System (Traditional) : *Sampling month* (September)	-0.697	0.262	-2.665	0.008	**
	Pairwise Abandoned – Traditional, February == 0	-0.035	0.188	-0.186	0.853	ns
	Abandoned – Traditional, May == 0	-0.242	0.158	-1.536	0.133	ns
	Abandoned – Traditional, July == 0	0.436	0.131	3.327	0.002	**
	Abandoned – Traditional, September == 0	0.662	0.182	3.642	<0.001	***
Parasitoid family richness (LME) (Square root) (varIdent (form=~1| Sampling month)	(Intercept)	2.853	0.183	15.572	<0.001	***
	System (Traditional)	-0.024	0.259	-0.093	0.928	ns
	Sampling month (May)	0.714	0.184	3.877	0.001	**
	Sampling month (July)	0.681	0.231	2.942	0.006	**
	Sampling month (September)	0.183	0.249	0.736	0.468	ns
	Level of SNH (Low)	-0.214	0.080	-2.666	0.029	*
	System (Traditional) : *Sampling month* (May)	0.077	0.260	0.296	0.769	ns
	System (Traditional) : *Sampling month* (July)	-0.369	0.327	-1.128	0.268	ns
	System (Traditional) : *Sampling month* (September)	-0.590	0.352	-1.678	0.104	ns
	System (Traditional) : *Level of SNH* (Low)	0.274	0.114	2.408	0.043	*
	Pairwise Abandoned – Traditional, February == 0	-0.113	0.253	-0.446	0.667	ns

	Abandoned – Traditional, May == 0	-0.190	0.063	-3.022	0.017	*
	Abandoned – Traditional, July == 0	0.257	0.208	1.234	0.252	ns
	Abandoned – Traditional, September == 0	0.478	0.245	1.953	0.087	•
	Abandoned – Traditional, High == 0	0.245	0.118	2.076	0.072	•
	Abandoned – Traditional, Low == 0	-0.029	0.118	-0.247	0.811	ns
	High – Low, Abandoned == 0	0.215	0.081	2.666	0.029	*
	High – Low, Traditional == 0	-0.060	0.081	-0.739	0.481	ns
Parasitoid abundance (LME) (varIdent (form=~1| Sampling month)	(Intercept)	24.167	8.528	2.834	0.009	**
	System (Traditional)	10.333	9.847	1.049	0.321	ns
	Sampling month (May)	86.833	18.344	4.734	<0.001	***
	Sampling month (July)	56.500	21.004	2.690	0.012	*
	Sampling month (September)	13.917	10.934	1.273	0.214	ns
	Level of SNH (Low)	-11.667	9.847	-1.185	0.266	ns
	System (Traditional) : *Sampling month* (May)	91.000	21.182	4.296	<0.001	***
	System (Traditional) : *Sampling month* (July)	-17.000	24.253	-0.701	0.489	ns
	System (Traditional) : *Sampling month* (September)	-30.500	12.626	-2.416	0.023	*
	Sampling month (May) : *Level of SNH* (Low)	-61.333	21.182	-2.896	0.007	**
	Sampling month (July) : *Level of SNH* (Low)	11.667	24.253	0.481	0.634	ns
	Sampling month (September) : *Level of SNH* (Low)	30.500	12.626	2.416	0.023	*
	Pairwise					
	Abandoned – Traditional, February == 0	-10.33	9.850	-1.049	0.321	ns
	Abandoned – Traditional, May == 0	-101.33	20.050	-5.055	<0.001	***
	Abandoned – Traditional, July == 0	6.670	23.27	0.287	0.781	ns
	Abandoned – Traditional, September == 0	20.170	10.61	1.900	0.090	•
	High – Low, February == 0	11.700	9.850	1.185	0.266	ns
	High – Low, May == 0	73.000	20.050	3.641	0.005	**
	High – Low, July == 0	0.000	23.270	0.000	1.000	ns
	High – Low, September == 0	-18.800	10.61	-1.775	0.110	ns
Bee genus richness (LME) (Square root)	(Intercept)	1.480	0.130	11.406	<0.001	***
	Sampling month (May)	0.506	0.158	3.205	0.003	**
	Sampling month (July)	0.737	0.158	4.670	<0.001	**
	Sampling month (September)	0.007	0.158	0.043	0.966	ns
Bee abundance (GLMM – poisson)	(Intercept)	3.485	0.195	17.832	<0.001	***
	Sampling month (May)	-0.966	0.129	-7.487	<0.001	***
	Sampling month (July)	-1.015	0.131	-7.729	<0.001	***
	Sampling month (September)	-2.551	0.252	-10.132	<0.001	***
	Level of SNH (Low)	-1.000	0.291	-3.441	<0.001	***

Sampling month (May) : *Level of SNH* (Low)	0.783	0.212	3.699	<0.001	***
Sampling month (July) : *Level of SNH* (Low)	0.962	0.209	4.61	<0.001	***
Sampling *month* (September) : *Level of SNH* (Low)	1.884	0.318	5.92	<0.001	***
Pairwise					
High – Low, February == 0	0.999	0.291	3.441	0.001	**
High – Low, May == 0	0.217	0.307	0.705	0.485	ns
High – Low, July == 0	0.038	0.305	0.123	0.903	ns
High – Low, September == 0	-0.884	0.388	-2.275	0.029	*

Table S2. Complete results of the different models for the richness and abundance of spiders, parasitoids, and bees. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables s*ystem*, *% of semi-natural habitats* at 150m or 500m, and the interaction (when significant). In the first column, the type of model (GLS, generalized least square model; GLM, generalized linear model) and the variance structure added to the model (if any) are given.

Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
Spider family richness (GLS) (varIdent (form=~1| System)	(Intercept)	20.729	0.756	27.408	0.000	***
	System (Traditional)	-3.245	1.170	-2.775	0.022	*
	% Semi-natural 150 m	-0.040	0.017	-2.359	0.043	*
Spider abundance (GLM – negative binomial) (dispformula = ~system)	(Intercept)	6.280	0.049	127.120	<0.001	***
	System (Traditional)	-0.467	0.080	-5.840	<0.001	***
	% Semi-natural 150 m	-0.005	0.001	-3.960	<0.001	***
	System (Traditional) : *% Semi-natural 150 m*	0.010	0.003	3.730	<0.001	***
Parasitoid family richness (GLS)	Nothing significant					
Parasitoid abundance (GLM – negative binomial)	(Intercept)	5.438	0.207	26.312	<0.001	***
	System (Traditional)	-0.030	0.271	-0.111	0.911	ns
	% Semi-natural 500 m	-0.002	0.005	-0.346	0.729	ns
	System (Traditional) : *% Semi-natural 500 m*	0.011	0.006	1.829	0.068	•
Bee genus richness (GLS)	(Intercept)	12.073	0.897	13.461	0.000	***
	System (Traditional)	-4.853	1.047	-4.634	0.002	**
	% Semi-natural 150 m	-0.066	0.020	-3.236	0.012	*
	System (Traditional) : *% Semi-natural 150 m*	0.093	0.029	3.170	0.013	*
Bee abundance (GLS)	(Intercept)	32.831	13.668	2.402	0.037	*
	% Semi-natural 500 m	0.601	0.319	1.884	0.089	•

Table S3. Complete results of the different models for the abundance of the most dominant families or genera. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables s*ystem*, the *sampling month*, *level of semi-natural habitats* (SNH), and their interactions (when significant) are provided. In the first column, the type of model (LME, linear mixed model; GLMM, generalized linear mixed model), the transformation applied on the explanatory variable (if any), and the correlation or variance structure added to the model (if any) are given.

Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
Araneidae abundance (GLMM – poisson)	(Intercept)	2.291	0.194	11.806	<0.001	***
	System (Traditional)	-0.407	0.178	-2.290	0.022	*
	Sampling month (May)	0.094	0.194	0.483	0.629	ns
	Sampling month (July)	0.487	0.178	2.737	0.006	**
	Sampling month (September)	-0.936	0.264	-3.548	<0.001	***
	Level of SNH (Low)	-0.430	0.268	-1.603	0.109	ns
	Sampling month (May) : *Level of SNH* (Low)	0.584	0.288	2.026	0.043	*
	Sampling month (July) : *Level of SNH* (Low)	0.435	0.272	1.6	0.110	ns
	Sampling *month* (September) : *Level of SNH* (Low)	0.874	0.364	2.403	0.016	*
	Pairwise					
	High – Low, February == 0	0.430	0.268	1.603	0.117	ns
	High – Low, May == 0	-0.155	0.235	-0.658	0.514	ns
	High – Low, July == 0	-0.006	0.215	-0.026	0.979	ns
	High – Low, September == 0	-0.444	0.323	-1.375	0.177	ns
Gnaphosidae abundance (GLMM – poisson)	(Intercept)	0.978	0.243	4.025	<0.001	***
	System (Traditional)	0.198	0.253	0.783	0.434	ns
	Sampling month (May)	1.379	0.189	7.292	<0.001	***
	Sampling month (July)	0.933	0.200	4.678	<0.001	***
	Sampling month (September)	0.337	0.221	1.520	0.1284	ns
	Level of SNH (Low)	-0.594	0.279	-2.13	0.033	*
	System (Traditional) : *Level of SNH* (Low)	0.796	0.370	2.15	0.032	*
	Pairwise					
	Abandoned – Traditional, High == 0	-0.198	0.253	-0.783	0.4383	ns
	Abandoned – Traditional, Low == 0	-0.994	0.270	-3.678	<0.001	***
	High – Low, Abandoned == 0	0.594	0.279	2.130	0.039	*
	High – Low, Traditional == 0	-0.202	0.243	-0.829	0.412	ns
Linyphiidae abundance (GLMM – poisson)	(Intercept)	2.094	0.242	8.653	<0.001	***
	System (Traditional)	0.442	0.268	1.649	0.099	•
	Sampling month (May)	0.410	0.221	1.856	0.063	•
	Sampling month (July)	0.113	0.231	0.491	0.624	ns
	Sampling month (September)	-0.196	0.259	-0.756	0.450	ns
	Level of SNH (Low)	-0.042	0.266	-0.157	0.875	ns
	System (Traditional) : *Sampling month* (May)	0.915	0.234	3.908	<0.001	***
	System (Traditional) : *Sampling month* (July)	-0.336	0.240	-1.405	0.160	ns
	System (Traditional) : *Sampling month* (September)	-0.590	0.283	-2.080	0.038	*

	Sampling month (May) : *Level of SNH* (Low)	-0.595	0.219	-2.714	0.007	**
	Sampling month (July) : *Level of SNH* (Low)	0.603	0.240	2.514	0.012	*
	Sampling month (September) : *Level of SNH* (Low)	0.200	0.282	0.710	0.478	ns
	Pairwise					
	Abandoned – Traditional, February == 0	-0.442	0.268	-1.649	0.108	ns
	Abandoned – Traditional, May == 0	-1.357	0.247	-5.500	<0.001	***
	Abandoned – Traditional, July == 0	-0.105	0.252	-0.417	0.679	ns
	Abandoned – Traditional, September == 0	0.148	0.294	0.503	0.618	ns
	High – Low, February == 0	0.042	0.266	0.157	0.876	ns
	High – Low, May == 0	0.6364	0.238	2.674	0.011	*
	High – Low, July == 0	-0.562	0.255	-2.204	0.034	*
	High – Low, September == 0	-0.158	0.294	-0.539	0.593	ns
Lycosidae abundance (GLMM – negative binomial)	(Intercept)	1.710	0.465	3.678	<0.001	***
	System (Traditional)	1.537	0.512	3.001	0.003	**
	Sampling month (May)	1.013	0.521	1.945	0.052	•
	Sampling month (July)	-0.536	0.565	-0.948	0.343	ns
	Sampling month (September)	-1.169	0.677	-1.726	0.084	•
	System (Traditional) : *Sampling month* (May)	-1.378	0.618	-2.230	0.026	*
	System (Traditional) : *Sampling month* (July)	-1.198	0.732	-1.637	0.102	ns
	System (Traditional) : *Sampling month* (September)	-2.720	1.243	-2.189	0.029	*
	Pairwise					
	Abandoned – Traditional, February == 0	-1.537	0.512	-3.001	0.005	**
	Abandoned – Traditional, May == 0	-0.159	0.431	-0.369	0.714	ns
	Abandoned – Traditional, July == 0	-0.339	0.614	-0.553	0.584	ns
	Abandoned – Traditional, September == 0	1.183	1.170	1.011	0.318	ns
Oxyopidae abundance (GLMM – poisson)	(Intercept)	3.000	0.218	13.745	<0.001	***
	System (Traditional)	-1.756	0.312	-5.633	<0.001	***
	Sampling month (May)	-1.119	0.227	-4.923	<0.001	***
	Sampling month (July)	1.232	0.139	8.883	<0.001	***
	Sampling month (September)	0.555	0.152	3.647	0.000	***
	Level of SNH (Low)	-0.119	0.272	-0.437	0.662	ns
	System (Traditional) : *Sampling month* (May)	2.076	0.313	6.630	<0.001	***
	System (Traditional) : *Sampling month* (July)	0.851	0.249	3.415	<0.001	***
	System (Traditional) : *Sampling month* (September)	0.465	0.265	1.759	0.079	•
	Sampling month (May) : *Level of SNH* (Low)	-0.012	0.274	-0.042	0.966	ns

	Sampling month (July) : *Level of SNH* (Low)	0.030	0.190	0.159	0.874	ns
	Sampling month (September) : *Level of SNH* (Low)	0.614	0.201	3.049	0.002	**
	Pairwise					
	Abandoned – Traditional, February == 0	1.756	0.312	5.633	<0.001	***
	Abandoned – Traditional, May == 0	-0.320	0.295	-1.083	0.286	ns
	Abandoned – Traditional, July == 0	0.905	0.226	4.001	<0.001	***
	Abandoned – Traditional, September == 0	1.291	0.242	5.327	<0.001	***
	High – Low, February == 0	0.119	0.272	0.437	0.665	ns
	High – Low, May == 0	0.130	0.293	0.445	0.659	ns
	High – Low, July == 0	0.089	0.225	0.394	0.696	ns
	High – Low, September == 0	-0.495	0.236	-2.099	0.043	*
Philodromidae abundance (GLMM – negative binomial)	(Intercept)	1.833	0.186	9.866	<0.001	***
	System (Traditional)	-0.254	0.133	-1.909	0.056	•
	Sampling month (May)	0.029	0.244	0.118	0.906	ns
	Sampling month (July)	1.157	0.202	5.725	<0.001	***
	Sampling month (September)	0.669	0.216	3.101	0.002	**
Salcitidae (GLMM – poisson)	(Intercept)	0.668	0.230	2.899	0.004	**
	System (Traditional)	-0.344	0.134	-2.565	0.010	*
	Sampling month (May)	0.095	0.309	0.308	0.758	ns
	Sampling month (July)	2.001	0.238	8.401	<0.001	***
	Sampling month (September)	0.668	0.275	2.428	0.015	*
Theridiidae (GLMM – poisson)	(Intercept)	1.065	0.325	3.273	0.001	**
	System (Traditional)	0.124	0.404	0.308	0.758	ns
	Sampling month (May)	-0.229	0.424	-0.540	0.589	ns
	Sampling month (July)	1.168	0.340	3.438	<0.001	***
	Sampling month (September)	0.983	0.356	2.761	0.006	**
	Level of SNH (Low)	0.308	0.398	0.774	0.439	ns
	System (Traditional) : *Sampling month* (May)	-0.304	0.448	-0.679	0.497	ns
	System (Traditional) : *Sampling month* (July)	-0.743	0.413	-1.799	0.072	•
	System (Traditional) : *Sampling month* (September)	-1.306	0.490	-2.667	0.008	**
	Sampling month (May) : *Level of SNH* (Low)	1.097	0.461	2.381	0.017	*
	Sampling month (July) : *Level of SNH* (Low)	-0.214	0.401	-0.535	0.593	ns
	Sampling month (September) : *Level of SNH* (Low)	-0.627	0.447	-1.402	0.161	ns
	System (Traditional) : *Level of SNH* (Low)	-0.690	0.400	-1.727	0.084	•
	Pairwise					
	Abandoned – Traditional, February == 0	0.221	0.354	0.623	0.537	ns
	Abandoned – Traditional, May == 0	0.525	0.325	1.615	0.116	ns
	Abandoned – Traditional, July == 0	0.963	0.276	3.487	0.001	**

	Abandoned – Traditional, September == 0	1.526	0.382	3.992	<0.001	***
	High – Low, February == 0	0.037	0.353	0.104	0.918	ns
	High – Low, May == 0	-1.060	0.346	-3.063	0.004	**
	High – Low, July == 0	0.251	0.264	0.952	0.348	ns
	High – Low, September == 0	0.664	0.332	1.999	0.054	•
	Abandoned – Traditional, High == 0	0.464	0.277	1.673	0.104	ns
	Abandoned – Traditional, Low == 0	1.154	0.286	4.038	<0.001	***
	High – Low, Abandoned == 0	-0.372	0.250	-1.489	0.146	ns
	High – Low, Traditional == 0	0.318	0.312	1.017	0.316	ns
Thomisidae abundance	(Intercept)	1.927	0.242	7.958	<0.001	***
	Sampling month (May)	0.516	0.309	1.671	0.095	•
	Sampling month (July)	-0.202	0.362	-0.558	0.577	ns
	Sampling month (September)	-0.545	0.402	-1.356	0.175	ns
	Level of SNH (Low)	-0.474	0.380	-1.248	0.212	ns
	Sampling month (May) : *Level of SNH* (Low)	-0.157	0.495	-0.317	0.751	ns
	Sampling month (July) : *Level of SNH* (Low)	0.766	0.523	1.464	0.143	ns
	Sampling month (September) : *Level of SNH* (Low)	1.079	0.554	1.950	0.051	•
	Pairwise					
	High – Low, February == 0	0.474	0.380	1.248	0.220	ns
	High – Low, May == 0	0.631	0.319	1.976	0.055	•
	High – Low, July == 0	-0.292	0.360	-0.811	0.422	ns
	High – Low, September == 0	-0.605	0.402	-1.504	0.141	ns
Zodariidae abundance (GLMM – poisson)	(Intercept)	-0.263	0.499	-0.527	0.598	ns
	Sampling month (May)	0.981	0.479	2.049	0.041	*
	Sampling month (July)	2.351	0.427	5.504	0.000	***
	Sampling month (September)	2.197	0.430	5.106	0.000	***
	Level of SNH (Low)	-1.717	1.153	-1.489	0.137	ns
	Sampling month (May) : *Level of SNH* (Low)	2.315	1.125	2.057	0.040	*
	Sampling month (July) : *Level of SNH* (Low)	1.966	1.094	1.798	0.072	•
	Sampling month (September) : *Level of SNH* (Low)	1.440	1.101	1.309	0.191	ns
	Pairwise					
	High – Low, February == 0	1.717	1.153	1.489	0.145	ns
	High – Low, May == 0	-0.598	0.513	-1.165	0.251	ns
	High – Low, July == 0	-0.249	0.439	-0.567	0.574	ns
	High – Low, September == 0	0.277	0.456	0.607	0.547	ns
Braconidae abundance (GLMM – poisson)	(Intercept)	1.808	0.256	7.059	<0.001	***
	System (Traditional)	-0.122	0.321	-0.380	0.704	ns
	Sampling month (May)	-0.032	0.293	-0.108	0.914	ns
	Sampling month (July)	-2.082	0.537	-3.876	<0.001	***
	Sampling month (September)	-1.998	0.628	-3.180	0.001	**
	Level of SNH (Low)	-0.687	0.332	-2.072	0.038	*
	System (Traditional) : *Sampling month* (May)	0.964	0.358	2.695	0.007	**
	System (Traditional) : *Sampling month* (July)	0.548	0.539	1.017	0.309	ns

	System (Traditional) : *Sampling month* (September)	-1.802	1.106	-1.630	0.103	ns
	Sampling month (May) : *Level of SNH* (Low)	-0.126	0.374	-0.336	0.737	ns
	Sampling month (July) : *Level of SNH* (Low)	1.538	0.568	2.709	0.007	**
	Sampling month (September) : *Level of SNH* (Low)	1.209	0.789	1.532	0.126	ns
	Pairwise					
	Abandoned – Traditional, February == 0	0.122	0.321	0.380	0.707	ns
	Abandoned – Traditional, May == 0	-0.842	0.287	-2.931	0.006	**
	Abandoned – Traditional, July == 0	-0.426	0.487	-0.875	0.388	ns
	Abandoned – Traditional, September == 0	1.924	1.082	1.778	0.084	•
	High – Low, February == 0	0.687	0.332	2.072	0.046	*
	High – Low, May == 0	0.813	0.286	2.838	0.008	**
	High – Low, July == 0	-0.851	0.515	-1.653	0.107	ns
	High – Low, September == 0	-0.522	0.754	-0.593	0.493	ns
Encyrtidae abundance (GLMM – poisson) (dispformula = ~sampling month)	(Intercept)	-0.508	0.530	-0.959	0.338	ns
	System (Traditional)	-0.253	0.802	-0.316	0.752	ns
	Sampling month (May)	1.609	0.548	2.938	0.003	**
	Sampling month (July)	3.209	0.510	6.292	<0.001	***
	Sampling month (September)	1.910	0.536	3.564	<0.001	***
	System (Traditional) : *Sampling month* (May)	0.182	0.830	0.220	0.826	ns
	System (Traditional) : *Sampling month* (July)	-0.752	0.789	-0.954	0.340	ns
	System (Traditional) : *Sampling month* (September)	-0.443	0.835	-0.531	0.596	ns
	Pairwise					
	Abandoned – Traditional, February == 0	0.253	0.802	0.316	0.754	ns
	Abandoned – Traditional, May == 0	0.071	0.407	0.175	0.862	ns
	Abandoned – Traditional, July == 0	1.005	0.314	3.203	0.003	**
	Abandoned – Traditional, September == 0	0.697	0.417	1.671	0.103	ns
Eulophidae abundance (GLMM – poisson)	(Intercept)	0.042	0.553	0.076	0.939	ns
	System (Traditional)	0.130	0.652	0.200	0.842	ns
	Sampling month (May)	2.479	0.537	4.615	<0.001	***
	Sampling month (July)	2.842	0.528	5.383	<0.001	***
	Sampling month (September)	1.980	0.549	3.604	<0.001	***
	Level of SNH (Low)	-0.627	0.671	-0.934	0.350	ns
	System (Traditional) : *Sampling month* (May)	0.264	0.636	0.415	0.678	ns
	System (Traditional) : *Sampling month* (July)	-0.209	0.623	-0.336	0.737	ns
	System (Traditional) : *Sampling month* (September)	-1.370	0.649	-2.111	0.035	*

	Sampling month (May) : *Level of SNH* (Low)	-0.747	0.666	-1.121	0.262	ns
	Sampling month (July) : *Level of SNH* (Low)	0.598	0.643	0.930	0.353	ns
	Sampling month (September) : *Level of SNH* (Low)	1.681	0.665	2.525	0.012	*
	Pairwise					
	Abandoned – Traditional, February == 0	-0.130	0.652	-0.200	0.843	ns
	Abandoned – Traditional, May == 0	-0.394	0.304	-1.297	0.203	ns
	Abandoned – Traditional, July == 0	0.079	0.271	0.292	0.772	ns
	Abandoned – Traditional, September == 0	1.239	0.323	3.832	<0.001	***
	High – Low, February == 0	0.627	0.671	0.934	0.357	ns
	High – Low, May == 0	1.374	0.323	4.252	<0.001	***
	High – Low, July == 0	0.029	0.272	0.108	0.945	ns
	High – Low, September == 0	-1.054	0.321	-3.286	0.002	**
Mymaridae abundance (GLMM – poisson)	(Intercept)	-0.049	0.586	-0.084	0.933	ns
	System (Traditional)	2.098	0.638	3.288	0.001	**
	Sampling month (May)	2.866	0.518	5.538	<0.001	***
	Sampling month (July)	1.213	0.572	2.121	0.034	*
	Sampling month (September)	0.419	0.655	0.639	0.523	ns
	Level of SNH (Low)	-1.434	0.528	-2.716	0.007	**
	System (Traditional) : *Sampling month* (May)	-0.914	0.548	-1.668	0.095	•
	System (Traditional) : *Sampling month* (July)	-2.567	0.638	-4.021	<0.001	***
	System (Traditional) : *Sampling month* (September)	-3.575	0.791	-4.522	<0.001	***
	Sampling month (May) : *Level of SNH* (Low)	0.677	0.404	1.677	0.094	•
	Sampling month (July) : *Level of SNH* (Low)	1.449	0.527	2.750	0.006	**
	Sampling month (September) : *Level of SNH* (Low)	2.149	0.657	3.271	0.001	**
	Pairwise					
	Abandoned – Traditional, February == 0	-2.098	0.638	-3.288	0.002	**
	Abandoned – Traditional, May == 0	-1.183	0.369	-3.209	0.003	**
	Abandoned – Traditional, July == 0	0.469	0.485	0.968	0.340	ns
	Abandoned – Traditional, September == 0	1.477	0.668	2.211	0.034	*
	High – Low, February == 0	1.434	0.528	2.716	0.010	*
	High – Low, May == 0	0.757	0.369	2.055	0.047	*
	High – Low, July == 0	-0.015	0.482	-0.031	0.976	ns
	High – Low, September == 0	-0.714	0.613	-1.164	0.252	ns
Platygastridae abundance (GLMM – poisson)	(Intercept)	-1.215	0.742	-1.638	0.102	ns
	System (Traditional)	0.383	0.965	0.397	0.692	ns
	Sampling month (May)	3.277	0.720	4.550	<0.001	***
	Sampling month (July)	1.705	0.769	2.218	0.027	*

	Sampling month (September)	0.000	1.000	0.000	1.000	ns
	System (Traditional) : *Sampling month* (May)	-0.569	0.935	-0.609	0.543	ns
	System (Traditional) : *Sampling month* (July)	1.047	0.972	1.077	0.282	ns
	System (Traditional) : *Sampling month* (September)	2.428	1.167	2.080	0.038	*
	Pairwise					
	Abandoned – Traditional, February == 0	-0.383	0.965	-0.397	0.694	ns
	Abandoned – Traditional, May == 0	0.186	0.372	0.501	0.619	ns
	Abandoned – Traditional, July == 0	-1.430	0.458	-3.123	0.003	**
	Abandoned – Traditional, September == 0	-2.811	0.792	-3.550	0.001	**
Pteromalidae abundance (GLMM – negative binomial)	(Intercept)	0.729	0.383	1.903	0.057	•
	System (Traditional)	0.882	0.235	3.750	<0.001	***
	Sampling month (May)	1.651	0.380	4.345	<0.001	***
	Sampling month (July)	-0.194	0.507	-0.383	0.701	ns
	Sampling month (September)	-20.618	8643.590	-0.002	0.998	ns
	Level of SNH (Low)	-0.054	0.486	-0.111	0.911	ns
	Sampling month (May) : *Level of SNH* (Low)	-1.226	0.592	-2.071	0.038	*
	Sampling month (July) : *Level of SNH* (Low)	0.465	0.688	0.676	0.499	ns
	Sampling month (September) : *Level of SNH* (Low)	19.282	8643.590	0.002	0.998	ns
	Pairwise					
	High – Low, February == 0	0.054	0.486	0.111	0.912	ns
	High – Low, May == 0	1.280	0.337	3.795	<0.001	***
	High – Low, July == 0	-0.411	0.484	-0.849	0.401	ns
	High – Low, September == 0	-19.228	8643.590	-0.002	0.998	ns
Scelionidae abundance (GLMM – poisson)	(Intercept)	1.539	0.279	5.513	<0.001	***
	System (Traditional)	0.799	0.314	2.546	0.011	*
	Sampling month (May)	1.577	0.242	6.505	<0.001	***
	Sampling month (July)	1.782	0.239	7.454	<0.001	***
	Sampling month (September)	1.272	0.252	5.056	<0.001	***
	Level of SNH (Low)	-0.452	0.307	-1.472	0.141	ns
	System (Traditional) : *Sampling month* (May)	0.507	0.267	1.897	0.058	•
	System (Traditional) : *Sampling month* (July)	-0.701	0.268	-2.616	0.009	**
	System (Traditional) : *Sampling month* (September)	-1.182	0.288	-4.108	<0.001	***
	Sampling month (May) : *Level of SNH* (Low)	-0.348	0.254	-1.369	0.171	ns
	Sampling month (July) : *Level of SNH* (Low)	0.151	0.260	0.579	0.563	ns
	Sampling month (September) : *Level of SNH* (Low)	0.466	0.280	1.665	0.096	•
	Pairwise					

	Abandoned – Traditional, February == 0	-0.799	0.314	-2.546	0.016	*
	Abandoned – Traditional, May == 0	-1.306	0.227	-5.742	<0.001	***
	Abandoned – Traditional, July == 0	-0.099	0.227	-0.434	0.667	ns
	Abandoned – Traditional, September == 0	0.383	0.250	1.533	0.134	ns
	High – Low, February == 0	0.452	0.307	1.472	0.150	ns
	High – Low, May == 0	0.800	0.224	3.575	0.001	**
	High – Low, July == 0	0.301	0.227	1.323	0.195	ns
	High – Low, September == 0	-0.014	0.248	-0.057	0.955	ns
Andrena abundance (GLMM – poisson)	(Intercept)	2.035	0.232	8.755	<0.001	***
	System (Traditional)	-0.346	0.301	-1.151	0.250	ns
	Sampling month (May)	-0.710	0.313	-2.266	0.023	*
	Sampling month (July)	-3.333	1.039	-3.209	0.001	**
	Sampling month (September)	-22.367	14840.820	-0.002	0.999	ns
	Level of SNH (Low)	-0.714	0.310	-2.299	0.022	*
	System (Traditional) : *Sampling month* (May)	1.036	0.366	2.830	0.005	**
	System (Traditional) : *Sampling month* (July)	-1.198	1.133	-1.057	0.290	ns
	System (Traditional) : *Sampling month* (September)	-1.450	35128.136	0.000	1.000	ns
	Sampling month (May) : *Level of SNH* (Low)	0.759	0.369	2.060	0.039	*
	Sampling month (July) : *Level of SNH* (Low)	2.267	1.131	2.005	0.045	*
	Sampling month (September) : *Level of SNH* (Low)	-0.726	30942.871	0.000	1.000	ns
	Pairwise					
	Abandoned – Traditional, February == 0	0.346	0.300	1.151	0.258	ns
	Abandoned – Traditional, May == 0	-0.690	0.290	-2.381	0.023	*
	Abandoned – Traditional, July == 0	1.544	1.110	1.393	0.173	ns
	Abandoned – Traditional, September == 0	1.796	35128.14	0.000	1.000	ns
	High – Low, February == 0	0.714	0.310	2.299	0.028	*
	High – Low, May == 0	-0.046	0.279	-0.163	0.871	ns
	High – Low, July == 0	-1.553	1.110	-1.402	0.170	ns
	High – Low, September == 0	1.440	0.000	0.000	1.000	ns
Eucera abundance (GLMM – poisson)	(Intercept)	2.053	0.562	3.652	<0.001	***
	Sampling month (May)	-2.833	0.460	-6.157	0.000	***
	Sampling month (July)	-23.918	16943.241	-0.001	0.999	ns
	Sampling month (September)	-23.918	16943.241	-0.001	0.999	ns
	Level of SNH (Low)	-1.854	0.847	-2.189	0.029	*
	Sampling month (May) : *Level of SNH* (Low)	1.889	0.641	2.949	0.003	**

	Sampling month (July) : *Level of SNH* (Low)	-1.187	68773.714	0.000	1.000	ns
	Sampling month (September) : *Level of SNH* (Low)	-1.187	68773.714	0.000	1.000	ns
	Pairwise					
	High – Low, February == 0	1.854	0.850	2.189	0.035	*
	High – Low, May == 0	-0.035	1.000	-0.035	0.973	ns
	High – Low, July == 0	3.041	68773.71	0.000	1.000	ns
	High – Low, September == 0	3.041	68773.71	0.000	1.000	ns
Lasioglossum abundance (GLMM – poisson) (dispformula = ~sampling month)	(Intercept)	2.592	0.231	11.201	<0.001	***
	Sampling month (May)	-1.144	0.213	-5.363	<0.001	***
	Sampling month (July)	-0.985	0.201	-4.898	<0.001	***
	Sampling month (September)	-2.565	0.392	-6.539	<0.001	***
	Level of SNH (Low)	-0.865	0.350	-2.470	0.014	*
	Sampling month (May) : *Level of SNH* (Low)	-0.415	0.444	-0.935	0.350	ns
	Sampling month (July) : *Level of SNH* (Low)	0.482	0.332	1.453	0.146	ns
	Sampling month (September) : *Level of SNH* (Low)	1.125	0.540	2.084	0.037	*
	Pairwise					
	High – Low, February == 0	0.865	0.350	2.470	0.018	*
	High – Low, May == 0	1.279	0.495	2.586	0.014	*
	High – Low, July == 0	0.382	0.398	0.961	0.342	ns
	High – Low, September == 0	-0.260	0.582	-0.446	0.658	ns

Table S4. Complete results of the different models for the abundance of the most dominant families or genera. Estimates, standard errors, test statistics, p-values, and significance levels (ns > 0.1, • < 0.1, * < 0.05, ** < 0.01, and *** < 0.001) for the intercept and the explanatory variables system, % of semi-natural habitats at 150m or 500m, and the interaction (when significant. In the first column, the type of model (GLS, generalized least square model; GLM, generalized linear model) and the variance or correlation structures added to the model (if any) are given.

Response variable	Explanatory variable	Value / Estimate	Std. error	t-value / z-value	p-value	*
Araneidae abundance (GLS) (correlation = corGaus(form =~ UTMX + UTMY)	(Intercept)	80.175	10.304	7.781	<0.001	***
	System (Traditional)	-43.262	2.793	-15.491	<0.001	***
	% Semi-natural 150 m	-0.707	0.080	-8.861	<0.001	***
	System (Traditional) : *% Semi-natural 150 m*	0.664	0.125	5.305	<0.001	***
Gnaphosidae abundance (GLM – negative binomial) (dispformula = ~semi150)	(Intercept)	2.158	0.606	3.562	0.000	***
	System (Traditional)	1.480	0.628	2.358	0.018	*
	% Semi-natural 150 m	0.018	0.012	1.519	0.129	ns
	System (Traditional) : *% Semi-natural 150 m*	-0.028	0.014	-2.052	0.040	*
Linyphiidae abundance (GLM – negative binomial) (dispformula = ~ semi150)	(Intercept)	4.247	0.267	15.927	<0.001	***
	System (Traditional)	-0.143	0.309	-0.463	0.643	ns
	% Semi-natural 150 m	-0.015	0.008	-1.905	0.057	.
	System (Traditional) : *% Semi-natural 150 m*	0.025	0.010	2.416	0.016	*
Lycosidae abundance (GLM – negative binomial)	(Intercept)	3.280	0.331	9.922	<0.001	***
	System (Traditional)	0.686	0.387	1.771	0.077	•
Oxyopidae abundance (GLM – poisson) (gaussian correlation)	(Intercept)	4.957	0.269	18.416	<0.001	***
	System (Traditional)	-1.415	0.184	-7.687	<0.001	***
	% Semi-natural 500 m	0.000	0.005	-0.078	0.938	ns
	System (Traditional) : *% Semi-natural 500 m*	0.010	0.005	2.124	0.034	*
Philodromidae abundance (GLM – negative binomial)	(Intercept)	3.867	0.165	23.421	<0.001	***
	System (Traditional)	-0.597	0.256	-2.338	0.019	*
	% Semi-natural 500 m	-0.002	0.004	-0.472	0.637	ns
	System (Traditional) : *% Semi-natural 500 m*	0.010	0.006	1.672	0.095	•
Salticidae abundance (GLM – gaussian) (square root transformed, gaussian correlation)	(Intercept)	4.891	0.229	21.341	<0.001	***
	System (Traditional)	-0.883	0.068	-12.937	<0.001	***
	% Semi-natural 150 m	-0.005	0.002	-2.728	0.006	**
	System (Traditional) : *% Semi-natural 150 m*	-0.008	0.002	-3.188	0.001	**
Theridiidae abundance (GLM – poisson)	(Intercept)	3.435	0.163	21.059	<0.001	***
	System (Traditional)	-1.294	0.242	-5.355	<0.001	***
	% Semi-natural 150 m	-0.004	0.004	-1.128	0.259	ns
	System (Traditional) : *% Semi-natural 150 m*	0.020	0.007	2.852	0.004	**
Thomisidae abundance (GLM – poisson)	(Intercept)	3.602	0.152	23.723	<0.001	***
	System (Traditional)	-0.542	0.190	-2.856	0.004	**
	% Semi-natural 150 m	-0.006	0.004	-1.682	0.093	•
	System (Traditional) : *% Semi-natural 150 m*	0.013	0.005	2.336	0.019	*

Zodariidae abundance (GLM – negative binomial)	Nothing significant					
Braconidae abundance (GLM – gaussian) (dispformula = ~system)	(Intercept)	4.296	3.761	1.142	0.253	ns
	System (Traditional)	6.114	3.196	1.913	0.056	•
	% Semi-natural 500 m	0.189	0.063	2.981	0.003	**
Encyrtidae abundance (GLM – poisson) (gaussian correlation)	(Intercept)	3.954	0.423	9.344	<0.001	***
	System (Traditional)	-1.605	0.240	-6.694	<0.001	***
	% Semi-natural 150 m	-0.021	0.005	-4.237	<0.001	***
	System (Traditional) : *% Semi-natural 150 m*	0.020	0.008	2.599	0.009	**
Eulophidae abundance (GLM – gaussian) (log transformed)	(Intercept)	4.192	0.323	12.972	<0.001	***
	System (Traditional)	-1.019	0.377	-2.701	0.007	**
	% Semi-natural 150 m	-0.013	0.007	-1.739	0.082	•
	System (Traditional) : *% Semi-natural 150 m*	0.031	0.011	2.885	0.004	**
Mymaridae abundance (GLM – negative binomial)	(Intercept)	3.201	0.300	10.674	<0.001	***
	System (Traditional)	0.707	0.356	1.985	0.047	*
Platygastridae abundance (GLS)	(Intercept)	24.963	3.737	6.680	<0.001	***
	% Semi-natural 150 m	-0.308	0.104	-2.973	0.014	*
Pteromalidae abundance (GLS)	(Intercept)	9.899	4.448	2.225	0.057	•
	System (Traditional)	1.490	6.140	0.243	0.814	ns
	% Semi-natural 500 m	0.007	0.095	0.071	0.946	ns
	System (Traditional) : *% Semi-natural 500 m*	0.524	0.145	3.609	0.007	**
Scelionidae abundance (GLM – negative binomial)	(Intercept)	4.188	0.185	22.605	<0.001	***
	System (Traditional)	0.513	0.231	2.219	0.027	*
Andrena abundance (GLM – poisson) (dispformula = ~system)	(Intercept)	2.753	0.239	11.526	<0.001	***
	System (Traditional)	-0.359	0.287	-1.250	0.211	ns
	% Semi-natural 150 m	-0.010	0.006	-1.779	0.075	•
	System (Traditional) : *% Semi-natural 150 m*	0.016	0.008	1.990	0.047	*
Eucera abundance (GLS)	(Intercept)	-1.465	5.743	-0.255	0.804	ns
	% Semi-natural 500 m	0.306	0.134	2.287	0.045	*
Lasioglossum abundance (GLS)	(Intercept)	6.761	6.070	1.114	0.291	ns
	% Semi-natural 500 m	0.365	0.142	2.576	0.028	*

Chapter III

TRADITIONAL ALMOND ORCHARDS IN CONTRASTING LANDSCAPES MAINTAIN EXTREMELY DIVERSE PARASITOID COMMUNITIES THREATENED BY ABANDONMENT

CULTIVOS TRADICIONALES DE ALMENDRO EN PAISAJES DIFERENTES MANTIENEN COMUNIDADES EXTREMADAMENTE DIVERSAS DE PARASITOIDES AMENAZADAS POR EL ABANDONO

Traditional almond orchards in contrasting landscapes maintain extremely diverse parasitoid communities threatened by abandonment

Cultivos tradicionales de almendro en paisajes diferentes mantienen comunidades extremadamente diversas de parasitoides amenazadas por el abandono

Resumen

Los himenópteros parasitoides son un grupo de insectos extremadamente diverso, esencial para el funcionamiento de los ecosistemas y el control de plagas. Debido a que pertenecen a un elevado nivel trófico y presentan un alto grado de especialización, los parasitoides son particularmente sensibles a las perturbaciones y a los eventos de extinción, lo que los convierte en buenos indicadores de la diversidad de artrópodos. Aunque varios estudios han demostrado que los parasitoides pueden verse afectados por las prácticas de manejo y la composición y configuración del paisaje, pocos han evaluado las consecuencias del abandono agrícola, un proceso que amenaza la elevada biodiversidad asociada a las áreas agrícolas de alto valor natural en Europa. En este contexto, nos propusimos determinar los efectos del abandono de parcelas tradicionales de almendro sobre la comunidad de himenópteros parasitoides (a nivel de género), así como el papel del porcentaje de hábitats seminaturales (SNH) en el paisaje modulando estos efectos y el efecto de diversas variables de uso del suelo a diferentes escalas. Realizamos cuatro muestreos entre la floración del almendro y la cosecha (febrero - septiembre de 2019) en 12 parcelas (6 abandonadas) situadas en paisajes tradicionales con diferentes porcentajes de SNH (paisajes simples vs. complejos). Las parcelas de almendro abandonadas albergaron comunidades de parasitoides diferentes a las tradicionales, aunque con valores de diversidad similares (excepto en mayo, cuando las tradicionales favorecieron notablemente a los parasitoides). El contexto paisajístico condicionó el papel del sistema agrícola, con las parcelas abandonadas actuando como refugio a finales de verano sólo en paisajes simples y los paisajes complejos favoreciendo la abundancia de parasitoides independientemente del sistema agrícola. La fuerte estacionalidad resultó en una alta tasa de recambio y condicionó las respuestas de la comunidad a las variables de uso del suelo a 150 m y 500 m. Nuestros resultados destacan la relevancia de los cultivos tradicionales de almendro y de los paisajes complejos para la conservación de los parasitoides, así como la importancia de trabajar a altas resoluciones taxonómicas para desentrañar las respuestas de los parasitoides al abandono agrícola y a la complejidad paisajística.

Abstract

Hymenopteran parasitoids are an extremely diverse insect group, crucial for ecosystem functioning and pest control. Due to their high trophic level and high degree of specialization, parasitoids are particularly sensitive to perturbation and extinction events, being good indicators of arthropod diversity. While several studies have shown that parasitoids can be affected by management practices and landscape composition and configuration, few have evaluated the consequences of agricultural abandonment, a process that threatens the high biodiversity associated with European High Nature Value Farmland. In this context, we aimed to determine the effects of traditional almond orchard abandonment on the hymenopteran parasitoid community (at genus level), the role of the percentage of semi-natural habitats (SNH) in the landscape in mediating these effects, and the effect of several land-use variables at different scales. We carried out four samplings between almond blooming and harvest (February – September 2019) in 12 orchards (6 abandoned) located in traditional landscapes with varying percentages of SNH (simple vs. complex landscapes). Abandoned and traditional almond orchards harbored different parasitoid communities but similar diversity measures, except in May, when traditional orchards clearly favored parasitoids. The landscape context conditioned the role of the farming system, abandoned orchards acting as a refuge in late summer only in simple landscapes, while complex landscapes favored parasitoid abundance irrespectively of the farming system. The strong seasonality drove a high turnover rate and conditioned community responses to land-use variables at 150 m and 500 m. Our results highlight the importance of traditional almond orchards and complex landscapes for parasitoid conservation and the relevance of working at high taxonomic resolutions to disentangle parasitoid responses to agricultural abandonment and landscape complexity.

Chapter IV

BEE TAXONOMIC AND TRAIT RESPONSES TO TRADITIONAL ALMOND ORCHARD ABANDONMENT IN CONTRASTING LANDSCAPES

RESPUESTAS EN LA COMPOSICIÓN TAXONÓMICA Y RASGOS FUNCIONALES DE LAS ABEJAS ANTE EL ABANDONO DE PARCELAS TRADICIONALES DE ALMENDRO EN PAISAJES CON DIFERENTE GRADO DE COMPLEJIDAD

Bee taxonomic and trait responses to traditional almond orchard abandonment in contrasting landscapes

Respuestas en la composición taxonómica y rasgos funcionales de las abejas ante el abandono de parcelas tradicionales de almendro en paisajes con diferente grado de complejidad

Resumen

La pérdida de hábitat y la intensificación son las principales causas del declive de las abejas silvestres, un grupo esencial para la polinización de cultivos y plantas silvestres. Los paisajes homogéneos que resultan de estos procesos se caracterizan por presentar grandes parcelas, escasa diversidad de cultivos, un elevado uso de agroquímicos y una baja biodiversidad, contrastando fuertemente con los paisajes agrícolas tradicionales a los que sustituyen. Aunque numerosos estudios se han centrado en las consecuencias de la intensificación agrícola sobre la diversidad taxonómica y funcional de las abejas silvestres, las consecuencias del abandono de parcelas tradicionales en este grupo aún no están claras, especialmente en cultivos permanentes y en regiones mediterráneas. En este contexto, nos propusimos determinar, en paisajes con diferentes niveles de complejidad (medida a través del porcentaje de hábitats seminaturales), los efectos del abandono de parcelas tradicionales de almendro sobre la composición taxonómica y los rasgos funcionales de la comunidad, la riqueza y la abundancia de abejas silvestres, así como los efectos de diversas variables de uso del suelo a diferentes escalas. Recolectamos abejas silvestres de febrero a septiembre en 12 parcelas de almendro (6 abandonadas) situadas en paisajes simples y complejos en el oeste de España. Nuestros resultados muestran una comunidad de abejas adaptada a la fenología del cultivo y a la estacionalidad mediterránea, con escasas diferencias entre las parcelas abandonadas y las tradicionales. Los hábitats seminaturales desempeñaron un papel clave, con los paisajes complejos albergando comunidades diferentes y más abundantes que los simples y favoreciendo a las abejas que nidifican en el suelo y a todos los gremios de tamaño corporal. Las abejas que nidifican en cavidades se vieron particularmente afectadas por la estacionalidad y demostraron ser especialmente sensibles a los cambios en el uso del suelo. Varias especies están asociadas a las parcelas tradicionales, incluida la única especie amenazada, mientras que las parcelas abandonadas constituyen hábitats importantes para las abejas, principalmente en paisajes simples. Nuestros resultados ponen de manifiesto el gran valor de estos paisajes culturales para la conservación de las abejas silvestres.

Abstract

Habitat loss and intensification are the main causes of the decline of wild bees, an essential group for the pollination of crops and wild plants. The homogeneous landscapes created, with large fields, low crop diversity, high agrochemical inputs, and low biodiversity, contrast sharply with the traditional agricultural landscapes they replace. While several studies have focused on the consequences of agricultural intensification on the taxonomic and functional diversity of wild bees, the implications of the abandonment of traditional agriculture on wild bees are still unclear, especially in permanent crops and Mediterranean regions. In this context, we attempted to determine, in landscapes with contrasting complexity (measured as the percentage of semi-natural habitats), the effects of traditional almond orchard abandonment on taxonomic and trait community composition, richness, and abundance of wild bees, as well as the effects of several land-use variables at different scales. We sampled wild bees from February to September in 12 almond orchards (6 abandoned) located in simple vs. complex landscapes in western Spain. Our results show a bee community adapted to the crop phenology and the Mediterranean seasonality, with few differences between abandoned and traditional orchards. Semi-natural habitats played a key role, with complex landscapes harboring different, more abundant communities than simple ones, favoring ground-nesting bees and all size guilds. Cavity nesting bees were particularly affected by the seasonality and proved to be especially sensitive to land-use changes. Several species were associated with traditional orchards, including the only threatened species, while abandoned orchards proved to be important habitats for bees, mainly in simple landscapes. Our results emphasize the high conservation value of these cultural landscapes.

Chapter V

DESCRIPTION OF THE FIRST BRACHYPTEROUS *LONCHIDIA* SPECIES (HYMENOPTERA: FIGITIDAE: FIGITINAE), WITH A KEY TO EUROPEAN SPECIES

DESCRIPCIÓN DE LA PRIMERA ESPECIE BRAQUÍPTERA DEL GÉNERO LONCHIDIA (HYMENOPTERA: FIGITIDAE: FIGITINAE), CON UNA CLAVE PARA LAS ESPECIES EUROPEAS

Description of the first *Lonchidia* brachypterous species (Hymenoptera: Figitidae: Figitinae), with a key to European species

Descripción de la primera especie braquíptera del género Lonchidia (Hymenoptera: Figitidae: Figitinae), con una clave para las especies europeas

Víctor De Paz, Laura Baños-Picón, Natalia Rosas-Ramos, Josep D. Asís, Irene Lobato-Vila, and Juli Pujade-Villar

This chapter is under review in the journal Zootaxa.

Resumen

Se describen el macho y la hembra de una nueva especie de *Lonchidia* Thomson, 1862, *L. atypica* Pujade-Villar & de Paz sp. nov., de las provincias de Salamanca y Cáceres (oeste de España). Los especímenes fueron recolectaron con un soplador de hojas modificado y trampas de caída en parcelas tradicionales de almendro y cerezo. Los caracteres diagnósticos de esta especie son: notaulos profundos pero cortos, alcanzando sólo la parte anterior del mesonoto, y alas braquípteras. Se ilustran ambos sexos y se propone una clave de identificación para diferenciar las especies europeas. También se discute la posibilidad de que el macho de *L. clavicornis* Thomson, 1862 corresponda a una especie diferente.

Abstract

The male and female of a new species of *Lonchidia* Thomson, 1862, *L. atypica* Pujade-Villar & de Paz sp. nov., are described from the provinces of Salamanca and Cáceres (Western Spain). Specimens were collected with a G-Vac suction sampler and pitfall traps from traditional almond and cherry orchards. The diagnostic characters of this species are: deep but short notauli, reaching only the anterior part of the mesoscutum, and brachypterous wings. Both sexes are illustrated and an identification key is proposed herein to differentiate the European species. The possibility that the male of *L. clavicornis* Thomson, 1862 corresponds to a different species is also discussed.

Key words: Hymenoptera, Figitidae, *Lonchidia*, new species, Spain.

Conclusions

1. Traditional almond and olive orchards maintain diverse and abundant arthropod communities of predators, parasitoids, and bees. The historical low-intensity management practices carried out in these orchards (mainly tillage) create stable open habitats with a diverse cover of annual plants, providing different resources, microhabitats, and niches. These characteristics allowed traditional orchards to harbor different but equally rich communities of natural enemies and pollinators than the more structurally complex abandoned orchards (Chapters 1-4).

2. Abandoned olive and almond orchards harbored diverse arthropod communities, with several unique parasitoid genera and bee species. A higher complexity in vegetation architecture greatly benefited spider communities, which were generally richer and more abundant than in traditional orchards. Abandoned orchards appear to be important landscape elements that provide complementary resources for many groups of beneficial arthropods, especially spiders. Moreover, abandoned olive groves are not reservoirs of the olive fruit fly and may even act as sink habitats due to their low olive production but high *Bactrocera oleae* numbers (Chapters 1-4).

3. Semi-natural habitats are crucial for the conservation of arthropods in traditional agricultural landscapes. They create complex landscapes that support different and more abundant bee communities and richer and more abundant parasitoid communities. Furthermore, landscape complexity mediated responses to orchard abandonment. In simple landscapes, abandoned orchards favored either richness or abundance of all studied groups by providing complementary resources and microhabitats, taking the role of semi-natural habitats. However, as the proportion of semi-natural habitats increases, abandoned orchards rapidly lose their relevance, while in traditional orchards diversity parameters increased, indicating a strong arthropod spillover from semi-natural habitats (Chapters 2-4).

4. The strong seasonality of the Mediterranean climate proved to be the most important variable explaining the variation in the communities studied. Drastic changes in the availability of floral resources and hosts or prey, as well as in climatic conditions (e.g., temperature, precipitation, humidity) resulted in changes in the structure, composition and diversity metrics of the arthropod communities and interacted with their responses to

agricultural abandonment and landscape complexity. This result was mainly observed for bees and parasitoids, which experienced high turnover rates between sampling periods that conditioned their responses to local and landscape variables (Chapters 1-4).

5. Parasitoids were extremely diverse in our study areas, especially in La Fregeneda, where abandoned and traditional almond orchards sustained at least 235 different genera and a minimum of three new species. This fact highlights the lack of knowledge about hymenopteran parasitoids and the need for further taxonomic studies of this group, which is crucial for ecosystem functioning. Community structure differed between systems, although diversity metrics remained similar throughout the season except in May. Specifically in this month, traditional orchards supported higher numbers of parasitoids of certain genera, resulting in a less uniform community. Parasitoid communities were also strongly affected by the seasonality, with high turnover rates, and by the landscape cover of semi-natural habitats, with complex landscapes maintaining richer and more abundant communities for the first half of the season. Working at the genus level provided further insights on parasitoid responses to agricultural abandonment and landscape complexity, implying that family-level assessments may not provide sufficient resolution to detect all these responses (Chapters 3 and 5).

6. Bees were very slightly affected by almond orchard abandonment. Although several species were associated with traditional orchards, including the only threatened species found in our study, both systems supported communities with similar composition and equal values of species richness and abundance. These results were also observed working at the genus level, suggesting that for bees, genus-level assessments may accurately reflect general species-level responses. Landscape cover of semi-natural habitats strongly influenced bees, with complex landscapes maintaining different and more abundant communities than simple landscapes. Functional traits mediated bee responses to landscape parameters, with species being affected by land-use variables at different landscape scales depending on their body size. Bee responses to local and landscape variables were conditioned by the seasonality. Communities differed greatly between sampling periods, with each community being influenced by a specific set of

land-use variables, among which shrubland cover and density of agricultural dirt-roads were particularly relevant (Chapter 4).

7. From a conservation perspective, abandoned orchards increase landscape heterogeneity and provide complementary habitats for some arthropod groups (e.g., spiders). However, this positive effect is limited to simple landscapes, where semi-natural habitats are scarce. In these landscapes, abandoned orchards are habitats of conservation value and they should be managed to ensure that they reach late successional stages. In complex landscapes, on the other hand, priority should be given to the conservation of traditional orchards. Furthermore, conservation measures designed in Mediterranean countries should take into account the high community turnover throughout the seasons, especially considering future climate scenarios. Landscape simplification through the loss of semi-natural habitats has negative consequences for arthropod biodiversity, even in traditional agricultural landscapes with small fields and high crop diversity. Our results suggest that maintaining both a high cover of semi-natural habitats and traditionally managed orchards in the landscape could have synergistic effects for arthropod conservation (Chapters 1-4).

Conclusiones

1. Las parcelas tradicionales de almendro y olivo presentaron comunidades diversas y abundantes de artrópodos depredadores, parasitoides y abejas. Las prácticas de manejo de baja intensidad llevadas a cabo históricamente en estas parcelas (principalmente, el arado) han generado hábitats abiertos y estables, con una cobertura diversa de plantas anuales, proporcionando diferentes recursos, microhábitats y nichos. Estas características han permitido que los cultivos tradicionales alberguen comunidades de enemigos naturales y polinizadores diferentes, pero igualmente ricas que las de las parcelas abandonadas, a pesar de que estas últimas son más complejas estructuralmente (Capítulos 1-4).

2. Las parcelas abandonadas de almendro y olivo albergaron comunidades de artrópodos diversas, con numerosos géneros de parasitoides y especies de abejas exclusivas. La mayor complejidad estructural de la vegetación en estas parcelas benefició en gran medida a las comunidades de arañas, que resultaron, en general, más ricas y abundantes que en los cultivos tradicionales. Las parcelas abandonadas parecen constituir elementos paisajísticos importantes, que proporcionan recursos complementarios para muchos grupos de artrópodos beneficiosos y, especialmente, para las arañas. Además, las parcelas de olivo abandonadas no constituyen reservorios de la mosca del olivo e incluso podrían actuar como hábitats sumidero, dado que su producción de aceituna es baja, pero la abundancia de *Bactrocera oleae* es elevada (Capítulos 1-4).

3. Los hábitats seminaturales son esenciales para la conservación de los artrópodos en paisajes agrícolas tradicionales. Estos hábitats generan paisajes complejos que sustentan comunidades de abejas diferentes y más abundantes y comunidades de parasitoides más ricas y abundantes. Además, la complejidad paisajística moduló las respuestas al abandono. En paisajes simples, las parcelas abandonadas favorecieron o bien la riqueza, o bien la abundancia de todos los grupos estudiados, al proporcionar recursos y microhábitats complementarios, asumiendo el papel de hábitats seminaturales. Sin embargo, a medida que aumenta la proporción de hábitats seminaturales, las parcelas abandonadas pierden rápidamente su relevancia, mientras que en las tradicionales aumentan los parámetros de diversidad, lo que indica una importante dispersión de artrópodos desde los hábitats seminaturales (Capítulos 2-4).

4. La marcada estacionalidad del clima mediterráneo resultó ser la variable más importante para explicar los cambios en las comunidades estudiadas. Las drásticas alteraciones en la disponibilidad de recursos florales y hospedadores o presas, así como en las condiciones climáticas (por ejemplo, temperatura, precipitación, humedad) provocaron cambios en la estructura, composición y diversidad de las comunidades de artrópodos e interaccionaron con sus respuestas al abandono y a la complejidad paisajística. Este resultado se observó principalmente para las abejas y los parasitoides, que experimentaron altas tasas de recambio entre los periodos de muestreo, lo que condicionó sus respuestas a las variables locales y paisajísticas (Capítulos 1-4).

5. Encontramos comunidades de parasitoides muy diversas en nuestras áreas de estudio, especialmente, en La Fregeneda, donde las parcelas abandonadas y tradicionales de almendro albergaron al menos 235 géneros diferentes y un mínimo de tres especies nuevas. Este hecho pone de manifiesto la falta de conocimiento acerca de los himenópteros parasitoides y la necesidad de realizar más estudios taxonómicos sobre este grupo fundamental para el funcionamiento de los ecosistemas. La estructura de la comunidad difirió entre sistemas, aunque las métricas de diversidad fueron similares durante toda la temporada, excepto en mayo. En este mes, las parcelas tradicionales albergaron un mayor número de parasitoides de algunos géneros, lo que resultó en una comunidad menos uniforme. Las comunidades de parasitoides también se vieron muy afectadas por la estacionalidad, presentando altas tasas de recambio, así como por la cobertura de hábitats seminaturales en el paisaje, ya que los paisajes complejos mantuvieron comunidades más ricas y abundantes durante la primera mitad de la temporada. Trabajar a nivel de género permitió obtener más información sobre las respuestas de los parasitoides al abandono agrícola y a la complejidad del paisaje, indicando que las evaluaciones a nivel de familia podrían carecer de la resolución suficiente para detectar todas estas respuestas (Capítulos 3 y 5).

6. Las abejas se vieron muy poco afectadas por el abandono de las parcelas de almendro. Aunque varias especies estaban asociadas a los cultivos tradicionales, incluida la única especie amenazada que se encontró en el estudio, ambos sistemas presentaron comunidades con composiciones y valores de riqueza y abundancia de especies similares.

Esto coincide con lo observado trabajando a nivel de género, lo que sugiere que, en el caso de las abejas, los estudios a nivel de género pueden reflejar con precisión las respuestas generales a nivel de especie. La cobertura de hábitats seminaturales en el paisaje afectó notablemente a las abejas, ya que los paisajes complejos mantuvieron comunidades diferentes y más abundantes que los paisajes simples. Las respuestas de las abejas a los parámetros del paisaje estuvieron moduladas por sus rasgos funcionales, afectando las variables de uso del suelo a las especies a diferentes escalas en función de su tamaño corporal. Por otro lado, las respuestas a las variables a escala local y paisajística estuvieron condicionadas por la estacionalidad. Las comunidades variaron mucho entre periodos de muestreo, cada una siendo afectada por un conjunto específico de variables de uso del suelo, entre las que destacaron la cobertura arbustiva y la densidad de caminos agrícolas sin asfaltar (Capítulo 4).

7. Desde el punto de vista de la conservación, las parcelas abandonadas aumentan la heterogeneidad del paisaje y proporcionan hábitats complementarios para algunos grupos de artrópodos (por ejemplo, las arañas). Sin embargo, este efecto positivo se limita a los paisajes simples, donde los hábitats seminaturales son escasos. En estos paisajes, los cultivos abandonados constituyen hábitats de gran valor desde el punto de vista de la conservación y deberían ser manejados para garantizar que alcancen etapas sucesionales tardías. En cambio, en paisajes complejos, convendría dar prioridad a la conservación de los cultivos tradicionales. Además, las medidas de conservación aplicadas en los países mediterráneos deberían tener en cuenta la elevada tasa de recambio que sufren las comunidades a lo largo de las estaciones, especialmente si se consideran los futuros escenarios climáticos. La simplificación del paisaje mediante la pérdida de hábitats seminaturales tiene consecuencias negativas para la biodiversidad de artrópodos, incluso en paisajes agrícolas tradicionales con un parcelario pequeño y gran diversidad de cultivos. Nuestros resultados sugieren que mantener en el paisaje una alta cobertura de hábitats seminaturales y de cultivos manejados de forma tradicional podría tener efectos sinérgicos para la conservación de los artrópodos (Capítulos 1-4).