

Semi-natural habitats and natural enemies in olive orchards:

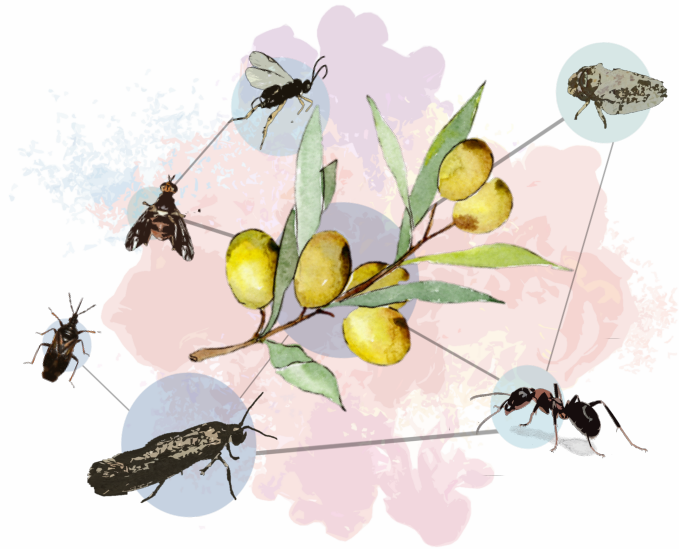
abundance, function, trophic interactions, and global climate change

Hugo Alejandro Alvarez
PhD Thesis



Semi-natural habitats and natural enemies in olive orchards: abundance, function, trophic interactions, and global climate change

Hábitats semi-naturales y enemigos naturales en los olivares: abundancia, función, interacciones tróficas y cambio climático global



by

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The present thesis has been carried out at the Department of Zoology, Faculty of Science, University of Granada, Spain. The research encompasses the data processing and analysis of the database of arthropod diversity (2001-2015) from the research group “Applied Ecology and Agroecosystems” (AGR-285); and the development of novel global warming experiments. The research was funded by the Excellence Project of the Andalusian Regional Government (AGR 1419); the Alhambra and Generalife Governing Board (contract 3548-00 and 3548-01); the Spanish Ministry of Science, Innovation, and Universities, General Sub-direction of Projects (AGL2009-09878); the project REN2002-03269/GLO (DGICYT); and by the individual economic support of the author and F. Ruano. The author was founded with an international PhD grant by CONACyT Mexico (registry 332659).

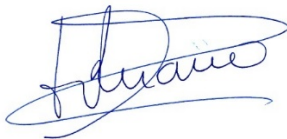
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a Sofia Daniela,

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"When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!... What a struggle must have gone on during long centuries between the several kinds of trees, each annually scattering its seeds by the thousand; what war between insect and insect – between insects, snails, and other animals with birds and beasts of prey – all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees. Throw up a handful of feathers, and all fall to the ground according to definite laws; but how simple is the problem where each shall fall compared to that of the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on... The dependency of one organic being on another, as of a parasite on its prey, lies generally between beings remote in the scale of nature. This is likewise sometimes the case with those which may strictly be said to struggle with each other for existence"

Charles Darwin, 1858,
On the Origin of Species by means of Natural Selection

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Summary

Within ecology, what and where are the predators of herbivores, is a classic question. In nature ecosystems are inherently dynamic and interact across spatial scales. As trophic relationships are a product of evolutionary and phylogenetic relationships between predators and prey, within ecosystems populations are naturally controlled by other organisms via trophic guilds across food chains. However, in human-managed ecosystems, such as agroecosystems, trophic interactions become highly simplified. As all ecosystems interact with each other, when there are managed ecosystems near to natural ecosystems organisms respond positively or negatively depending on resource availability or environmental conditions. Humans had exploited the properties of ecosystem, i.e., ecosystem-services, and the interaction between different ecosystems to provide human well-being, but the modern demand on food has led to agriculture intensification, which results in the loss and fragmentation of natural habitats and therefore biodiversity loss and extinction. Such a process alters the benefits provided by biodiversity, amongst other ecosystem-services, to control non-beneficial (detrimental) organisms to humans. Accordingly, conservation biological control aims to exploit the functions of natural enemies of a given ecosystem and landscape by restoring or maintaining natural and semi-natural habitats near or within agroecosystems to provide places in which natural enemies can feed, overwinter, or complete their life cycles.

In order to enhance conservation biological control, this thesis has focused on the ecological processes that underlie such an ecosystem-service, aiming to provide a detailed overview of the influence of natural and semi-natural habitats on natural enemy-pest interactions in organically managed crops, which in this case it was used an historic and economically important crop in the Mediterranean basin, the olive orchard *Olea europaea* L. Thus, the thesis tries to respond, what and where are the “natural enemies” of herbivores and how habitat structure and climate change will affect higher trophic levels within agroecosystems? So, the thesis was separated into three general parts. The first part comprise studies based on the relation of abundance and ecosystem function (biological control), with focus on the interaction amongst natural enemies, herbivores, agroecosystems, semi-natural habitats, and landscapes (Chapters 1 to 4). The second part focus on the trophic roles and trophic interactions amongst natural enemies and herbivores (Chapters 5 and 6). And the third part focus on the response of natural enemies to a scenario of global climate change (Chapter 7).

The outcomes generated here suggested that (1) semi-natural habitats contribute to the establishment of different guilds of natural enemies (NE) positively affecting the abundance and movement of NE into the orchard; (2) abundance of key NE is affected by habitat complexity being influenced differently by plant richness and plant arrangement and scattering; (3) the establishment of ground covers positively affect key NE and promote the biological control of specialist herbivores (SH) by means of egg predation; (4) landscape composition and configuration affect key NE abundance and predation, and SH abundance and damage, so diversified landscapes with dense edges reduce the adult SH, and the proportion of sparse scrubland in the landscape may be the main factor driving biological control; (5) the maturity of the ground cover positively affects the structure and complexity of the olive canopy trophic network and promotes the establishment of key NE that are related to natural habitats; (6) the trophic role of omnivores ants expresses a predator isotopic profile rather than being a hyper-predator, so they can be considered as NE; and (7) under a global warming scenario, predators (larvae) individuals express phenotypic plasticity and a down-regulation in their metabolism, but endogamy reduces the potential of thermal plasticity, and therefore its evolvability, when predator individuals are subjected to thermal stress during ontogeny expressing trade-offs and constrains in order to improve survival.

Resumen

En ecología, ¿cuáles son y dónde se encuentran los depredadores de los herbívoros? es una pregunta clásica. En la naturaleza los ecosistemas son dinámicos e interactúan en el espacio. Dado que las relaciones tróficas son producto de relaciones filogenéticas y evolutivas entre depredador y presa, dentro de los ecosistemas, las poblaciones son controladas naturalmente por otros organismos por medio de gremios tróficos a través de las cadenas alimentarias. Sin embargo, en ecosistemas manejados por el humano, como serían los agroecosistemas, las relaciones tróficas se vuelven altamente simplificadas. Dado a que todos los ecosistemas interactúan, donde existen ecosistemas naturales cerca de ecosistemas manejados los organismos responden positiva o negativamente dependiendo de la disponibilidad de recursos o las condiciones ambientales. Los humanos han explotado las propiedades de los ecosistemas, es decir, los servicios ecosistémicos, y la interacción entre ecosistemas para proveerse de bienes, no obstante, la demanda moderna de alimentos ha llevado a la intensificación de la agricultura, lo que resulta en la pérdida y fragmentación de los hábitats naturales y por consiguiente a la pérdida y extinción de la biodiversidad. Dicho proceso altera los beneficios que la biodiversidad provee, entre otros servicios ecosistémicos, para controlar organismos perjudiciales que afectan a los humanos. Respectivamente, el control biológico por conservación tiene por objetivo explotar las funciones de los hábitats naturales que estén cerca o dentro de los agroecosistemas para proporcionar lugares en donde los enemigos naturales puedan alimentarse, protegerse en el invierno o completar su ciclo de vida.

Con el fin de mejorar el control biológico por conservación, la presente tesis se centra en los procesos ecológicos que subyacen a dicho servicio ecosistémico, con el objetivo de proporcionar una descripción detallada de la influencia de los hábitats naturales y semi-naturales en las interacciones entre enemigos naturales y plagas en cultivos manejados orgánicamente, por lo que en este caso se usó un cultivo histórico y de importancia económica en el Mediterráneo, el olivar *Olea europaea* L. Así, la tesis trata de responder ¿cuáles son y dónde se encuentran los “enemigos naturales” de los herbívoros y cómo la estructura del hábitat y el cambio climático afectarán a los niveles tróficos más altos dentro de los agroecosistemas? De manera que, la tesis se separó en tres partes generales. La primera parte incluye estudios basados en la relación de la abundancia con la función ecosistémica (control biológico), enfocándose en la interacción entre enemigos naturales, herbívoros, agroecosistemas, hábitats semi-naturales y paisajes (Capítulos 1 a 4). La segunda parte se enfoca en los roles e interacciones tróficas entre enemigos naturales y herbívoros (Capítulos 5 y 6). Y la tercera parte se enfoca en la respuesta de los enemigos naturales a un escenario de cambio climático global (Capítulo 7).

Los resultados generados aquí sugieren que (1) los hábitats semi-naturales contribuyen al establecimiento de diferentes gremios de enemigos naturales (EN) afectando positivamente el movimiento y la abundancia de EN hacia el cultivo; (2) la abundancia de EN clave es afectada por la complejidad del hábitat siendo influenciados de manera diferente por la riqueza y el arreglo y esparcimiento de las plantas; (3) el establecimiento de cubiertas vegetales afecta positivamente a los EN clave y promueve el control biológico de los herbívoros especialistas (HE) por medio de la depredación de huevos; (4) la composición y configuración del paisaje afectan a la abundancia de EN clave y la depredación, así como a la abundancia de HE y el daño al cultivo, por lo que los paisajes diversos con bordes densos reducen a los HE adultos y la proporción de matorral disperso en el paisaje puede ser el factor principal que promueva el control biológico; (5) la madurez de la cubierta vegetal afecta positivamente la estructura y complejidad de la red trófica de la copa del olivo y promueve el establecimiento de EN clave relacionados con los hábitats naturales; (6) el rol trófico de las hormigas omnívoras muestra un perfil isotópico de depredador más que ser un híperdepredador, por lo que pueden ser consideradas como un EN; y (7) bajo

un escenario de cambio climático global, los depredadores (larvas) expresan plasticidad fenotípica y una regulación a la baja en su metabolismo, no obstante la endogamia reduce el potencial de la plasticidad térmica, y por consiguiente su capacidad evolutiva, cuando los individuos depredadores son sometidos a estrés térmico durante la ontogenia expresando así compensaciones y limitaciones para mejorar su supervivencia.

General Introduction

A service from the ecosystem

In ecology, it can be considered that a set of living organisms and a set of abiotic factors structure ecosystems across space and time (Holling, 1992; Riser, 1995). Ecosystems are inherently dynamic and interact across spatial scales (Holling, 1992; Riser, 1995), so the structure and processes within ecosystems and their spatiotemporal variability encompass the ecosystem properties, e.g., soil features, biomass production, nutrient cycles, or biodiversity (Bastian et al., 2012). Thus, ecosystems (natural or managed) can support a variety of services that, actively or passively, can provide human well-being, namely ecosystem-services (Daily et al., 2000; Fisher et al., 2009).

Indeed, ecosystem-services are actually ecosystem processes or functions based on ecosystem properties. If one takes into account that within ecosystems populations are “naturally controlled” by other organisms (natural control, Thompson, 1965) via trophic guilds across food chains, then humans can exploit such a feature aiming to reduce populations of detrimental organisms related to human activities (e.g., agriculture), hence, biological control.

Biological control is characteristic of agroecosystems, commonly used to reduce or maintain herbivores or weeds (pests) by their natural enemies, i.e., predators, parasitoids, or infectious agents (DeBach, 1964). By control it is meant maintaining the population of a detrimental organism below the numerical level at which it begins to cause measurable economic damage. Though, there are three forms of biological control: classical, augmentative, and conservational. For our purposes, here I will focus on conservation biological control.

Natural enemies and the “natural habitat problematic”

Conservation biological control aims to exploit the functions of natural enemies of a given ecosystem and landscape by restoring or maintaining natural and semi-natural habitats (i.e., cropland boundaries-hedges, ground covers, floral stripes, fallows, grasslands, woodlands, wetlands, scrublands, or forests) near or within agroecosystems to provide places in which natural enemies can feed, overwinter, or complete their life cycles (Tscharrntke et al., 2012; 2016). We the ecologists and conservationists commonly bet for the conservation of natural and semi-natural habitats and appreciate their

contribution to biodiversity and potential ecosystem-services in human dominated landscapes. For example, there is sufficient scientific evidence suggesting that, overall, semi-natural habitats provide great benefits to enhance ecosystem-services in agricultural landscapes (Tscharntke et al., 2012). Indeed, Bianchi et al. (2006) proposed a hypothesis relating the presence of semi-natural habitats with the abundance of natural enemies in an agroecosystem. This hypothesis suggests that complex low-fragmented landscapes with a high proportion of semi-natural habitats boost the populations of natural enemies within agroecosystems and therefore enhance biological control reducing herbivores abundance (Bianchi et al., 2006; Rusch et al., 2010). Thus, there is the notion that the higher the abundance of natural enemies, the higher the biological control.

However, despite that great amount of studies have showed that the presence of semi-natural habitats indeed increase the richness and abundance of natural enemies, recent accounts showed that these habitats may fail to support biological control, which relies on the type of crop, detrimental-organism, natural enemy, land management, and landscape structure in the area of study. Moreover, it suggests that a higher abundance of natural enemies does not always suppress herbivore abundance and damage (Karp et al., 2018; Rusch et al., 2010; Tscharntke et al., 2016). This is, amongst other factors, due to (1) natural enemies may not disperse from natural and semi-natural habitats; (2) natural and semi-natural habitats may provide a more suitable environment for a large number of herbivore species at several key stages of their life cycles; or (3) herbivore density may be driven by factors other than biological control, such as environmental conditions, crop susceptibility, agricultural practices, adjacent growing areas, or intraguild predation (Tscharntke et al., 2016).

In order to enhance conservation biological control, it is important to focus on the ecological processes that underlie such an ecosystem-service. As terrestrial habitats, which are part of a given ecosystem, are structured at their base commonly by plants (amongst other primary producers), some studies have showed that changes in primary and secondary consumer communities (abundance and richness) may be driven by changes in the number of plant species and/or changes in plant community composition (usually associated with changes in plant diversity). From a “biodiversity-ecosystem function” point of view, plant richness produces a positive relationship with ecosystem function, although some researchers argue that it is the underlying diversity of functional traits amongst species present, not the number of taxonomic units, the driver of such a relationship (Hooper et al., 2005; Flynn et al., 2009). Thus, plant functional groups, i.e., groups of species that differ in physiology,

phenology, and morphology, and plant functional groups composition within a habitat, must be considered in biological control studies. For example, greater diversity of plants provides a diversity of resources for insects, especially for the specialist herbivores, and thus, this must support a higher diversity of predators and parasitoids (Knops et al., 1999). Nonetheless, herbivore insects should respond to plant functional groups composition due to two reasons: (1) tissue quality and plant resource use, and (2) similarities in plant taxonomy, i.e., insect abundance respond to plant functional groups due to its form of feeding and its status as specialist within a plant genus or family (Haddad et al., 1999). Therefore, the type of plants within a given habitat (and consequently within the agroecosystem) should determine the amount of biological control in agroecosystems.

Climate change and trophic interactions

To date, it is undeniable that global temperatures are increasing, and thus, global climate change mediated by human activity is a real process (Harvey et al., 2020; Thompson et al., 2012). This is, the increasement of temperatures associated with more frequent, stronger, and rapid events of climate extremes in a very short period of time (geological time scale). So, species subjected to continuous temperature extremes may not adapt well in a short time scale. However, animals can exploit the thermal diversity of their microhabitats to avoid thermal extremes, and thus, the role of natural and semi-natural habitats appears to be paramount for natural enemies in such a scenario. There is evidence that temperature extremes can affect trophic networks and trophic interactions (Harvey et al., 2020). Accordingly, it is known that the sensitivity of species to high temperatures increases with trophic level (Voigt et al., 2003), and natural enemies such as predators, parasitoids, or hyper-predators and hyper-parasitoids will be more affected than herbivores, hence affecting biological control (Harvey et al., 2020; Thompson et al., 2012). Therefore, predicting how animal populations will respond to warming temperatures, and thus global climate change, is amongst the most pressing challenges in current ecology.

Organic olive orchards

Olea europaea L. is a small, slow-growing, long-lived evergreen tree (8 - 15 m), with a large trunk, which develops multiple branches with cascading twigs. As a thermophile species is adapted to tolerate drought and salinity stress, growing on a wide range of soils, with a preference for sandy loam soils of moderate depth. Typical from the Mediterranean basin, it is found to

inhabit in places with continental Mediterranean climate (warm, dry summers and rainy, cool winters) up to 2000 m.a.s.l. Native from minor Asia, the *O. europaea*, as a tree crop spread from the eastern Mediterranean basin to the west of Europe reaching Greece, Italy, France, Spain, and Portugal.

This species is wind-pollinated, commonly helped by bees and hoverflies, and spread by bird-dispersed seed.

It is an economic important plant species, of which it can be harvested olives fruits, olive oil, and wood. Mediterranean countries produce more than 70 % of the total world supply of olive oil, and near 95 % of the European production is concentrated in Spain, Italy and Greece.

The organic management of agroecosystems has been increasing in the Mediterranean region. In Europe this type of management frequently involves abandoning the use of chemical supplies, herbicides, and pesticides (with some exceptions) using natural agents for controlling detrimental-organisms, but if wanted it also involves the establishment of ground covers within the orchard and the conservation and restoring of adjacent semi-natural habitats (Boller et al., 2004; Landis et al., 2005; Malavolta and Perdakis, 2018), all in accordance to the policies currently being implemented by the European Union (IOBC, 2012).

Interestingly, the increase in modern demand for organic food and economic subventions encourages olive producers to start managing olive orchards in an organic manner (Alonso Mielgo et al., 2001; Torres-Miralles et al., 2017), and thus, the proportion of organic olive orchards has increased exponentially. So, the need for a better understand of this agroecosystem in the most natural conditions is paramount.

Thesis outline

The production of this thesis was motivated by a central question within biological control theory: what and where are the natural enemies of herbivores? Whereas this question may seem simple, its answer relies on a myriad of factors which suppose a great amount of human and economic investment for its research. Moreover, one current ecological question drives the objectives of this thesis, which is, how habitat structure and climate change will affect higher trophic levels within managed ecosystems? Though, through the next seven chapters I will try to answer such questions for the specific case of the organic olive orchards in Mediterranean areas.

The thesis was separated into three general parts. The first part comprise studies based on the relation of abundance and ecosystem function (biological control), with focus on the interaction amongst natural enemies, herbivores, agroecosystems, semi-natural habitats, and landscapes (Chapters 1 to 4). The second part focus on the trophic roles and trophic interactions amongst natural enemies and herbivores (Chapters 5 and 6). And the third part focus on the response of natural enemies to a scenario of global climate change (Chapter 7).

In Chapter 1 it was aimed to establish the effects that plants as individual species and as habitat assemblages have on the abundance, presence, and movement of natural enemy trophic guilds.

- (1) Different semi-natural habitats will contribute to the establishment of different guilds of natural enemies.
- (2) The higher the complexity of a habitat the higher the abundance of arthropods and natural enemy guilds.

In Chapter 2 it was evaluated the influence of plant structure, plant richness, and plant attraction on the natural enemies and pollinators, in olive trees and semi-natural habitats.

- (1) Natural enemies respond to the level of plant richness and plant arrangement and scattering in semi-natural habitats.
- (2) Habitat complexity modulates the type of natural enemies found in semi-natural habitats.

The Chapter 3 focus on the function provided by semi-natural habitats to biological control, it was investigated the effectiveness of the biological control of herbivores (i.e., *Prays oleae*) by means of egg predation.

When a ground cover is mowed in orchards surrounded by natural vegetation:

- (1) Key taxa of natural enemies would be positively affected.
- (2) The biological control of *P. oleae*, by means of egg predation, would increase.

Chapter 4 aims to further extend the knowledge of species–environment relationships in organic olive orchard landscapes, assessing which vegetation within semi-natural habitats is the best ecological infrastructure to avoid herbivore pressures (i.e., *Prays oleae*) and increase biological control at the landscape scale.

- (1) What effects are produced by semi-natural habitats when they are divided into specific cover categories?
- (2) Is the patch configuration of such categories an important factor in the landscape?
- (3) How do these effects vary at different spatial scales of study?

In Chapter 5 it was assessed the effects of maturity of semi-natural habitats on the trophic network of the olive canopy, especially the natural enemies at two periods of time separated by more than 10 years.

- (1) The presence of mature ground covers will increase the diversity of arthropods in olive orchards
- (2) The maturity of a ground cover will affect the structure and complexity of the olive canopy trophic network
- (3) The maturity of a ground cover will favour the establishment of natural enemies into the olive canopy

Chapter 6 aims to disentangle the trophic function of natural enemies in olive orchards assessing, within omnivory, whether natural enemies (i.e., ants) could be predators or hyper-predators, and therefore if ants are beneficial organisms or not, by using stable isotopes analysis.

- (1) Ant isotopic signature will vary across diets and locations.
- (2) Ants will reflect a predator signature rather than a herbivore or a hyper-predator one.

Finally, Chapter 7 aims to assess within population genetic variance produced by endogamy in the functional traits, metabolic rate allometries, and survival of natural enemies (i.e., green lacewings) estimating the effects of temperature rising on a transgenerational thermal acclimated population based on the A1B scenario of the United Nations.

- (1) Are thermal extremes modifying the metabolic rates of green lacewings larvae?

- (2) Are green lacewing larvae maintaining or modifying their metabolism under thermal extremes, and if so, will there be counteracting costs to deal with this?
- (3) Is survival of green lacewing larvae inherently affected by thermal extremes and metabolism?

General Methodology

In this thesis it was used two approaches. Firstly, from Chapter 1 to 5 a field approach was used, the studies were conducted in organic olive orchards located in the province of Granada, southern Spain. Olive orchards were selected based on (1) the presence of patches of adjacent vegetation, and (2) the use of mowing techniques and no herbicides, maintaining the ground cover. Efforts were focused on collecting samples of arthropods (1) in the most abundant and recognizable (blossom) plant species within adjacent vegetation and ground cover, and (2) in the canopy of the olive trees. Samples in this study were collected, weather permitting (once a month) from May to July, which are the months of highest arthropod abundance. The differences in species composition in both adjacent vegetation and ground cover, and the structure of the adjacent vegetation were also recorded and used to establish different gradients at habitat and landscape scale. Difference in arthropod abundance was subjected to several analyses to determine habitat complexity effects, landscape scale effects, and trophic interactions. Secondly, for Chapter 6 and 7 a laboratory approach was used. In Chapter 6 it was collected nests inhabiting olive orchards and produced a rearing protocol and diet experiments. It was compared the isotopic signature of ants feeding on natural diets, experimental diets in the laboratory across a gradient of time, and natural diets of ants inhabiting natural habitats and olive orchards with different agricultural managements. Then, it was contrasted the results with ant foraging surveys. In Chapter 7 it was assessed within population genetic variance produced by endogamy in the (a) functional traits, (b) metabolic rate allometries, and (c) larvae survival of green lacewings through a series of experiments at different temperatures based on the A1B scenario of global warming. The collection and rearing of *Chrysoperla* lacewings were established to produce endogamic and exogamic genetic lines from 5 generations. Then larvae were subjected to three different experiments with different temperatures based on maximum temperatures and 1.8°C surpassing maximum temperatures. Then overall effect of warming temperatures, estimations of the variance in the intercepts and slopes of the allometric relationships of metabolic rates, and effects of warming temperatures on the survival and its interaction with functional traits, were analysed.

Part One:

Abundance and Function

Chapter 1

Semi-natural habitat complexity affects abundance and movement of natural enemies in organic olive orchards

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Abstract

Olive orchards have been shown to be able to improve the abundance of natural enemies due to the establishment of adjacent vegetation and ground cover in recent years. Yet evidence regarding the positive effects that such semi-natural habitats provide to the presence and movement of the trophic guilds of the arthropod community is lacking. In this study we assess the effects that plants, both as individual species and as semi-natural habitat assemblages, have on the abundance, presence, and movement of the arthropod community in organic olive orchards. We collected 97 families of arthropods from the canopy of olive trees and the foliage of plants in the ground cover and adjacent vegetation. We analysed the data in relation to habitat complexity. Our results show that the abundance of natural enemies is higher in areas with more complex semi-natural habitats. Parasitoids were able to colonize the olive trees, irrespective of the area or type of vegetation. Predators and parasitoids occurred in the ground cover and adjacent vegetation, but not in the orchard. The adjacent vegetation mainly acted as an important sink for natural enemies when the ground cover withered in June-July, and thus, ground cover and adjacent vegetation may serve as a source of parasitoids and predators for colonizing olive trees. Overall, the density of the natural enemies in organic olive orchards is better enhanced by

complex stands of ground cover and natural adjacent vegetation, which gives support to the complex-habitat hypothesis.

Introduction

Agroecological theory suggests that semi-natural habitats provide food and shelter to natural enemies of insect pests (Altieri, 1999, 2000; Tscharntke et al., 2012, 2016; Wan et al., 2018a). It has been suggested that some natural enemies (i.e., arthropods) respond negatively to the presence of semi-natural habitats (Karp et al., 2018), which is a problem in conservation biological control. A positive or negative response shown by an organism to a nearby habitat could be driven by the structure of such a habitat (Laurance, 2007; López-Barrera et al., 2007; Broadbent et al., 2008; Balmford et al., 2012; Álvarez et al., 2016, 2017a; Wan et al., 2019). Indeed, arthropod richness responds negatively to fragmentation and disturbance (Hogsden and Hutchinson, 2004; Dallimer et al., 2012) but arthropod abundance has complex and controversial patterns (Ries and Sisk, 2004), which are conditioned by factors related to landscape complexity (Rusch et al., 2010; Tscharntke et al., 2012, 2016). Bianchi et al. (2006) proposed a hypothesis relating the presence of semi-natural habitats with an abundance of natural enemies in an agroecosystem. This hypothesis (hereafter referred to as the complex-habitat hypothesis) suggests that complex low-fragmented landscapes with a high proportion of semi-natural habitats boost the populations of natural enemies within agroecosystems (Bianchi et al., 2006; Rusch et al., 2010).

In perennial crops, controversial results have been reported about the effects of semi-natural habitats on the abundance of natural enemies. For example, some studies have reported an increase in abundance (Danne et al., 2010; Silva et al., 2010; Karp et al., 2018; Wan et al., 2014a, 2014b, 2018b), whereas others have reported no effects (Costello and Daane, 1998; Bone et al., 2009; Karp et al., 2018). In olive orchards recent studies have suggested an improvement in the abundance of natural enemies due to the presence of ground cover and adjacent vegetation in and around orchards (Ruano et al., 2004; Paredes et al., 2013a; Gkissakis et al., 2016; 2018). Indeed, landscape structure and the management of the ground cover positively affect the abundance and variability of natural enemies (Gkissakis et al., 2016; Villa et al., 2016). However, the synergy between both habitats may have an important role in predicting the type of organisms that can be found in an olive tree (Paredes et al., 2013a, 2013b). Thus, an increase in natural enemy abundance would reduce populations of herbivore insects.

Despite the efforts of different authors to assess the effects of ground cover and adjacent vegetation on natural enemies and olive pests (Paredes et al., 2013a; Jiménez-Muñoz et al., 2017; Manjón Cabezas Córdoba et al., 2017; Villa et al., 2016a; 2016b; Porcel et al., 2017; Gkissakis et al., 2016, 2018), to the best of our knowledge there is no study that has focussed on the abundance, presence, and movement of the overall arthropod community in both habitats and their interaction with olive orchards. This point of view is of great importance because, unlike insect pests, natural enemies require a non-crop environment at one or more stages of their life cycle (Keller and Häni, 2000; Rusch et al., 2010). Furthermore, spill over is based on the ability of organisms to move between vegetations, which is driven by the trophic level (i.e., organisms at higher trophic levels operate at a larger spatial scale, Holt, 1996) and body size (Tscharntke et al., 2005).

Empirical data are needed to understand the interaction amongst ground cover, adjacent vegetation, and all types of olive orchards. However, this study just focuses on organic olive orchards. A decision motivated by (1) the need to understand the system in the most natural conditions, (2) the increase in modern demand for organic food, and (3) the policies currently being implemented with the aim of restoring native habitats (e.g., the European Union, IOBC, 2012), which encourages producers to start managing olive orchards in an organic manner (Alonso Mielgo et al., 2001; Torres-Miralles et al., 2017). The aim of this study is to establish the effects that plants as individual species and as habitat assemblages i.e., ground cover and adjacent vegetation, have on the abundance, presence, and movement of the arthropod community, especially the guilds of natural enemies, in organically managed olive orchards.

Material and methods

Study area

The study was conducted in organic olive orchards (186.45ha, Fig. 1), located in the province of Granada, southern Spain. Olive orchards were selected based on (1) the presence of patches of adjacent vegetation, and (2) the use of mowing techniques and no herbicides, and thus maintaining the ground cover for at least three consecutive years (Fig. A1.1 of supplementary data in Appendix). Four patches of adjacent vegetation (study areas) were found amongst three olive orchards: three patches in the locality of Piñar (37°24'N and 3°29'W) and one in the locality of Deifontes (37°19'N and 3°34'W).

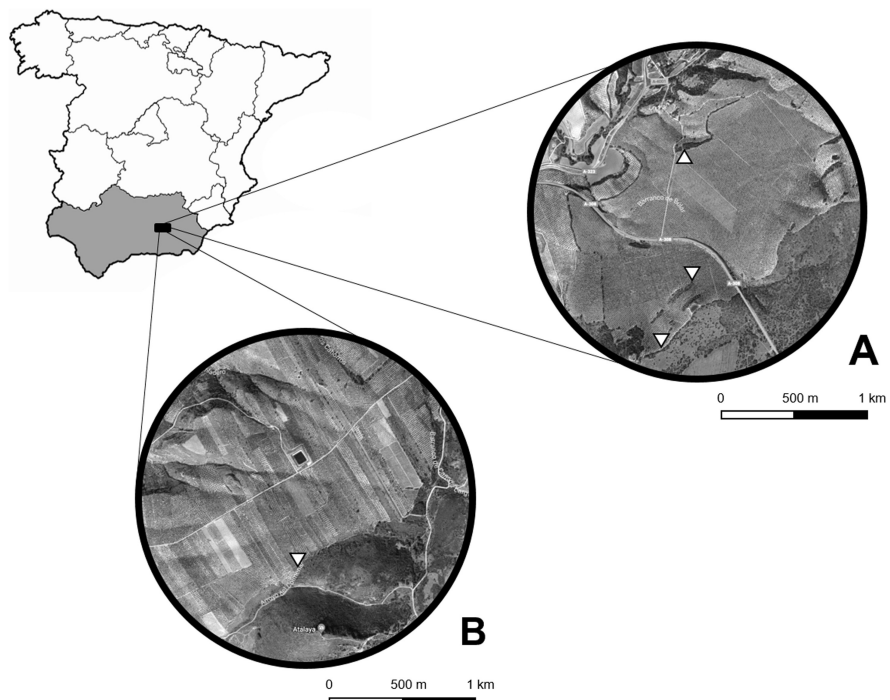


Figure 1. Location of the study areas in southern Spain. Distribution of the patches of adjacent vegetation (triangles) in Piñar (A) and Deifontes (B).

Bacillus thuringiensis was sprayed in randomly selected sections (but not all the area) in July. This was used as a preventive pest control for the carpophagous generation of *Prays oleae* (larvae) Bern (Lepidoptera: Plutellidae) in the orchards of Piñar. Climatic conditions for the hydrological year of 2014 – 2015 in the region were: 16.0 °C mean annual temperature, 31.9 °C – 15.9 °C mean maximum and minimum temperatures from May to July, and 429.6 mm mean annual precipitation. In this area the main insect pest that damages olives is the olive moth, *Prays oleae* (Red de alerta e Información fitosanitaria de Andalucía (RAIF, 2018), which is widely distributed in the circum-Mediterranean region (Tzanakakis, 2006).

Plant composition and structure

Eight plant species were abundant in the adjacent vegetation: *Cistus albidus* L., *Prunus dulcis* (Mill.) D. A. Webb, *Quercus rotundifolia* Lam., *Retama sphaerocarpa* (L.) Boiss., *Rosmarinus officinalis* L., *Thymus mastichina* (L.) L., *Thymus zygis gracilis* (Boiss.) R. Morales, and *Ulex parviflorus* Pourr. Six species of

herbaceous plants were found in the blossom period in the ground cover: *Anacyclus radiatus* Loisel, *Centaurea melitensis* L., *Diplotaxis catholica* (L.) DC., *Erodium cicutarium* (L.) L'Hér, *Leontodon longirostris* (Finch & P.D. Sell) Talavera, and *Senecio vulgaris* L. The structure of the vegetation within the patches showed differences. In Piñar 1 (PI-1) and Piñar 2 (PI-2) the structure was similar, plants were distributed and scattered all over the patches, but the plants in PI-1 were gathered in clusters of vegetation. Conversely, in Deifontes (DEI) most of the patch was occupied by two tree species and the rest of the species were gathered in one cluster of vegetation. Finally, Piñar 3 (PI-3) was occupied mostly by one species. Table 1 summarizes plant species composition and the structure of the semi-natural habitats in the study areas.

The differences in species composition in both adjacent vegetation and ground cover, and the structure of the adjacent vegetation (Table 1) were used to establish a qualitative gradient of complexity. We arranged the study areas from most to least complex as: PI-2, PI-1, DEI and PI-3.

Specimen collection and sampling design

We focussed our efforts on collecting samples of arthropods (1) in the most abundant and recognizable (blossom) plant species within adjacent vegetation and ground cover, and (2) in the canopy of the olive trees. Our experimental unit (sample) was a suction plot that was a 30 s-suction in a 50 × 50 cm surface of plant foliage. We used a modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA). This method allows us to standardize sampling amongst different types of plants (i.e., herbaceous, shrubs, and trees) (Fig. A1.2 of supplementary data in Appendix).

Samples in this study were collected, weather permitting (once a month) from May to July 2015, which are the months of highest arthropod abundance (Ruano et al., 2004; Santos et al., 2007a). We collected 20 randomly distributed samples per plant species, depending on plant species availability (Table 1). In addition, in order to test edge effects between adjacent vegetation and the olive trees, we collected 40 randomly distributed samples in the olive trees per patch of adjacent vegetation. These samples were taken in trees near to the adjacent vegetation (edge trees) and trees far from the adjacent vegetation near to the centre of the orchard (inner trees) (20 samples per section). The edge trees had a separation of 550 m from the inner trees (approximately). The samples were stored individually and maintained at -20°C until the specimens were classified.

Table 1. Plant species composition and structure in the four study areas of organic olive orchards: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). Plant species in adjacent vegetation: *C. albidus* (Ca), *P. dulcis* (Pd), *Q. rotundifolia* (Qr), *R. sphaerocarpa* (Rs), *R. officinalis* (Ro), *T. mastichina* (Tm), *T. z. gracilis* (Tzg), *U. parviflorus* (Up). Plant species in ground cover: *A. radiatus* (Ar), *C. melitensis* (Cm), *D. catholica* (Dc), *E. cicutarium* (Ec), *L. longirostris* (Ll), *S. vulgaris* (Sv).

Site	Plant species composition		
	Adjacent vegetation	Ground cover	Patch structure
DEI	Qr - Rs - Ro - Tzg - Up - Ca - Pd - Tm	Ll - Dc - Cm - Ec - Sv	Dominated by Qr and Pd, others gathered in one cluster
PI-1	Qr - Rs - Ro - Tzg - Up	Ll - Dc - Ar	Gathered into clusters
PI-2	Qr - Rs - Ro - Tzg - Up	Ll - Dc	All scattered
PI-3	Qr - Rs	Ll	Dominated by Qr

The arthropods were identified to family level, unless otherwise specified, and classified by trophic guilds i.e., omnivore, parasitoid, predator (natural enemies) and specialist olive pests. The families that were identified as neither natural enemies nor pests were gathered together in a group named neutral arthropods (Wan et al., 2014a). Guild classification was based on literature data (see Table A1.1 of supplementary data in Appendix, also available at <https://doi.org/10.1016/j.agee.2019.106618>). Raw sample data was used to conduct analyses.

Differences in arthropod abundance

Arthropod abundance was analysed by comparing the study areas and the types of vegetation, for which several generalised linear models (GLMs) were constructed using “quasi-likelihood” with Poisson-like assumptions (quasi-Poisson) tendency (for justification on this approach see Ver Hoef and Boveng, 2007). Firstly, to compare (1) overall arthropod abundance, (2) total abundance of natural enemies (i.e., omnivores, parasitoids, and predators together), and (3) abundance of omnivores, parasitoids, and predators, we fitted models including abundance as the dependent variable and type of vegetation and study area as factors. Secondly, to compare the total abundance of natural enemies amongst plant species, we fitted a model including abundance as the dependent variable and the plant species and study area as factors. In all the GLMs the sampling date was controlled using the month as a factor. Further differences between the groups in each model were tested using analyses of deviance and the Tukey *post hoc* (contrasts) test. The R software v 3.5.0 (R Developmental Core Team, 2018) was used to

compute all the analyses. Tukey test was computed using the “multcomp” package (Hothorn et al., 2008).

Arthropod presence and movement

To understand and visualize differences in abundance amongst the study areas and the types of vegetation, multivariate techniques were used. Family level abundance was pulled together by the type of vegetation per month in each study area, and then it was subjected to principal component analysis (PCA) in R software v 3.5.0 (R Developmental Core Team, 2018). We analysed the interrelation between the abundance of all the trophic guilds and the type of vegetation in each study area (per month), by using a correspondence analysis (CA) approach (Greenacre, 2013). CA was used to describe the movement of arthropods across the vegetation by direct effects of abundance on ordination. This was achieved by introducing categorical data of presence in each type of vegetation and ID data of each trophic guild. Then, abundance scores were used to weight the data. One of the goals of CA is to describe the relationships between two nominal variables in a low-dimensional space, whilst describing the relationships between the categories for each variable. CA as an eigenvector technique also weights sites and organisms (using Chi-square metrics) by their totals in eigen analysis (Legendre and Gallagher, 2001; Greenacre, 2013). CA was carried out in SPSS software v 19 (IBM Corp., 2010).

Distance with adjacent vegetation

We compared the abundance of each guild of natural enemies (i.e., omnivores, parasitoids, and predators) between inner and edge (olive) trees in the four study areas. A Wilcoxon-Mann-Whitney rank sum test was computed, using the data of the three months together, in R software v 3.5.0 (R Developmental Core Team, 2018).

Results

A total of 7381 individuals were collected in 1856 suction samples. The arthropods were comprised in 12 orders: Araneae, Blattodea, Coleoptera, Diptera, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, Phasmida, Raphidioptera, and Thysanoptera. Table 2 summarizes information regarding the relative abundance and trophic guild for each arthropod family. Overall, 97 families were identified.

Table 2. Relative abundance and trophic guilds of all the families of arthropods ($n = 97$) identified in organic olive orchards and semi-natural habitats.

Name		Guild	Relative Abundance (%)	
Arachnida				
Araneae	Amaurobiidae	Predator	0.041	
	Araneidae	Predator	0.352	
	Dyctinidae	Predator	0.027	
	Linyphiidae	Predator	0.176	
	Mimetidae	Predator	0.014	
	Oxyopidae	Predator	1.016	
	Philodromidae	Predator	0.257	
	Salticidae	Predator	0.379	
	Sicariidae	Predator	0.014	
	Thomisidae	Predator	2.940	
	Uloboridae	Predator	0.339	
	Zodaridae	Predator	0.054	
Insecta				
Blattodea	Blattellidae	Neutral arthropod	0.108	
Coleoptera	Alleculidae	Neutral arthropod	0.095	
	Anthicidae	Neutral arthropod	0.068	
	Apionidae	Neutral arthropod	0.081	
	Cantharidae	Predator	0.041	
	Catopidae	Neutral arthropod	0.068	
	Chrysomelidae	Neutral arthropod	0.975	
	Cleridae	Predator	0.041	
	Coccinelidae	Predator	0.921	
	Curculionidae	Neutral arthropod	1.612	
	Dasytidae	Predator	0.135	
	Dermestidae	Neutral arthropod	0.041	
	Elateridae	Predator	0.014	
	Malachiidae	Predator	0.027	
	Monotomidae	Neutral arthropod	0.014	
	Mycetophagidae	Neutral arthropod	0.014	
	Nitidulidae	Neutral arthropod	0.027	
	Phalacridae	Neutral arthropod	0.718	
	Ptinidae	Neutral arthropod	0.014	
	Scarabaeidae	Neutral arthropod	0.014	
	Staphylinidae	Predator	0.054	
	Dermaptera	Forficulidae	Omnivore	0.014
	Diptera	Agromyzidae	Neutral arthropod	0.027
Asilidae		Predator	0.014	
Bibionidae		Neutral arthropod	0.014	
Bombyliidae		Neutral arthropod	0.108	
Calliphoridae		Neutral arthropod	0.014	
Camillidae		Neutral arthropod	0.135	

	Cecidomyiidae	Neutral arthropod	0.217
	Ceratopogonidae	Neutral arthropod	0.014
	Chamaemyiidae	Predator	0.014
	Chironomidae	Neutral arthropod	0.054
	Chloropidae	Neutral arthropod	0.230
	Dolichopodidae	Predator	0.163
	Empididae	Neutral arthropod	0.095
	Heleomyzidae	Neutral arthropod	0.014
	Limoniidae	Neutral arthropod	0.027
	Muscidae	Neutral arthropod	0.068
	Opomyzidae	Neutral arthropod	0.014
	Phoridae	Neutral arthropod	0.014
	Sciaridae	Neutral arthropod	0.095
	Tephritidae	Neutral arthropod	0.271
Hemiptera	Anthocoridae	Predator	0.122
	Aphididae	Neutral arthropod	18.493
	Berytidae	Neutral arthropod	0.122
	Coccidae	Neutral arthropod	0.312
	Cydnidae	Neutral arthropod	0.014
	Fulgoromorpha	Neutral arthropod	13.887
	Geocoridae	Predator	0.027
	Lygaeidae	Predator (facultative)	0.610
	Miridae	Predator	3.943
	Nabidae	Predator	0.027
	Pentatomidae	Neutral arthropod	0.542
	Psyllidae	Neutral arthropod	14.564
	Rhopalidae	Neutral arthropod	0.339
	Tingidae	Neutral arthropod	0.244
Hymenoptera	Aphelinidae	Neutral arthropod	0.054
	Apidae	Neutral arthropod	0.447
	Bethylidae	Parasitoid	0.149
	Braconidae	Parasitoid	0.528
	Ceraphronidae	Neutral arthropod	0.014
	Chrysididae	Parasitoid	0.014
	Cynipidae	Neutral arthropod	0.027
	Diapriidae	Parasitoid	0.027
	Elasmidae	Parasitoid	0.095
	Encyrtidae	Parasitoid	0.854
	Eulophidae	Parasitoid	0.122
	Eupelmidae	Parasitoid	0.027
	Eurytomidae	Parasitoid	0.041
	Formicidae	Omnivore	22.246
	Ichneumonidae	Parasitoid	0.054
	Mymaridae	Parasitoid	0.068
	Platygastridae	Parasitoid	0.041
	Pompilidae	Neutral arthropod	0.014
	Pteromalidae	Parasitoid	0.406

	Scelionidae	Parasitoid	0.528
Lepidoptera	Plutellidae	Neutral arthropod	0.406
Mantodea	Mantidae	Predator	0.054
Neuroptera	Chrysopidae	Predator	0.434
	Coniopterygidae	Predator	0.027
Phasmatodea	Phasmatidae	Neutral arthropod	0.014
Raphidioptera	Raphidiidae	Predator	0.027
Thysanoptera	Aeolothripidae	Predator	2.642
	Phlaeothripidae	Neutral arthropod	1.057
	Thripidae	Neutral arthropod	4.037

Then, 49 families were classified as natural enemies in three trophic guilds: 2 omnivores, 15 parasitoids, and 32 predators. 2 families were identified as specialist pests of olive orchards, the rest of the families were grouped as neutral arthropods.

Differences in arthropod abundance

Areas and vegetation

The arthropod abundance differed amongst study areas and showed a positive relation with the level of complexity. The study area had a significant effect on the overall abundance ($F_{3,1850} = 8.464$, $p = 0.001$) (Table 3). PI-1 and PI-2 had higher abundance than PI-3 (Tukey test, $p = 0.001$) and DEI ($p < 0.004$) but there were no differences between PI-1 and PI-2 ($p = 0.999$) and between PI-3 and DEI ($p = 0.245$). Secondly, the study area had a significant effect on the abundance of natural enemies (total abundance: $F_{3,1850} = 26.743$, $p = 0.001$), which was similar to the pattern of overall abundance (Fig. 2). However, when separated by guild, this pattern was only significant for omnivores and predators (Fig. 2). Indeed, omnivore abundance showed significant differences ($F_{3,1850} = 27.946$, $p = 0.001$). PI-2 had higher abundance than the rest of the areas (DEI and PI-3, $p = 0.001$; PI-1, $p = 0.002$) but PI-1 had higher abundance than DEI ($p = 0.001$). There were no differences between PI-3 and DEI ($p = 0.86$) and between PI-1 and PI-3 ($p = 0.072$). Likewise, predator abundance showed significant differences ($F_{3,1850} = 3.924$, $p = 0.008$). PI-1 had higher abundance than PI-3 ($p = 0.023$) and DEI ($p = 0.031$) but there were no differences for the rest of the combinations. Conversely, parasitoid abundance was not significantly different amongst the study areas ($F_{3,1850} = 1.341$, $p = 0.259$).

On the other hand, the type of vegetation had a significant effect on the overall abundance ($F_{2,1853} = 60.075$, $p = 0.001$) (Table 3). Ground cover had higher arthropod abundance than adjacent vegetation (Tukey test: $p =$

0.001) and olive trees ($p = 0.001$) but there were no differences between adjacent vegetation and olive trees ($p = 0.589$). The type of vegetation also had a significant effect on the abundance of natural enemies ($F_{2,1853} = 70.737$, $p = 0.001$) (Table 4). When separated by guild, omnivore abundance showed significant differences ($F_{2,1853} = 25.149$, $p = 0.001$). Olive trees had lower omnivore abundance than the adjacent vegetation (Tukey test: $p = 0.001$) and ground cover ($p = 0.001$) but there were no differences between adjacent vegetation and ground cover ($p=0.154$). Significant differences were found though in the same pattern for both parasitoid abundance ($F_{2,1853} = 11.672$, $p = 0.001$) and predator abundance ($F_{2,1853} = 105.615$, $p = 0.001$). Ground cover had a higher abundance of parasitoids and predators than the adjacent vegetation ($p = 0.001$) and the olive trees ($p < 0.027$) but there were no differences between the adjacent vegetation and the olive trees (parasitoids, $p = 0.047$; predators, $p = 0.138$).

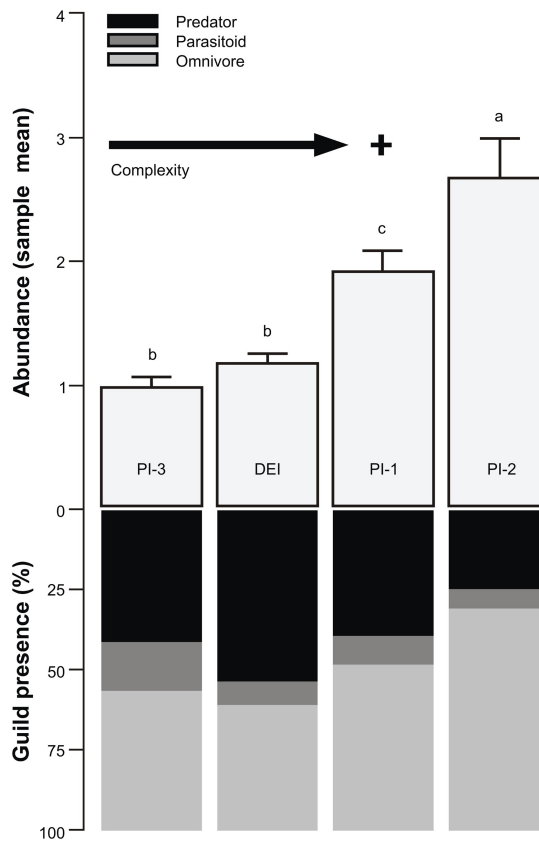


Figure 2. Overall abundance of natural enemies amongst study areas. Mean sample ($n = 1\ 856$), standard deviation, and percentage of guild presence in each study area: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). Study areas are arranged from most to least complex.

Plant species

Plant species had a significant effect on the abundance of natural enemies (total abundance: $F_{14,1841} = 16.428$, $p = 0.001$) (Fig. 3). Firstly, *O. europaea* had a lower abundance than the shrubs *C. albidus*, *R. officinalis*, *R. sphaerocarpa*, *T. mastichina*, and *T. z. gracilis* and the herbaceous plants *A. radiatus*, *D. catholica*, *L. longirostris*, and *S. vulgaris* (Tukey test: $p < 0.037$). These herbaceous plants had the highest abundance of natural enemies. Secondly, *Q. rotundifolia* had a lower abundance than *A. radiatus*, *C. albidus*, *D. catholica*, *L. longirostris*, *R. sphaerocarpa*, *S. vulgaris*, and *T. z. gracilis* ($p < 0.018$). On the other hand, *L. longirostris* had a higher abundance than *P. dulcis*, *R. officinalis*, *R. sphaerocarpa*, *T. z. gracilis*, and *U. parviflorus* ($p < 0.020$). Finally, *A. radiatus* and *D. catholica* had a higher abundance than *R. officinalis* and *U. parviflorus* ($p = 0.001$). Overall, almost all the species in adjacent vegetation and ground cover had high abundances of the three natural enemies guilds compared with those found in the olive trees. Four species of herbaceous plants contributed to the increase of predator abundance in ground cover more than the other guilds (Fig. 3). Moreover, all the shrub plants contributed to the increase of omnivore abundance in adjacent vegetation (Fig. 3).

Table 3. Descriptive statistics of overall arthropod abundance compared in GLM analyses amongst types of vegetation and study areas: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3).

Type	Type of vegetation		
	Adjacent	Ground cover	Olive
NE Total	1.57 ± 5.00	3.75 ± 5.49	0.68 ± 1.13
Omnivore	1.01 ± 4.61	1.42 ± 4.23	0.26 ± 0.69
Parasitoid	0.06 ± 0.41	0.27 ± 0.61	0.14 ± 0.46
Predator	0.39 ± 1.18	2.05 ± 3.46	0.27 ± 0.67

Table 4. Descriptive statistics of abundance (Mean ± SD) of natural enemy (NE) guilds compared in GLM analyses amongst types of vegetation.

	Mean	SD
Deifontes	3.74	8.72
Piñar 1	4.73	12.65
Piñar 2	5.11	9.83
Piñar 3	2.25	2.48
Adjacent vegetation	3.09	10.03
Ground cover	9.45	12.34
Olive	3.20	3.42

Arthropod presence and movement

The PCA showed that the difference between the study areas was explained by the variance of overall arthropod abundance in the ground cover of DEI and PI-1, and the adjacent vegetation of PI-2 (Fig. 4). 49.31% of the variance was explained by PC1, and 39.40% by PC2. The families that showed the highest loadings in variance were Aphididae, Formicidae, Fulgoromorpha, Miridae, Psyllidae, and Thripidae. Accordingly, Aphididae, Fulgoromorpha, Miridae, and Thripidae contributed mainly to the variance of ground cover, Formicidae to adjacent vegetation and Psyllidae to olive trees (Fig. 4).

Fig. 5 shows the results of 12 correspondence analyses (CAs) separated by months for each study area. It represents a pattern of increase or decrease in abundance (that can be interpreted as movement) in the three types of vegetation, which includes all the guilds of arthropods in a low dimensional space. This separation was made in order to simplify the tendencies in the data. Overall, the CAs showed that dimension one explained almost the total of the inertia in all the study areas and months. The CAs showed differences by month and study area. The number of families was higher in May for most of the areas, except for DEI, which had a higher number of families in June. On the other hand, the correspondence between guilds and the types of vegetation presented some tendencies. In May, omnivores were related with adjacent vegetation, and the other guilds were linked with ground cover (except parasitoids in DEI). In June parasitoids were mostly present in the olive trees, and the predators, omnivores and neutrals in adjacent vegetation (except predators in PI-3 and neutrals in DEI). In July most predators, neutrals, and parasitoids were found in the adjacent vegetation (except parasitoids in PI-3) but the omnivores showed no pattern. Finally, in the three months studied the pests were only related with olive trees. Moreover, in almost all the areas the ground cover started to wither in June, and thus by July the ground cover was almost empty of natural enemies. Therefore, the guilds moved across the different types of vegetation. For example (1) the predators moved from ground cover to adjacent vegetation from May to June, with the possibility of moving to the olive trees when the ground cover withered; (2) the omnivores moved from the adjacent vegetation to the ground cover and olive trees in July; and (3) the parasitoids moved from the ground cover to the olive trees from May to June when the ground cover withered (Fig. 6).

Distance with adjacent vegetation

Overall, the abundance of natural enemies within an olive tree was not related with the distance of the trees to the adjacent vegetation. However, only omnivores showed higher abundance within the canopy of the inner trees rather than the edge trees in PI-1 and PI-2 (Wilcoxon-Mahn-Whitney: $W = 1505$, $p = 0.005$; $W = 1385$, $p = 0.005$, respectively).

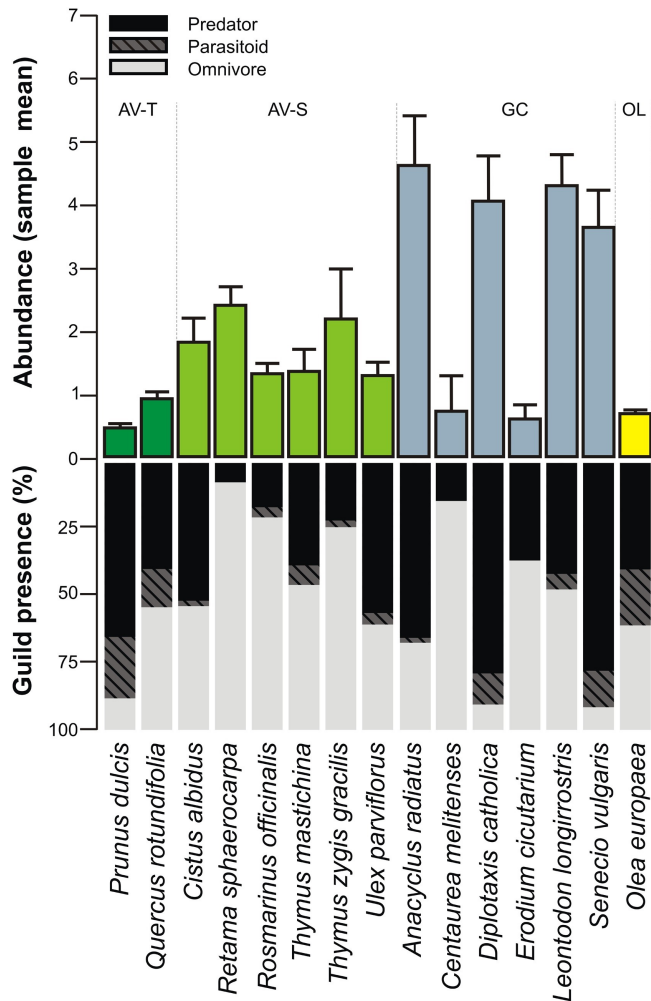


Figure 3. Overall abundance of natural enemies amongst plant species. Mean sample ($n = 1\ 856$), standard deviation, and percentage of guild presence in each plant. Plants are arranged by type of vegetation: ground cover (GC), olive orchard (OL), and adjacent vegetation was separated for more detail in trees (AV-T) and shrubs (AV-S).

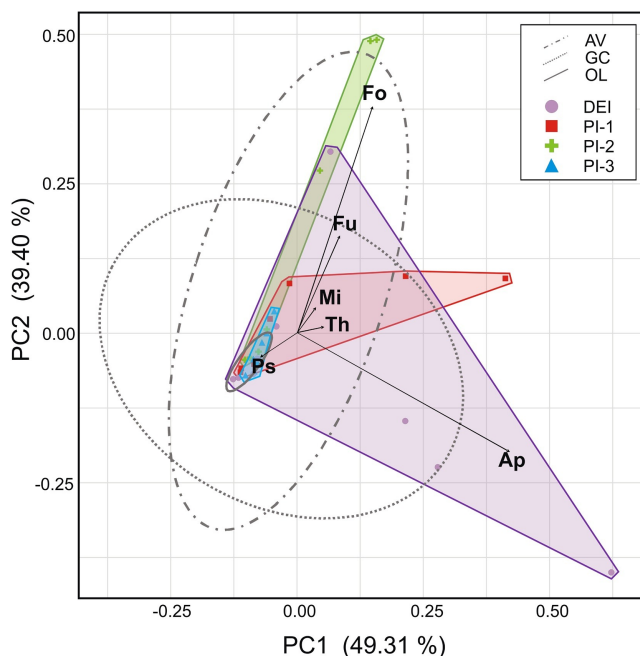


Figure 4. Principal component analysis. Data clustered by study areas: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). The calculated ellipses assume a multivariate t distribution and represent the type of vegetation: adjacent vegetation (AV), ground cover (GC), and olive orchards (OL). Arthropod families: Aphididae (Ap), Formicidae (Fo), Fulgoromorpha (Fu), Miridae (Mi), Psyllidae (Ps), and Thripidae (Th).

Discussion

Habitat complexity

The presence of natural enemies in organic olive orchards, and their relationship with adjacent vegetation and ground cover, correlates with habitat complexity. There is more abundance when semi-natural habitats have high numbers of plant species and plants are arranged and dispersed across the entire area (Fig. 6). This was reflected in the predators and omnivores (Fig. 2). It has been shown that the structure of non-crop vegetation has a direct effect on an enemy's preference for a habitat, specifically, hedgerow plots with mixed plant species have a greater presence of natural enemies than plots with a single species (Campbell et al., 2012; Miñarro and Prida, 2013; Morandin et al., 2014; Cotes et al., 2018). This tendency has also been seen in the ground cover of olive orchards (Gómez et al., 2018). Nonetheless, the difference in plant species composition and structure between our study areas seemed to have no effect on parasitoid abundance (Fig. 6). This could be explained, firstly, by the fact that our sample method is not the optimum for flying hymenopterans, and secondly, because such insects have a wide range of movement (Rusch et al., 2010).

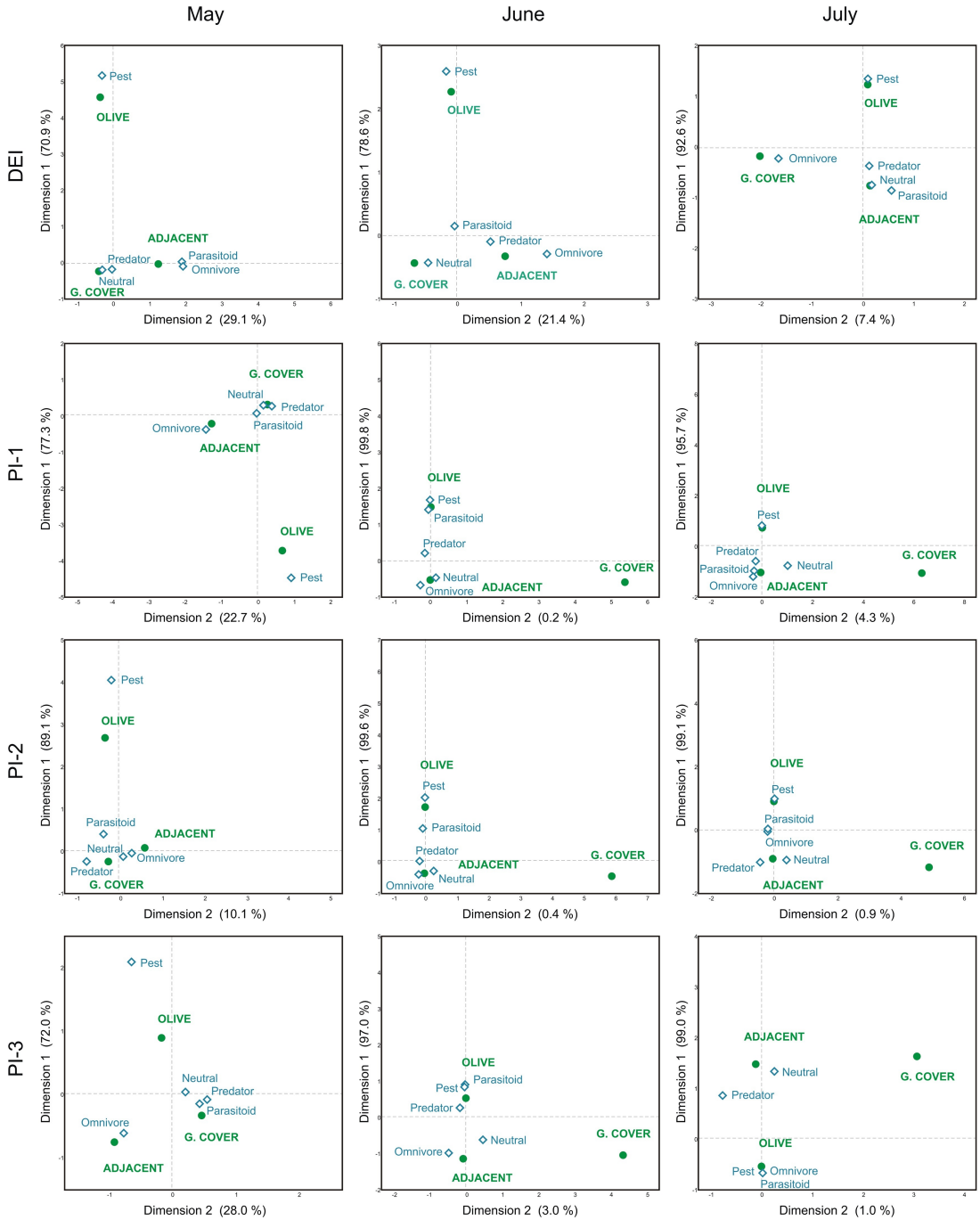


Figure 5. Correspondence analyses. Rhomboids represent overall abundances separated by trophic guilds, circles represent each type of vegetation. Data is presented by month and study area: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3).

Relationship with vegetation

Overall, abundance is affected by the type of vegetation. Most plant species had a higher abundance of natural enemies than the olive trees, although each trophic guild had a specific relationship with a type of vegetation. For example, it is known that parasitoids and some predators greatly benefit from the presence of sources of pollen and nectar inside crops (Wäckers, 2001; Berndt et al., 2006; Winkler et al., 2006; Rusch et al., 2010). In olive orchards this tendency is due to the relationship between floral architecture and insect morphology (Nave et al., 2016), which in some cases increases the parasitism rate (Villa et al., 2016). This could explain why, in our case, the herbaceous plants in the ground cover maintained the presence (percentage) and abundance of parasitoids (Fig. 3). Paredes et al. (2013a) showed, by modelling, that adjacent vegetation positively affected the abundance of parasitoids within the olive orchard, but also that parasitoids had a stronger dependence on herbaceous habitats (i.e., ground cover). In their study, when such habitats were missing the predicted abundance was zero. This pattern is in accordance with our results. Furthermore, Paredes et al. (2013a) showed that parasitoid abundance dropped in July, which matches with the tendencies shown by our CAs in the same month.

It has been reported that alternative prey for predators is of great importance when the enhancement of biological control in agroecosystems is desired (Rusch et al., 2010). For example, some species of predator coccinellids are affected by prey availability in non-crop habitats when their primary source of food is not present, becoming increasingly dependent on alternative sources (Bianchi and van der Werf, 2004; Rand et al., 2006), which can, in some cases, increase their fitness (Rusch et al., 2010). However, the dependence of a natural enemy on alternative prey is greater for a generalist predator than for a specialist predator (Rusch et al., 2010). In our study the predator families were mostly generalists which could explain the differences for the abundance of predators in ground cover.

On the other hand, the adjacent vegetation showed the highest abundance of omnivores, which are mainly represented by the ant family Formicidae. It has been suggested that the formicids which inhabit olive orchards (mainly in Spain) are facultatively predatory, although some genera are mainly granivorous (Redolfi et al., 1999). In this case, such features may drive formicids to establish their colonies in adjacent vegetation, due to the availability of potential sources of food. The tendency of our results, which point out the preference of formicids for adjacent vegetation rather than olive trees, may explain the non-conclusive patterns for the abundance of ants within olive orchards shown in a previous study (Paredes et al., 2013a).

Movement of natural enemies

How arthropod presence and abundance interact with the type of vegetation is an issue to consider. Overall, the patterns of movement appear to be related with the (life-cycle) developmental requirements of each guild of natural enemies. Predators and parasitoids are the guilds that moved the most between the types of vegetation (Fig. 6). From May to July the predators moved mainly from ground cover to adjacent vegetation, but also to the olive trees. This movement is related with the abundance of the neutral arthropods (Fig. 5). There is evidence that the predator *Anthocoris nemoralis* and some chrysopids showed this movement in olive orchards (Plata et al., 2017; Porcel et al., 2017). This pattern suggests that some neutral arthropods may be acting as an alternative source of food for predator insects, thus maintaining the predator population when pests are not available in the olive orchard (Chang and Kareiva, 1999; Ives et al., 2005). This is supported by the tendencies in the abundance of predators (such as Miridae) and phytophagous (such as Thripidae and Fulgoromorpha) shown in our analysis (Fig. 4).

On the other hand, from May to June, but mostly in June, parasitoids moved from ground cover to olive trees, which corresponds with the time that *P. oleae* lay their eggs on young olive fruits (Ramos et al., 1978; 1987) but also when the ground cover starts to wither. This pattern is possibly a consequence of the movement of the specialist parasitoids of olive pests, whose abundance is boosted by ground cover (Rodríguez et al., 2012; Villa et al., 2016).

In July, the omnivores moved from adjacent vegetation to ground cover and the olive trees (Fig. 6). Omnivores are mainly represented here by formicid ants, so this tendency could be a consequence of the large range of movement that formicids may present when searching for food (Plowes et al., 2013) within the olive orchard (Redolfi et al., 1999). Moreover, the movement mainly happened when the ground cover withered (Fig. 5), which may be an effect generated by the resources produced by herbaceous plants. For example, granivorous ants such as *Messor*, tend to put their nests inside the olive orchard and form big paths spreading for great distances. Conversely, facultatively predator ants such as *Tapinoma* and *Crematogaster*, can feed primarily on the honeydew of herbaceous plants but when the abundance of a pest increases they turn to feeding on such a source of food (Cerdá et al., 1989) moving towards it. This pattern increases the role of formicids to control pests within the olive trees, which can be boosted by the nearness of the adjacent vegetation (edge effects). However, this tendency needs to be investigated more thoroughly.

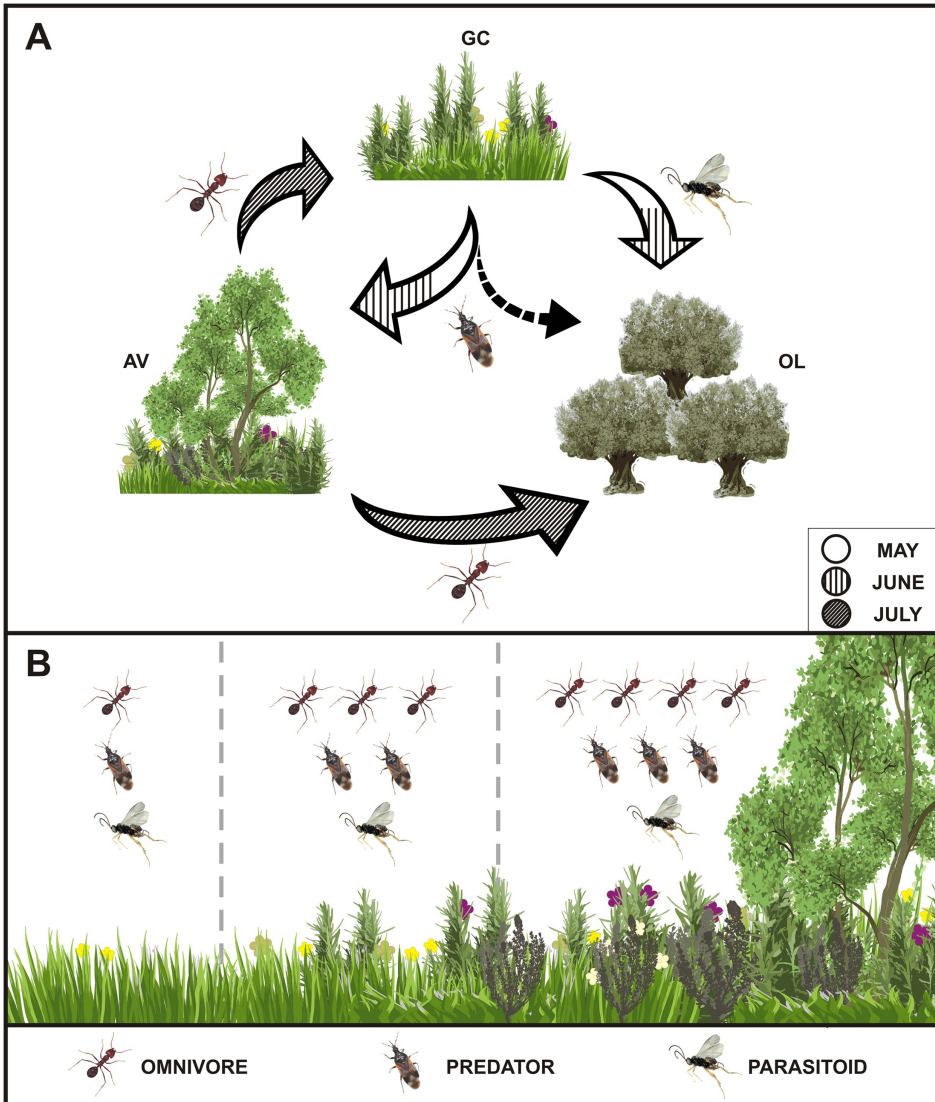


Figure 6. Graphic representation of movement of natural enemies (A) and abundance response to habitat complexity (B). Movement across adjacent vegetation (AV), ground cover (GC), and olive orchards (OL). Arrows indicate the direction of the movement and the plot inside the arrows shows the month in which the movement happens. A dotted arrow indicates the possibility of movement.

Resource availability

A resource availability and distribution mechanism provided by the resource-based model (Ries and Sisk, 2004; Ries et al., 2004) including edge effects (López-Barrera et al., 2007; Malanson et al., 2006; Laurance, 2007; Broadbent et al., 2008) and perturbation gradients (Colwell et al., 2004;

Hogsden and Hutchinson, 2004; Dallimer et al., 2012), provides a framework with which it is possible to explain the trend of our results. For example, resource distribution refers to a scenario where two adjacent habitats have different resource availability (quantity and quality). When these habitats are significantly different (high and low quality) a complementary resource distribution will drive a positive response, i.e., the low-quality habitat will have a lesser abundance of natural enemies than the other whilst the natural enemies living at the boundaries will have the advantage to boost their populations due to new resources. The resource-based model also shows that resources could be concentrated at an edge, hence increasing the abundance of natural enemies in that edge. In this context, if we consider the ground cover not only as a single habitat but also as an ecotone, we can establish that the features of the most complex study areas in our analysis (PI-1 and PI-2) match model predictions. Conversely, when the resource availability is relatively equal in two different habitats, the abundance will be the same in both habitats, i.e., the response is neutral, which is the case of the less-complex study areas in our analysis (PI-3 and DEI). It is important to point out that changes in availability of resources may affect the multitrophic interactions in the food web, resulting in intra-guild predation between natural enemies (Tschardt et al., 2016; Morente et al., 2018), which is a topic that needs to be investigated more thoroughly.

Conclusions

Our findings show the importance of the presence of ground cover and adjacent vegetation in organic olive orchards. Different plant species contribute to the establishment of different guilds of natural enemies. Accordingly, our data support the complex-habitat hypothesis in organic olive orchards. When both ground cover and adjacent vegetation are maintained (functioning as a sink for natural enemies), they produce a complementary distribution of resources that needs to be maximised by high levels of complexity in order to increase the abundance of natural enemies in the orchard. To the best of our knowledge this is the first time that this type of empirical data has been recorded for organic olive orchards. Further research is needed to investigate the efficiency of this type of arrangement and the effects of habitat complexity on pest predation in organic olive orchards.

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Chapter 2

Habitat complexity in organic olive orchards modulates the abundance of natural enemies but not the attraction to plant species

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Abstract

Semi-natural habitat complexity and organic management could affect the abundance and diversity of natural enemies and pollinators in olive orchards. Nonetheless, in such agroecosystems the effect of plant structure, plant richness, and plant attraction on the arthropod fauna has been poorly documented. Here we evaluate the influence of those effects jointly as an expression of arthropod abundance and richness in olive trees, ground cover, and adjacent vegetation within organic olive orchards. For this, we used generalized linear models and non-metric multidimensional scaling (NMDS) integrating generalized additive models. Our results suggest that natural enemies and pollinators are mainly attracted to *A. radiatus*, *D. catholica*, and *L. longirostris* within ground cover and *G. cinerea speciosa*, *Q. rotundifolia*, *R. officinalis*, *T. zygis gracilis*, and *U. parviflorus* within adjacent vegetation. Accordingly, habitat complexity showed a positive relationship with the abundance of key families of natural enemies and pollinators but not with the number of taxa. NMDS showed that plant richness and plant arrangement and scattering affected the key families differently, suggesting that each key family responds to their individual needs for plant resources but forming groups modulated by complexity. This pattern was especially seeing in predators and omnivores. Our findings support that the higher the plant richness and structure of a semi-natural habitat within an olive orchard, the higher the abundance and richness of a given arthropod community (a pattern found in natural ecosystems). The information presented here can be used by producers and technicians to increase the presence and abundance of

natural enemies and pollinators within organic olive orchards, and thus improve the ecosystem services provided by semi-natural habitats.

Introduction

Recent studies have suggested an improvement in the abundance of natural enemies and pollinators due to the presence of semi-natural habitats in agroecosystems (Clemente-Orta and Álvarez, 2019; Karp et al., 2018; Tschardt et al., 2016). In the European Union policies are currently being implemented with the aim of restoring semi-natural habitats, such as ground cover and adjacent vegetation within vineyards, citrus, almond, and olive orchards (Malavolta and Perdakis, 2018). Especially, there is a growing interest in suitable plant species for ecological restoration and ecosystem services, for example, to prevent soil erosion, maintain soil fertility and control insect pests (biological control) (Oldfield, 2019; Pedrini et al., 2019).

Semi-natural habitat complexity and the management of the ground cover positively affect abundance and variability of natural enemies and pollinators in olive orchards (Álvarez et al., 2019a; 2019b; 2021a; Gkissakis et al., 2016; Karamaouna et al., 2019; Villa et al., 2016a). However, a positive or negative response shown by an organism to a nearby habitat could be driven by the structure and composition of such a habitat (Álvarez et al., 2016; 2017; 2021; Balmford et al., 2012; Clemente-Orta et al., 2020; Laurance, 2007; López-Barrera et al., 2007; Wan et al., 2018a). Indeed, the composition and dominance of plant species are key factors in natural habitats that drive the richness and abundance of insects, i.e., the higher the plant species richness in a habitat, the higher the richness and abundance of a given insect community. Interestingly, this pattern is especially reflected on predator insects (Haddad et al., 2001; Knops et al., 1999).

It is known that some plant species can attract more natural enemies and pollinators than others, which is due to the form of functional traits of flowers or prey presence, amongst other factors (Hatt et al., 2017; Nave et al., 2016; Van Rijn and Wackers, 2016). In olive orchards some plant species within ground cover and adjacent vegetation have shown positive effects on predators, omnivores (Torres, 2006), and pollinators (Karamaouna et al., 2019). For example, in a previous study Álvarez et al. (2019a) suggested that arthropod abundance is affected by the type of vegetation, i.e., most plant species within ground cover and adjacent vegetation had a higher abundance of natural enemies than the olive trees, although each trophic guild of natural enemies (e.g., omnivores, parasitoids, and predators) had a specific

relationship with a type of vegetation. They showed that four herbaceous species within ground cover attract more predators than others, and six shrubby species within adjacent vegetation attract more omnivores than others. Nevertheless, there is no characterization of the arthropod fauna that is attracted to such plants and no quantification of the effects of those plants on arthropod abundance.

Despite the efforts of different authors to assess the effects of ground cover and adjacent vegetation on natural enemies, pollinators, and olive pests, to the best of our knowledge there is no study that has focused on (1) the attraction of the (whole) arthropod fauna to key plant species within ground cover and adjacent vegetation and (2) the effects of habitat complexity on arthropod attraction. This is of great importance because identifying habitat features and plant species that could attract more key (beneficial) arthropods will be paramount to improve the organic management of olive orchards by means of conserving and planning ground cover and adjacent vegetation, given the fact that, for example, not all natural enemies in a semi-natural habitat are able to produce an effective biological control of pests (Karp et al., 2018; Rusch et al., 2010). Based on the above, the aim of this study was to assess the potential effects of plant species within the ground cover and adjacent vegetation, and the influence of habitat complexity, to attract natural enemies of olive pests and pollinators within organic olive orchards.

Material and methods

Study area

The study was conducted in organic olive orchards (186.45 ha), in the localities of Piñar (37°24'N, 3°29'W) and Deifontes (37°19'N, 3°34'W), in the province of Granada (southern Spain). The orchards maintained a ground cover for at least three consecutive years. *Bacillus thuringiensis* was used as a preventive pest control for the carpophagous generation of *Prays oleae* (larvae) in July in the orchards of Piñar (for detailed information on climatic conditions and sample areas see Álvarez et al., 2019a). Five different areas with patches and/or hedgerows of adjacent vegetation were sampled within the olive orchards: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), Piñar 3 (PI-3) and Piñar 5 (PI-5). Based on the soil uses for Andalusia obtained from the information system of occupation of the Spanish soil database at 1:10 000 (SIOSE, www.siose.com) in ArcGis software, and following the definition of classes in the technical guide of the Andalusian soil vegetation cover and uses map (Junta de Andalucía, 2007), we found three soil uses in the sampled areas: (1) woody-sparse scrub: sparse oak (WSS); woody-dense scrub: sparse

oak (WDS); and sparse scrub with grass and rocks (SSGR). Accordingly, the structure of the adjacent vegetation was different for each area, i.e., DEI had a surface of WSS and SSGR, PI-1 had a surface of WSS, and PI-2 had a surface of WDS, in contrast PI-3 and PI-5 had one hedgerow (formed primarily by oak trees) and the difference between PI-3 and PI-5 is that the hedgerow in PI-5 is entirely linear (Table 1).

Sampling design and habitat classification

We focussed our efforts on collecting samples of arthropods (1) in the most abundant and recognizable (blossom) plant species within adjacent vegetation and ground cover, and (2) in the canopy of the olive trees. Nine plant species were abundant enough in the adjacent vegetation for sampling, i.e., two species of trees: *Prunus dulcis* (Mill.) D.A. Webb, and *Quercus rotundifolia* Lam., and seven species of bushes: *Cistus albidus* L., *Genista cinerea speciosa* Rivar Mart. & al., *Retama sphaerocarpa* (L.) Boiss., *Rosmarinus officinalis* L., *Thymus mastichina* L., *Thymus zygis gracilis* (Boiss.) R. Morales and *Ulex parviflorus* Pourr. Six species of herbaceous plants were abundant enough in the blossom period in the ground cover: *Anacyclus radiatus* Loisel, *Centaurea melitenses* L., *Diplotaxis catholica* (L.) DC., *Erodium cicutarium* (L.) L'Hér, *Leontodon longirostris* (Finch & P.D. Sell) Talavera, and *Senecio vulgaris* L. In addition, we collected samples in sections of the ground cover located under the canopy of olive trees, i.e., evergreen plants (due to the drip irrigation of the olive trees and their shade) which did not present blooming flowers but formed a distinctive stratum, and thus it was considered as another plant-category named “miscellaneous”. Overall, 17 different plants were measured.

We used as an experimental unit (sample) a suction plot that was a 30 s-suction in a 50 × 50 cm surface of foliage. We used a modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA) to collect the arthropods. This method allows us to standardize sampling amongst different types of plants (i.e., herbaceous, shrubs, and trees). Samples in this study were collected, weather permitting (once a month) from May to July 2015, which are the months of highest arthropod abundance in olive orchards (Ruano et al., 2004; Santos et al., 2007a). We collected 20 randomly distributed samples per plant species in each sample area, depending on plant species availability (see Table 1), and 40 randomly distributed samples in the olive trees. The samples were stored individually and maintained at -20°C until the specimens were classified.

Table 1. Plant species richness, arrangement, and scattering in the five study areas of organic olive orchards: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), Piñar 3 (PI-3), and Piñar 5 (PI-5). Plant species in adjacent vegetation: *C. albidus* (Ca), *G. cinerea speciosa* (Gcs), *P. dulcis* (Pd), *Q. rotundifolia* (Qr), *R. sphaerocarpa* (Rs), *R. officinalis* (Ro), *T. mastichina* (Tm), *T. gracilis* (Tzg), *U. parviflorus* (Up). Plant species in ground cover: *A. radiatus* (Ar), *C. melitenses* (Cm), *D. catholica* (Dc), *E. cicutarium* (Ec), *L. longirostris* (Ll), *S. vulgaris* (Sv), and the miscellaneous plants (mi).

Area	Adjacent vegetation		Ground cover	Level of richness	Level of arrangement and scattering	Complexity
	Richness	Arrangement				
DEI	Qr - Rs - Ro - Tzg - Up - Ca - Pd - Tm	Surface: sparse. All plants gathered into clusters	Ll - Dc - Cm - Ec - Sv - mi	3	3	+ + + + + +
PI-1	Qr - Rs - Ro - Tzg - Up	Surface: sparse. All plants gathered into clusters	Ll - Dc - Ar - mi	2	3	+ + + +
PI-2	Qr - Rs - Ro - Tzg - Up - Gcs	Surface: dense. All scattered	Ll - Dc - mi	2	4	+ + + + + +
PI-3	Qr - Ro	Edge	Ll - mi	1	2	+ + +
PI-5	Qr - Ro	Edge (lineal)	Ll - mi	1	1	+ +

The arthropods were identified to family level, unless otherwise specified and classified by trophic guilds, i.e., natural enemies: omnivores, parasitoids, and predators; pollinators and specialist olive pests. The families that were identified as neither natural enemies nor pests were gathered in a group named neutral arthropods (Wan et al., 2014a). Guild classification was based on literature data (see Table A1.1 of supplementary data in Appendix). We pooled together raw sample data by plant species and month.

On the other hand, we followed Álvarez et al. (2019a) to establish a gradient of habitat complexity, however we did not quantify it directly but rather its components, i.e., plant species composition (e.g. plant richness) and habitat structure (e.g. plant arrangement and scattering) for each study area. Table 1 summarizes the different features of each study area and shows the resulting amount of habitat complexity and the level of its components. The level of richness follows the number of plant species in each study area, and then areas were numbered from most to least. The level of arrangement and scattering is based on the information of the structure of the adjacent vegetation given by the SIOSE database (see above). The variables used were (1) surface or hedgerow, where the former is more important, (2) type of soil use: dense or sparse (and their features), where a dense vegetation with woods is more important, and (3) plants scattered across the area or gathered into one or several clusters, where the former is more important. Then the areas were numbered from most to least. We gave the same weight to plant richness and plant arrangement and scattering to express the amount of habitat

complexity. Finally, the study areas can be arranged from most to least complex as: PI-2 and DEI (equal), PI-1, PI-3, and PI-5 (Table 1).

Data analysis

Contrary to Álvarez et al. (2019a), we analysed the effects of plant-species attraction and habitat complexity on each family of beneficial arthropods. Firstly, to see plant-species effects on arthropod abundance we analysed family abundance per guild (i.e., omnivores, parasitoids, predators, and pollinators) per plant species, for which several generalised linear models (GLMs) were constructed using “quasi-likelihood” with Poisson-like assumptions (quasi-Poisson) tendency (for justification on this approach see Ver Hoef and Boveng, 2007). We fitted models including abundance as the dependent variable and family (per guild) as the independent variable. In this study we considered month samples as independent. Nonetheless, the presence and abundance of the total arthropod community by family in plants was still recorded and reported (see chapter appendix).

Secondly, to see habitat effects on arthropod abundance we used the data of the resulting arthropod families that showed the best effects (hereafter called key families), for which four GLMs were constructed using “quasi-likelihood” with Poisson-like assumptions (quasi-Poisson) tendency. Two GLMs were fitted including (1) total abundance of key families and (2) the number of key families as the dependent variables and study area as the independent variable. The next two GLMs were fitted including (1) total abundance of key families and (2) the number of key families as the dependent variables and the level of richness plus the level of arrangement and scattering and their interaction as independent variables. There was no interaction between the two levels, then it was not integrated in further analyses.

Finally, to assess how plant richness and plant arrangement and scattering affect arthropod abundance, the composition of key families and the plants per area were subjected to a non-metric multidimensional scaling (NMDS). Based on the NMDS, smooth surfaces were generated with the data of abundance for each key family. Smooth surfaces result from fitting thin plate splines in two dimensions using generalized additive models. The function selects the degree of smoothing by generalized cross-validation and interpolates the fitted values on the NMDS plot represented by lines ranking in a gradient (Oksanen et al., 2018). Key families were grouped based on the topology of the smooth surfaces in NMDS plots because its form is driven by the maximum abundance showed by plants and study areas.

Then, key families were ordered following their relationship with study areas, and therefore, with the level of richness and the level of arrangement and scattering.

All analyses were computed in the R software v.3.6.2 (R Developmental Core Team, 2019). The “vegan” package (Oksanen et al., 2018) was used to compute NMDS and smooth surfaces.

Results

A total of 9,279 individuals were collected. The arthropods were comprised in 12 orders: Araneae, Blattodea, Coleoptera, Diptera, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, Phasmida, Raphidioptera, and Thysanoptera. Overall, 106 families were identified, 51 families were identified as natural enemies and grouped in three trophic guilds: 2 omnivores, 17 parasitoids, and 32 predators. Two families were identified as specialist pests of olive orchards and 1 family as a pollinator. The rest of the families were grouped as neutral arthropods. The chapter appendix summarizes information of each arthropod family regarding their relative abundance, trophic guild, and records in plants and months. In addition, the plants that showed more abundance and the type of vegetation in which each family was present is detailed.

Difference in arthropod abundance amongst plants

Predators

We found that the abundance amongst families of predators significantly increased in olive trees ($F_{30,62} = 6.212$, $p = 0.001$), the miscellaneous plants ($F_{30,62} = 4.659$, $p = 0.001$), and 8 of the 15 plant species sampled, i.e., within the adjacent vegetation family abundance was different in *G. cinerea speciosa* ($F_{30,62} = 6.537$, $p = 0.001$), *Q. rotundifolia* ($F_{30,62} = 7.951$, $p = 0.001$), *R. officinalis* ($F_{30,62} = 7.742$, $p = 0.001$), *T. zygis gracilis* ($F_{30,62} = 6.786$, $p = 0.001$), and *U. parvijlorus* ($F_{30,62} = 2.956$, $p = 0.001$), but within ground cover family abundance was different in *A. radiatus* ($F_{30,62} = 4.703$, $p = 0.001$), *D. catholica* ($F_{30,62} = 4.804$, $p = 0.001$), and *L. longirrostris* ($F_{30,62} = 4.185$, $p = 0.001$).

Figure 1 and 2 graphically summarizes the proportion of the families of predators and parasitoids, respectively, that were the most abundant in plant species (i.e., plants with high arthropod abundances). The families of predators were: Anthocoridae, Miridae (Hemiptera); Oxiopidae, Salticidae, Thomisidae, Uloboridae (Araneae); Aeolothripidae (Thysanoptera);

Coccinellidae (Coleoptera); and Chrysopidae (Neuroptera). However, the most representative families of predators were (from most to least abundant): Miridae, Aeolothripidae, and Thomisidae.

Parasitoids, omnivores, and pollinators

The families of parasitoids were significantly more abundant in olive trees ($F_{13, 28} = 4.505, p = 0.001$), with Encyrtidae and Scelionidae being the families that showed high abundances.

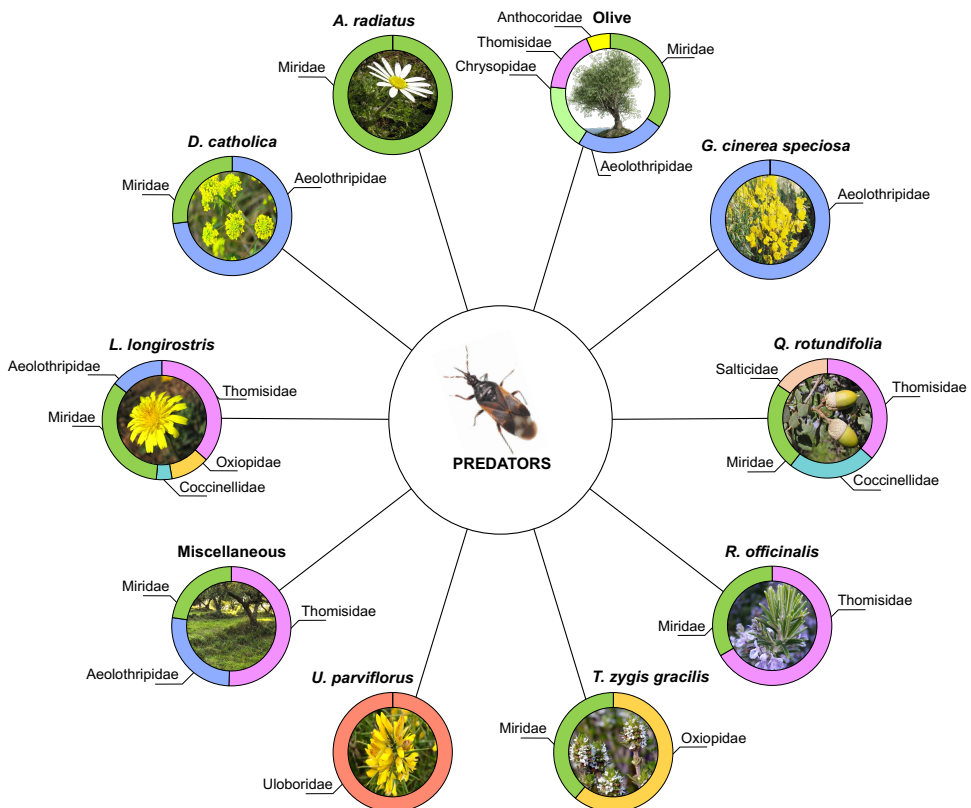


Figure 1. Families of predators that had the highest abundance per plant species within organic olive orchards. The circles show the proportion of the abundance amongst such families.

On the other hand, only two families were identified as omnivores: Formicidae (Hymenoptera) and Forficulidae (Dermaptera), the former had very high abundance and the latter almost none ($n = 1$). Formicidae was present in all plants, tending to have more abundance in *R. sphaerocarpa*, *R. officinalis*, *T. zygis gracilis*, *L. longirrostris*, and the miscellaneous plants (see chapter appendix).

Finally, only bees (Hymenoptera: Apidae) were identified as pollinators. Apidae was present in three plants within adjacent vegetation, four plants within ground cover, the miscellaneous plants and the olive trees, tending to have more abundance in *L. longirrostris* and olive trees (see chapter appendix).

Effects of habitat complexity

The abundance of the key families showed significant differences amongst study areas ($F_{4,40} = 2.708, p = 0.043$), i.e., the areas with the highest complexity had the highest abundance (PI-2 and DEI: Tukey *post hoc* test, $p = 0.037$) (Fig. 3). Moreover, key family abundance had a positive relationship with the level of (plant) arrangement and scattering ($F_{1,42} = 10.661, p = 0.002$) (Fig. 3) but not with the level of (plant) richness. On the other hand, the number of key families (number of taxa) did not follow any pattern, i.e., there is no difference amongst study areas ($F_{1,43} = 0.236, p = 0.915$) and no relationship with the level of richness nor the level of arrangement and scattering.

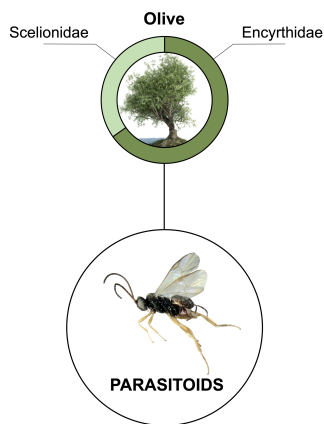


Figure 2. Families of parasitoids that had the highest abundance in olive trees within the organic olive orchards. The circles show the proportion of the abundance amongst such families.

In addition, we found that the key families can be separated in four groups based on the form and topology of the smooth surfaces (Fig. 4). The NMDS showed that plant richness and plant arrangement and scattering affected differently the key families. For example, ants, ladybeetles, and uloborid spiders were mostly influenced by plant arrangement and scattering followed by the aeolothrips. Conversely, mirids and oxyopid and thomisid spiders were mostly influenced by plant richness followed by anthocorids, lacewings, parasitoids, and salticid spiders. Contrary to the anterior, the pollinator abundance was influenced by the less rich areas, where *L. longirrostris* had more presence. NMDS results suggest that the abundance and presence of each key family responds to the presence of specific plant species in each study area but key families form groups modulated by habitat complexity (primarily affected by the level of arrangement and scattering) (Fig. 4).

Discussion

In this study we have assessed the effects that several plants within ground cover and adjacent vegetation may have to attract natural enemies and pollinators to olive orchards. We have also, assessed the effects of the components of habitat complexity on key families of natural enemies and pollinators.

Overall, from the 15 most representative plants in our study areas, only *A. radiatus*, *D. catholica*, and *L. longirrostris* showed effects to attract natural enemies and pollinators within ground cover and *G. cinerea speciosa*, *Q. rotundifolia*, *R. officinalis*, *T. zygis gracilis*, and *U. parviflorus* showed such an effect within adjacent vegetation. Moreover, the miscellaneous plants also showed effects. This suggests that there are more plants in the adjacent vegetation that can attract beneficial arthropods compared with the ground cover. Perhaps, this is why in some modelling adjacent vegetation produced greater (positive) effects on predators than the ground cover, especially in shrubby habitats (Paredes et al., 2013; 2015). However, it has been shown that the ground cover maintains the highest abundance of natural enemies, i.e., parasitoids, predators, and omnivores together rather than the adjacent vegetation (Álvarez et al., 2019a), also it integrates more predators into the trophic network of the olive tree canopy (when ground cover is mature, Álvarez et al., 2019b), and promotes an effective predation of the olive moth *P. oleae* (Álvarez et al., 2021a).

Based on the type of beneficial arthropod, our results are in agreement with the findings of Álvarez et al., (2019a; 2021a), Karamaouna et al., (2019),

and Paredes et al., (2013). Accordingly, shrubby habitats had more attraction for spiders (predators) and ants (omnivores) but the ground cover had more attraction for bees (pollinators), heteropterans (predators), and members of Aeolothripidae (predators). This supports the idea that adjacent vegetation and ground cover are different types of habitats, with different types of resources (and availability), which stay in synergy with the olive orchard. Nonetheless, habitat complexity plays an important role modulating the abundance of beneficial arthropods. Our results showed that abundance tend to increase as complexity increase when total abundance is measured (Fig. 3).

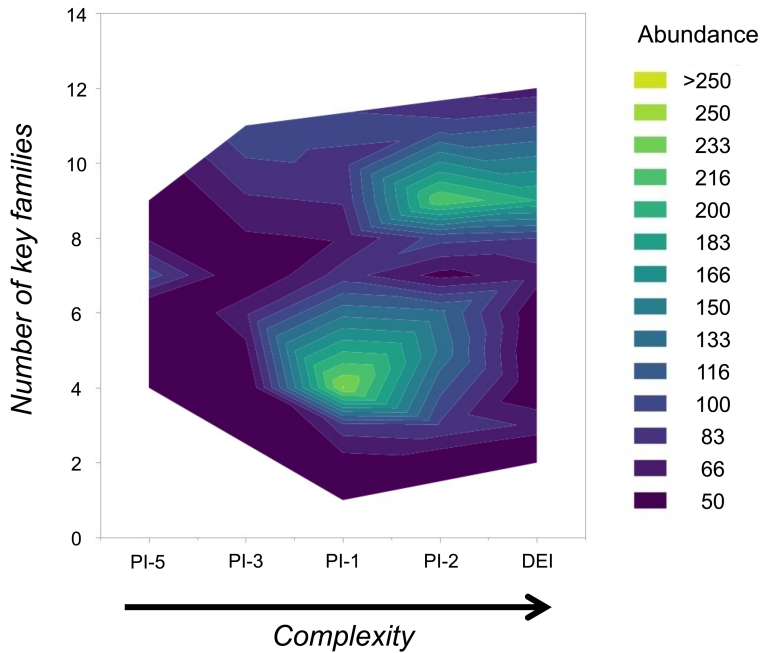


Figure 3. Contour plot showing the response values and desirable operating conditions. The contour plot contains the following elements: predictors on X (study areas arranged according to complexity) and T (number of key families and abundance) axes. Contour lines connect points that have the same adjusted response value integrating data of total abundance of key families, i.e., the lines and its form is given by the proportion of the abundance amongst areas. The form of the aggregate is given by the number of families.

Furthermore, it was interesting that only plant arrangement and scattering affected abundance rather than plant richness. This can be explained due to the fact that organic olive orchards are highly similar (e.g., management and structure). This is why there are no differences amongst our study areas when we use the level of richness, all areas are similar in their plant richness. Moreover, the richest areas turned to be the ones with higher abundance (Fig. 3) and according to NMDS analyses, richness do affect abundance specially the abundance of generalist and specialist predators, which is in agreement with theory (Haddad et al., 2001; Knops et al., 1999).

In regard to the anterior, Álvarez et al. (2019a) showed that the natural enemies of olive pests are more abundant in complex habitats and that they move across orchards and vegetations throughout the months of highest arthropod abundance. It seems that parasitoids, predators, and omnivores overwinter in the adjacent vegetation and when the temperature increases, they move to the ground cover, and as a result of spill over, they can invade the olive trees preying new preys (such as olive pests). However, this movement is modulated only by the ground cover, i.e., predators and parasitoids invade the ground cover when it is growing, but when ground cover starts to wither the predators tend to return to the adjacent vegetation. Conversely, it is only at this time that parasitoids and omnivores move to the olive trees, which corresponds with the time that *P. oleae* lay their eggs on young olive fruit (Ramos et al., 1978). Accordingly, the synergy between adjacent vegetation and ground cover implies that complex habitats are paramount in order to increase natural enemy abundance as suggested by studies on natural ecosystems (Haddad et al., 2001; Knops et al., 1999), being the generalist arthropods the ones that will respond to such an effect. However, one has to take into account that the pattern showed here by abundance could be drove by few of the taxa present in one area and if it is wanted to increase the number of families or specific predators within olive orchards plant richness is of great importance as suggested by the NMDS (Fig. 4).

On the other hand, specialist predators of olive pests and parasitoids such as Anthocoridae, Chrysopidae (predators), Encyrtidae, and Scelionidae (parasitoids) showed effects for olive trees and tend to be (1) related with plant richness and (2) less affected by plant arrangement and scattering than other families (Fig. 4). For example, it is known that *Anthocoris nemoralis* (Anthocoridae) and *Chrysoperla carnea s.l.* (Chrysopidae) are important natural enemies that predate eggs and adults of *Prays oleae* (Morris et al., 1999; Villa et al., 2016b). In addition, the wasp *Ageniaspis fuscicollis* (Encyrtidae) is a polyembryonic parasitoid that lays its eggs on the eggs of *P. oleae* (Arambourg,

1984), and the wasp *Telenomus acrobater* (Scelionidae) is a hyperparasitoid that parasites the larvae of Chrysopidae (Campos, 1986). Hence, the specialist predators and parasitoids are linked to olive trees due to their need for specific prey, and thus, it is possible to enhance the abundance of such families by increasing habitat complexity but it would be paramount to increase the presence of the plant species in which these families have been recorded, aside from olive trees, within ground cover and adjacent vegetation (Alcalá-Herrera et al., 2019a; Álvarez et al., 2021a).

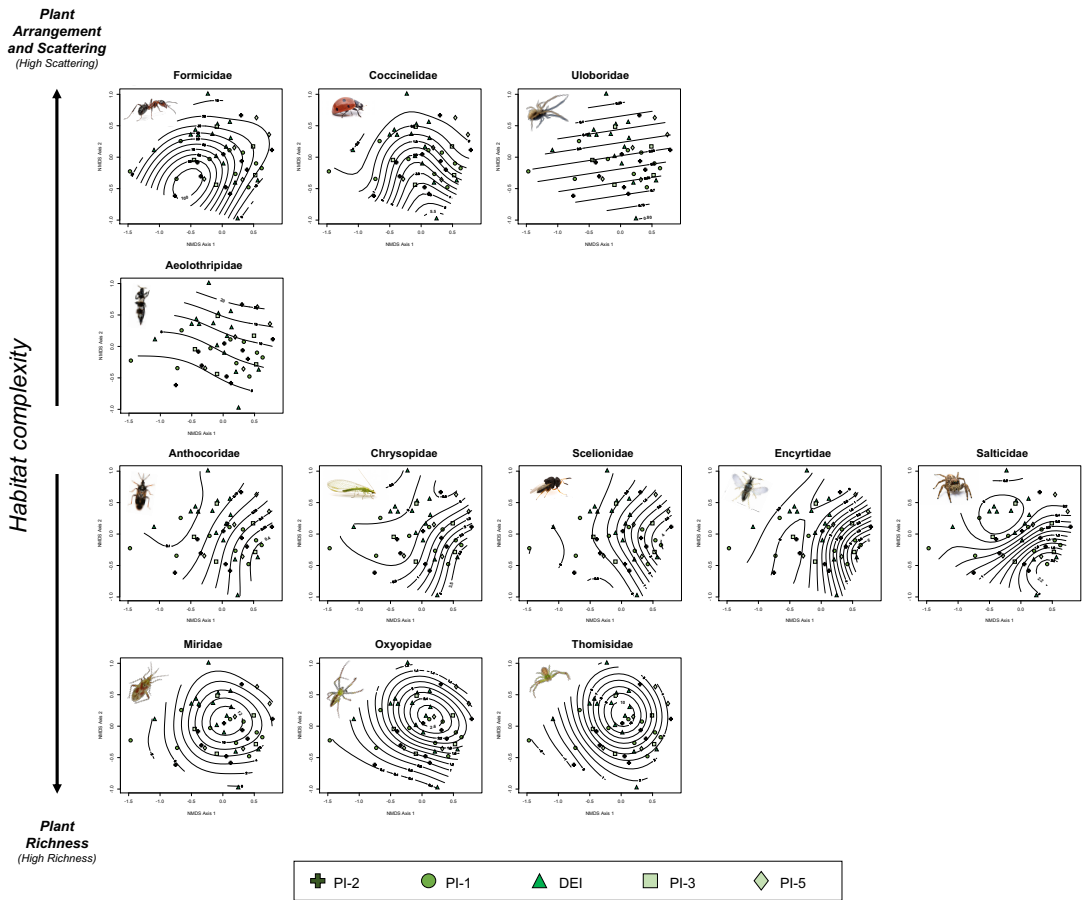


Figure 4. Non-metric multidimensional scaling (NMDS) of the total abundance of natural enemies. Lines (smooth surfaces) represent different levels in the form of a gradient of each key family according to generalised additive models. Aggregates of families are given by the tendency in the smooth surface and arranged according to effects of plant richness or patch structure. Areas are arranged from most to least complex. To see details in each graph, proceed to the digital version of the figure in high definition.

It is important to note that several of the natural enemies and the pollinators that have been recorded in this study had previously been known to inhabit the olive orchards and help to control olive pests (Torres, 2006). However, in our study Aeolothripidae showed a strong presence within the olive orchards. The role of the Aeolothripidae as natural enemies of olive pests has been poorly documented (reviewed by Torres, 2006). It is known that Aeolothripidae attack other Thysanoptera, but it has also been shown that some genera of Aeolothripidae can feed on mites, larvae, whiteflies, and aphids, as well as on the eggs of psyllids and lepidopterans (Lewis, 1973; Trdan et al., 2005). Their abundance suggests that they may be important assets amongst the natural enemies of olive pests as a parallel study suggests (Álvarez et al., 2021a).

In regard to pollinators, we recorded the family Apidae as the only representative of this guild. Olive flowers are wind pollinated (Lavee, 1996) and insect pollination may supplement wind pollination. In the Mediterranean basin few insect pollinators of olive trees are known, the primary recorded groups are (1) bees of the families Apidae, Adrenidae, and Halictidae, and (2) hoverflies (Syrphidae), with the most representative being the honeybee *Apis mellifera* L. (Canale and Loni, 2010; Karamaouna et al., 2019). Apidae in this study were recorded in almost all the flowering plants, however, it seems that they are attracted to the ground cover because of the presence of yellowish flowers such as *L. longirostris*, but they did visit the olive trees, which supports the results found by previous studies (Canale and Loni, 2010; Karamaouna et al., 2019).

Conclusions

Nine plant species showed the best results regarding attracting beneficial arthropods within organic olive orchards. Key family abundance is affected by habitat complexity, i.e., the highest the complexity in a habitat the highest the abundances of natural enemies and pollinators, however, they are influenced differently by plant richness and plant arrangement and scattering. Our findings could be used by producers and technicians to increase the abundance of natural enemies and pollinators within olive orchards. We agree that these plant species have the potential to boost abundance in adjacent vegetation and ground cover, however high levels of complexity to conserve areas of natural habitats are paramount to produce such results, i.e., ground cover and adjacent vegetation must have several plant species within them, then they can be planned in order to integrate such plants according to the best features of arrangement and scattering.

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Chapter appendix

Records and relative abundance (RA) of arthropod families on vegetations, plants species, and months. The highest abundances on plant species and months are showed in bold.

Name	ID	RA (%)	Record on Type of vegetation : Plant	Month
Arachnida				
Araneae	Amaurobiidae	Predator	0.03 ADJACENT: <i>U. parviflorus</i> .	June
	Araneidae	Predator	0.30 ADJACENT: <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>L.</i> <i>longirostris</i> . OLIVE.	May , June, July
	Dyctinidae	Predator	0.02 ADJACENT: <i>Q. rotundifolia</i> .	June, July
	Linyphiidae	Predator	0.14 ADJACENT: <i>C. albidus</i> , <i>R.</i> <i>officinalis</i> , <i>T. zygis gracilis</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , <i>L. longirostris</i> .	May , June
	Mimetidae	Predator	0.02 G. COVER: <i>D. catholica</i> , miscellaneous.	May, June
	Oxyopidae	Predator	0.86 ADJACENT: <i>C. albidus</i> , <i>R.</i> <i>officinalis</i> , <i>R. sphaerocarpa</i> , <i>T.</i> <i>mastichina</i> , <i>T. zygis gracilis</i> , <i>U.</i> <i>parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>L. longirostris</i> , miscellaneous. OLIVE.	May , June, July
	Philodromidae	Predator	0.23 ADJACENT: <i>C. albidus</i> , <i>G. cinerea</i> <i>speciosa</i> , <i>Q. rotundifolia</i> , <i>R.</i> <i>sphaerocarpa</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>R. officinalis</i> , <i>S. vulgaris</i> , miscellaneous. OLIVE.	May, June, July

	Salticidae	Predator	0.37	ADJACENT: <i>P. dulcis</i> , Q. rotundifolia *, <i>R. officinalis</i> , <i>R. sphaerocarpa</i> , <i>T. mastichina</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>L. longirrostris</i> , miscellaneous. OLIVE *.	May, June, July
	Sicariidae	Predator	0.01	ADJACENT: <i>U. parviflorus</i> .	June
	Thomisidae	Predator	2.88	ADJACENT: <i>C. albidus</i> , <i>G. cinerea speciosa</i> , <i>P. dulcis</i> , Q. rotundifolia , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , <i>E. cicutarium</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous . OLIVE.	May, June, July
	Uloboridae	Predator	0.27	ADJACENT: <i>U. parviflorus</i> .	July
	Zodariidae	Predator	0.04	ADJACENT: U. parviflorus . G. COVER: <i>L. longirrostris</i> .	June, July
Insecta					
Blattodea	Blattellidae	Neutral	0.09	ADJACENT: <i>P. dulcis</i> , Q. rotundifolia , <i>R. officinalis</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> .	May, June , July
Coleoptera	Alleculidae	Neutral	0.08	ADJACENT: <i>C. albidus</i> , R. sphaerocarpa . G. COVER: <i>A. radiatus</i> .	May, June
	Anthicidae	Neutral	0.08	ADJACENT: <i>T. zygis gracilis</i> . G. COVER: <i>L. longirrostris</i> , miscellaneous.	May , June, July
	Apionidae	Neutral	0.06	ADJACENT: <i>C. albidus</i> .	June , July
	Cantharidae	Predator	0.03	ADJACENT: R. officinalis *, <i>T. zygis gracilis</i> .	May
	Catopidae	Neutral	0.09	ADJACENT: Q. rotundifolia , <i>G. cinerea speciosa</i> , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> .	May, June
	Cerambycidae	Neutral	0.91	G. COVER: <i>L. longirrostris</i> .	May
	Chrysomelidae	Neutral	0.01	ADJACENT: <i>C. albidus</i> , <i>P. dulcis</i> , Q. rotundifolia , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , L. longirrostris *, miscellaneous. OLIVE.	May , June, July
	Cleridae	Predator	0.04	G. COVER: L. longirrostris *. OLIVE.	May
	Coccinellidae	Predator	0.81	ADJACENT: <i>C. albidus</i> , <i>P. dulcis</i> , Q. rotundifolia , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , L. longirrostris , miscellaneous. OLIVE.	May , June, July
	Curculionidae	Neutral	1.86	ADJACENT: <i>C. albidus</i> , G. cinerea speciosa , <i>P. dulcis</i> , Q. rotundifolia , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zygis gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , <i>E. cicutarium</i> , L. longirrostris , miscellaneous. OLIVE.	May , June, July

	Dasytidae	Predator	0.12	ADJACENT: <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. zigys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , L. longirrostris .	May, June
	Dermestidae	Neutral	0.03	ADJACENT: <i>Q. rotundifolia</i> . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> .	May, June
	Elateridae	Predator	0.01	G. COVER: <i>L. longirrostris</i> .	May
	Malachiidae	Predator	0.02	ADJACENT: <i>U. parviflorus</i> . G. COVER: <i>L. longirrostris</i> .	May, June
	Monotomidae	Neutral	0.02	G. COVER: miscellaneous. OLIVE.	June
	Mycetophagidae	Neutral	0.01	ADJACENT: <i>Q. rotundifolia</i> .	May
	Nitidulidae	Neutral	0.03	ADJACENT: <i>G. cinerea speciosa</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> .	May
	Phalacridae	Neutral	0.61	ADJACENT: Q. rotundifolia , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , L. longirrostris . OLIVE.	May, June, July
	Ptinidae	Neutral	0.01	ADJACENT: <i>P. dulcis</i> .	June
	Scarabaeidae	Neutral	0.01	G. COVER: <i>D. catholica</i> .	May
	Staphylinidae	Predator	0.04	ADJACENT: R. officinalis* . G. COVER: <i>A. radiatus</i> , <i>L. longirrostris</i> .	May
Dermaptera	Forficulidae	Neutral	0.02	ADJACENT: <i>P. dulcis</i> , <i>G. cinerea speciosa</i> .	May, June
Diptera	Agromyzidae	Neutral	0.02	OLIVE.	June, July
	Asilidae	Predator	0.01	ADJACENT: <i>Q. rotundifolia</i> .	May
	Bibionidae	Neutral	0.03	ADJACENT: <i>Q. rotundifolia</i> , <i>R. officinalis</i> . OLIVE.	May, July
	Bombyliidae	Neutral	0.09	ADJACENT: <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>U. parviflorus</i> . G. COVER: <i>L. longirrostris</i> . OLIVE.	May, June, July
	Calliphoridae	Neutral	0.13	ADJACENT: <i>Q. rotundifolia</i> .	June
	Camillidae	Neutral	0.01	G. COVER: D. catholica , <i>E. cicutarium</i> , <i>L. longirrostris</i> , miscellaneous.	May, June
	Cecidomyiidae	Neutral	0.36	ADJACENT: <i>G. cinerea speciosa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zigys gracilis</i> , U. parviflorus . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> , miscellaneous.	May, June, July
	Ceratopogonidae	Neutral	0.01	ADJACENT: <i>T. zigys gracilis</i> .	June
	Chamaemyiidae	Predator	0.01	ADJACENT: <i>T. zigys gracilis</i> .	June
	Chironomidae	Neutral	0.06	ADJACENT: <i>Q. rotundifolia</i> . G. COVER: miscellaneous. OLIVE.	May, June
	Chloropidae	Neutral	0.22	ADJACENT: <i>P. dulcis</i> , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> . G. COVER: C. melitenses , L. longirrostris , miscellaneous. OLIVE.	May, June, July

	Dolichopodidae	Predator	0.16	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>T. zigys gracilis</i> . G. COVER: <i>C. melitenses</i> , L. longirrostris* ; miscellaneous.	May, June, July
	Empididae	Neutral	0.08	ADJACENT: <i>P. dulcis</i> , Q. rotundifolia* ; <i>T. zigys gracilis</i> . OLIVE.	May, June
	Lauxaniidae		0.01	G. COVER: miscellaneous.	June
	Limonidae	Neutral	0.02	ADJACENT: <i>P. ducis</i> .	May, June
	Muscidae	Neutral	0.05	ADJACENT: <i>Q. rotundifolia</i> . G. COVER: <i>D. catholica</i> . OLIVE.	May, June, July
	Mythicompyiidae		0.05	G. COVER: miscellaneous.	July
	Opomyzidae	Neutral	0.01	G. COVER: <i>D. catholica</i> .	May
	Phoridae	Predator	0.01	ADJACENT: <i>Q. rotundifolia</i> .	May
	Sciariidae	Neutral	0.12	ADJACENT: <i>R. officinalis</i> , <i>U. parviflorus</i> . G. COVER: D. catholica , <i>E. cicutarium</i> , miscellaneous .	May, June, July
	Tephritidae	Neutral	0.22	ADJACENT: P. dulcis* , Q. rotundifolia* ; <i>R. officinalis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> , <i>S. vulgaris</i> . OLIVE.	May, June
	Trioxscelidae		0.04	G. COVER: <i>D. catholica</i> , miscellaneous.	May, June
Hemiptera	Anthorcoridae	Predator	0.11	ADJACENT: <i>C. albidus</i> , <i>T. zigys gracilis</i> . G. COVER: miscellaneous. OLIVE .	May, June
	Aphididae	Neutral	21.11	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> , R. sphaerocarpa , <i>R. officinalis</i> , <i>T. matchina</i> , <i>T. zigys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , E. cicutarium , L. longirrostris , S. vulgaris , miscellaneous . OLIVE.	May, June, July
	Berytidae	Neutral	0.20	ADJACENT: <i>T. zigys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous .	May, June, July
	Coccidae	Neutral	0.28	ADJACENT: <i>C. albidus</i> , <i>T. zigys gracilis</i> , U. parviflorus . G. COVER: <i>D. catholica</i> , miscellaneous. OLIVE .	May, June, July
	Coreidae		0.01	G. COVER: miscellaneous.	June
	Cydnidae	Neutral	0.01	ADJACENT: <i>T. zigys gracilis</i> .	May
	Fulgoromorpha	Neutral	13.56	ADJACENT: <i>C. albidus</i> , <i>G. cinerea speciosa</i> , <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> , R. officinalis , <i>T. matchina</i> , T. zigys gracilis , U. parviflorus . G. COVER: A. radiatus , <i>C. melitenses</i> , <i>D. catholica</i> , <i>E. cicutarium</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous. OLIVE .	May, June, July
	Geocoridae	Predator	0.02	ADJACENT: <i>U. parviflorus</i> .	July

Lygaeidae	Neutral and predator (facultative)	0.56	ADJACENT: <i>C. albidus</i> , <i>R. officinalis</i> , T. mastichina , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>C. melitenses</i> , <i>A. radiatus</i> , L. longirrostris , S. vulgaris , miscellaneous . OLIVE.	May, June , July	
Miridae	Neutral and predator (Facultative)	3.55	ADJACENT: C. albidus , <i>G. cinerea speciosa</i> , <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: A. radiatus , <i>C. melitenses</i> , D. catholica , <i>E. cicutarium</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous . OLIVE .	May, June , July	
Nabidae	Predator	0.03	ADJACENT: <i>P. dulcis</i> , <i>U. parviflorus</i> . G. COVER: miscellaneous .	May, June	
Pentatomidae	Neutral (some predators / pests)	0.53	ADJACENT: <i>G. cinerea speciosa</i> , <i>R. sphaerocarpa</i> , R. officinalis , <i>T. mastichina</i> , T. zizys gracilis , U. parviflorus . G. COVER: <i>A. radiatus</i> , D. catholica , L. longirrostris , miscellaneous .	May , June, July	
Plataspidae		0.01	G. COVER: miscellaneous .	July	
Psyllidae	Pest	12.52	ADJACENT: <i>C. albidus</i> , <i>G. cinerea speciosa</i> , <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>C. melitenses</i> , <i>L. longirrostris</i> , miscellaneous . OLIVE .	May, June, July	
Rhopalidae	Neutral	0.32	ADJACENT: <i>Q. rotundifolia</i> , <i>R. officinalis</i> , T. zizys gracilis , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>E. cicutarium</i> , <i>S. vulgaris</i> , miscellaneous . OLIVE.	May, June , July	
Tingidae	Neutral	0.20	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>L. longirrostris</i> .	May , June, July	
Hymenoptera	Aphelinidae	Parasitoid	0.05	OLIVE.	June
	Apidae	Pollinator	0.51	ADJACENT: <i>C. albidus</i> , <i>Q. rotundifolia</i> , <i>R. officinalis</i> . G. COVER: <i>A. radiatus</i> , <i>D. catholica</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous . OLIVE .	May , June, July
	Bethylidae	Parasitoid	0.14	ADJACENT: <i>R. officinalis</i> . G. COVER: L. longirrostris . OLIVE.	May
	Braconidae	Parasitoid	0.45	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , D. catholica *, L. longirrostris *, <i>S. vulgaris</i> , miscellaneous . OLIVE.	May , June
	Ceraphronidae	Hyper-parasitoid	0.01	ADJACENT: <i>R. officinalis</i> .	May
	Chrysididae	Parasitoid	0.02	ADJACENT: <i>Q. rotundifolia</i> . OLIVE.	May
	Cynipidae	Neutral	0.02	ADJACENT: <i>Q. rotundifolia</i> , <i>U. parviflorus</i> .	June
	Diapriidae	Parasitoid	0.02	G. COVER: <i>D. catholica</i> , <i>S. vulgaris</i> .	May, June

Elasmidae	Parasitoid	0.10	ADJACENT: <i>Q. rotundifolia</i> , <i>T. mastichina</i> . G. COVER: miscellaneous. OLIVE .	May, June	
Encyrtidae	Parasitoid	0.83	ADJACENT: <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> , miscellaneous. OLIVE .	May, June , July	
Eulophidae	Parasitoid	0.13	ADJACENT: <i>P. dulcis</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zizys gracilis</i> . G. COVER: <i>D. catholica</i> , miscellaneous.	May , June	
Eupelmidae	Parasitoid	0.02	ADJACENT: <i>T. zizys gracilis</i> .	June	
Eurytomidae	Parasitoid	0.03	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> .	May, June	
Figitidae	Parasitoid	0.01	G. COVER: miscellaneous.	June	
Formicidae	Omnivore	21.55	ADJACENT: <i>C. albidus</i> , <i>G. cinerea speciosa</i> , <i>Q. rotundifolia</i> , <i>P. dulcis</i> , <i>R. sphaerocarpa</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , <i>C. melitense</i> , <i>D. catholica</i> , <i>E. cicutarium</i> , <i>L. longirrostris</i> , <i>S. vulgaris</i> , miscellaneous. OLIVE .	May , June , July	
Ichneumonidae	Parasitoid	0.04	ADJACENT: <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> . G. COVER: <i>L. longirrostris</i> .	May , June	
Leucospidae	Hyper-parasitoid	0.01	ADJACENT: <i>Q. rotundifolia</i> .	June	
Megaspilidae	Parasitoid	0.01	ADJACENT: <i>Q. rotundifolia</i> .	May	
Mymaridae	Parasitoid	0.09	ADJACENT: <i>R. officinalis</i> . G. COVER: <i>S. vulgaris</i> , miscellaneous. OLIVE .	May, June	
Platygastridae	Parasitoid	0.04	ADJACENT: <i>G. cinerea speciosa</i> , <i>Q. rotundifolia</i> . G. COVER: <i>L. longirrostris</i> .	May, June	
Pompilidae	Predator	0.02	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> .	June	
Pteromalidae	Parasitoid	0.45	ADJACENT: <i>C. albidus</i> , <i>G. cinerea speciosa</i> , <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>T. mastichina</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> , <i>S. vulgaris</i> , miscellaneous. OLIVE .	May, June , July	
Scelionidae	Parasitoid	0.63	ADJACENT: <i>G. cinerea speciosa</i> , <i>Q. rotundifolia</i> , <i>T. mastichina</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>D. catholica</i> , <i>L. longirrostris</i> , <i>S. vulgaris</i> , miscellaneous. OLIVE .	May, June , July	
Sphecidae	Parasitoid and predator	0.01	ADJACENT: <i>R. officinalis</i> .	May	
Lepidoptera	Praydidae	Pest	0.33	ADJACENT: <i>R. officinalis</i> . G. COVER: miscellaneous. OLIVE .	May, June
Mantodea	Mantidae	Predator	0.08	ADJACENT: <i>P. dulcis</i> , <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>T. zizys gracilis</i> , <i>U. parviflorus</i> . G. COVER: miscellaneous.	June , July

Neuroptera	Chrysopidae	Predator	0.37	ADJACENT: <i>C. albidus</i> , Q. rotundifolia , <i>P. dulcis</i> , <i>T. zigys gracilis</i> . G. COVER: <i>D. catholica</i> , miscellaneous. OLIVE .	May, June , July
	Coniopterygidae	Predator	0.03	ADJACENT: <i>Q. rotundifolia</i> .	May, June
Phasmida	Phasmatidae	Neutral	0.01	ADJACENT: <i>T. zigys gracilis</i> .	June
Raphidioptera	Raphidiidae	Predator	0.02	ADJACENT: <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> .	May, June
Thysanoptera	Acolothripidae	Predator	3.47	ADJACENT: G. cinerea speciosa , <i>Q. rotundifolia</i> , <i>R. officinalis</i> , <i>T. zigys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>A. radiatus</i> , D. catholica , <i>E. cicutarium</i> , L. longirrostris , miscellaneous. OLIVE.	May , June, July
	Phlacothripidae	Neutral	1.39	ADJACENT: G. cinerea speciosa , <i>Q. rotundifolia</i> , <i>R. sphaerocarpa</i> , <i>T. mastichina</i> , T. zigys gracilis , U. parviflorus . G. COVER: <i>A. radiatus</i> , <i>C. melitenses</i> , <i>D. catholica</i> , <i>L. longirrostris</i> , miscellaneous. OLIVE.	May , June, July
	Thripidae	Neutral	4.16	ADJACENT: <i>Q. rotundifolia</i> , R. sphaerocarpa , <i>R. officinalis</i> , <i>T. zigys gracilis</i> , <i>U. parviflorus</i> . G. COVER: <i>C. melitenses</i> , <i>D. catholica</i> , <i>E. cicutarium</i> , L. longirrostris , <i>S. vulgaris</i> , miscellaneous . OLIVE.	May, June , July

Chapter 3

Ground cover presence in organic olive orchards affects the interaction of natural enemies against *Prays oleae*, promoting an effective egg predation

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Abstract

The olive moth, *Prays oleae*, is one of the most common insects that damages olives in the Mediterranean region. The establishment of ground cover within olive orchards has been promoted in this region in recent years to avoid erosion and soil degradation. Nevertheless, its role as a shelter for natural enemies of pests has been controversial. In this study, we have investigated the effectiveness of the biological control of *P. oleae* in organic olive orchards with ground cover (mowed) and without ground cover (tilled). For this, (1) we assessed the relationship between predated eggs and the abundance of natural enemies in both types of orchards; (2) we compared both the potential damage of the pest and the egg hatching in the two types of orchards; and (3) we examined the interaction amongst families of natural enemies and *P. oleae* (as adults and as predated eggs). The results showed that there is a high rate of predation in the studied olive orchards, 81% of the eggs were predated, 12.2% hatched, and 6.9% were live eggs. However, mowed orchards were more effective for controlling *P. oleae* by means of egg predation rather than tilled orchards, i.e., in mowed orchards, whilst the potential damage of the pest was higher, egg hatching was rather low. The structure of the adult arthropod community, i.e., the composition and abundance of families of natural enemies did not differ between the orchards, but the abundance of the

families Anthocoridae, Miridae, and Scelionidae was significantly higher in the mowed orchards. Finally, the interaction amongst natural enemies and *P. oleae* showed that the families that better explained the effects on egg predation were Aeolothripidae, Anthocoridae, Miridae, Chrysopidae (predators), and Formicidae (omnivore). We discuss the results in terms of ecological interactions of trophic guilds and we conclude that the establishment and maintenance of ground cover in organic olive orchards, at least in June and July, is of great significance because it positively affects the egg predation of *P. oleae*. This effect is especially significant when there is a low abundance of natural enemies in the olive orchards.

Introduction

The organic management in olive orchards has been increasing in the Mediterranean region in recent years (Alonso-Mielgo et al., 2001; Torres-Miralles et al., 2017). This type of management frequently involves the establishment of ground cover within the orchard, and when possible, the conservation of adjacent semi-natural habitats (Boller et al., 2004; Landis et al., 2005; Malavolta and Perdakis, 2018). In this region, one of the most common insects that damages olives is the olive moth, *Prays oleae* Bern (Lepidoptera: Praydidae) (Tzanakakis, 2006; Red de alerta e Información fitosanitaria de Andalucía (RAIF), 2018). *Prays oleae*, produces three generations per year: (1) the phyllophagous generation (feeds on olive leaves from November to April, and over-winters in the canopy); (2) the anthophagous generation (feeds on floral buttons from April to June and is the one that lays eggs mainly on the chalice of the olive fruits); and (3) the carpophagous generation (larvae penetrate the fruit and feed on the stone from June to October). All three generations can cause damage to olive orchards and each generation plays an important role in configuring the size of the next generation. However, the carpophagous larvae can generate significant damage to olives, which potentially reduces the yield production. Thus, much of the efforts of pest control are focused on the anthophagous and carpophagous generations (Ramos et al., 1998; Bento et al., 2001).

Recently, it has been observed that olive orchards have great potential to boost populations of natural enemies within the orchard, especially when ground cover is present rather than orchards with bare ground (Herz et al., 2005; Lousão et al., 2007; Cárdenas et al., 2012; Rodríguez et al., 2005; Paredes et al., 2013a). From a “biodiversity-ecosystem function” point of view, semi-natural vegetation interspersed within the growing area or located

at their margins can reinforce microclimate conditions in crops and orchards, and thus provide food and shelter to natural enemies of insect pests (Tscharntke et al., 2012; Wan et al., 2018a). Accordingly, in olive orchards ground cover plays a major role in modulating such a tendency. For example, it has been suggested the existence of synergistic effects between ground cover and natural adjacent vegetation, which jointly promote a high abundance of some (but not all) predator arthropods of *P. oleae* and *Euphyllura olivina* Costa (Hemiptera: Psyllidae) within the olive-tree canopy (Paredes et al., 2013a). Recently, Álvarez et al. (2019a) demonstrated such a synergistic relationship by describing the abundance and movement of the natural enemies which are boosted by the ground cover. Moreover, Villa et al. (2016a) observed that ground cover favoured the parasitism of *P. oleae* larvae by *Ageniaspis fuscicollis* (Dalman) (Hymenoptera: Encyrtidae), whereas herbicide applications had negative effects.

Nonetheless, a higher abundance of natural enemies does not always suppress pest abundance and pest damage, which is a problem that has arisen in conservational biological control (Karp et al., 2018; Rusch et al., 2010). In addition, and unfortunately, it has been recognized that the positive effects generated by a higher biodiversity on ecosystem function, i.e., the control of pests, are conditioned by a myriad of factors (Bianchi et al., 2006; Karp et al., 2018; Rusch et al., 2010; Tscharntke et al., 2016).

Significant efforts have been made by various authors to describe the effects of semi-natural habitats on the abundance of natural enemies and olive pests (Ruano et al., 2004; Paredes et al., 2013a; 2013b; Gkisakis et al., 2016; Villa et al., 2016a; 2016b; Porcel et al., 2017; Álvarez et al., 2019a). However, to the best of our knowledge, there is no study that has focussed on jointly assessing the effects of ground cover on both the abundance of natural enemies and the egg predation of *P. oleae*. The aim of this study was to assess the effectiveness of predation in organic olive orchards with both tilled and mowed management of the ground cover. Specific goals of the study were: (1) to assess the relationship between the abundance of natural enemies and egg predation in both managements, (2) to compare the effectiveness of egg predation between both managements, and (3) to explore the interaction amongst families of natural enemies and *P. oleae* adults and predated eggs using unconstrained ordination. We have hypothesized that when a ground cover is mowed (1) key taxa of natural enemies would be positively affected; therefore (2) the biological control of *P. oleae*, by means of egg predation, would increase.

Material and methods

Study area and sampling design

The study was conducted in three consecutive years from 2011 to 2013 in southern Spain, in the province of Granada. We selected eight organic olive orchards based on (1) the absence of ground cover (tillage in late spring: tilled) and (2) the use of mowing techniques during late spring to maintain the ground cover (mowed) (see Table A3.1 of supplementary data in Appendix; also available at <https://doi.org/10.1016/j.agee.2021.107441>). All the orchards were located in areas surrounded by extended semi-natural habitats interspersed in an olive-orchard matrix including different management systems (Fig. 1). Agricultural management in these organic orchards was based on a system of natural regulation (*sensu* Pajarón Sotomayor, 2006), and thus, pest management did not differ amongst the orchards in the years of study. The distance of planting was 10×10 m, and two varieties of olive trees were grown: Picual (location Deifontes) and Lucio (location Granada). The climatic and topographic conditions were typical of the olive orchards in the study area (see Paredes et al., 2013a; Álvarez et al., 2019a).

June and July are the months when the anthophagous generation of *P. oleae* laid their eggs on newly growing olives. We carried out three different types of sampling in both months per year. Firstly, adult arthropods were collected twice a month by batting four branches per tree over an entomological net (a sample per tree). Olive trees were sampled in randomly selected plots formed by four parallel transects with a separation of 100 m between the transects. Each transect consisted of ten trees of which only five trees were sampled, following a discontinuous sequence, i.e., 20 samples per plot. After being collected, the samples were transported to the Department of Zoology, University of Granada and the Zaidin Experimental Station. The samples were stored individually and maintained at -20°C until the specimens were identified. The arthropods were identified to family level, otherwise specified, and the natural enemies were separated and used for this study. Identification of the natural enemies was based on literature data (see Table A1.1 of supplementary data in appendix). Secondly, 200 olives were collected from four trees (total of 50 olives per tree) randomly selected in each orchard per month (June and July) and the same tree was never re-sampled. The olives were collected to examine the eggs laid by *P. oleae*. Thirdly, *P. oleae* adults were collected using pheromone traps (2 traps per orchard), which were randomly distributed in each orchard and changed every 10 days in June and July. Adults and eggs of *P. oleae* were stored and identified at the Zaidin Experimental Station (CSIC).

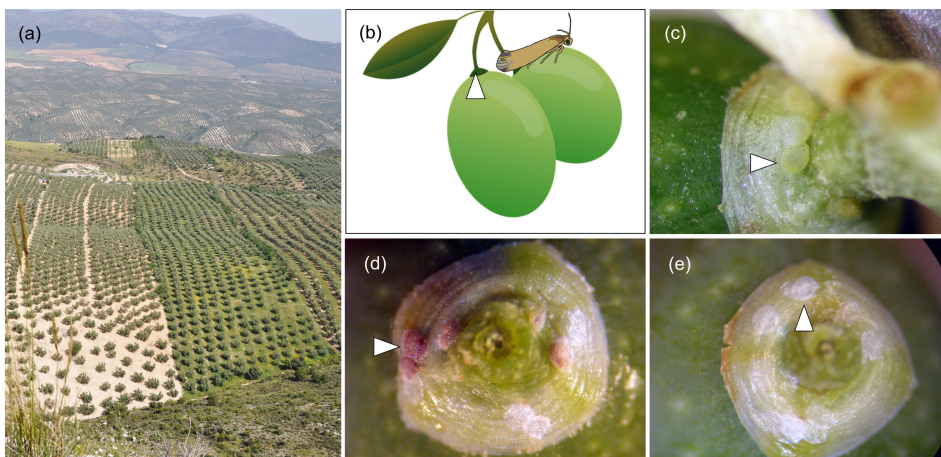


Figure 1. Panoramic view of tilled (left) and mowed (right) organic olive orchards (a). Oviposition site of *Prays oleae* on an olive (b). Appearance of laid eggs of *P. oleae* on an olive: live egg (c), hatched egg (d), and predated egg (e). Site and eggs are indicated by triangles.

Identification of egg damage

The olives were observed with the help of a microscope-sterescoscope to record the number of olives with laid eggs of *P. oleae*, and to characterize the appearance of the eggs (Fig. 1). Then, the number of (1) eggs that had hatched and give place to a larva inside the olive was recorded (hatched eggs); (2) eggs that had not hatched and were still alive (live eggs) and showed a white to yellowish colour; and (3) eggs that had been damaged by predators (predated eggs) and of which only the translucent chorion adhering to the fruit remained.

Data analysis

For comparison purposes the site (orchard) was used as our experimental unit. Thus, we pooled together samples by (1) orchard and (2) months for the three years to avoid pseudo-replication. The orchards were not always the same throughout years, of the eight orchards, four were sampled in 2011 (2 tilled and 2 mowed), five in 2012 (3 tilled and 2 mowed, of which 2 were new), and seven in 2013 (2 tilled and 5 mowed, of which 2 were new) (see Table A3.1 of supplementary data in Appendix; also available at <https://doi.org/10.1016/j.agee.2021.107441>). Monthly samples were considered independently. Therefore, for each site we obtained a representative measure of arthropod abundance and *P. oleae* egg counts.

Raw data of the abundance of natural enemies and *P. oleae* adults was subjected to a logistic regression approach in order to detect differences

between managements. We used this method instead of mean or median comparison because it is a more suitable method to detect statistical differences due to the nature of our experimental unit (see Peng et al., 2002).

We used two approaches to assess the differences in egg predation between the tilled and mowed managements. Firstly, we fitted a generalized linear mixed model (GLMM) using a Poisson tendency to test whether or not the relationship between the abundance of natural enemies and the amount of the predation changed in the two types of managements. We used a GLMM approach because our experimental unit (orchard) changed throughout the years of study, in some of the re-sampled orchards farmers passed from a tilled to a mowed management. Then, to control for such inter-annual variation and site-management variation we included in the model year and site as nested random effects. The number of predated eggs was included as the dependent variable and the type of management and the total abundance of natural enemies were included as fixed effects (see Table A3.2 of supplementary data in Appendix; also available at <https://doi.org/10.1016/j.agee.2021.107441>). Secondly, we assessed the effectiveness of predation by analysing the potential damage of the pest (number of olives with any kind of eggs laid \times 100 / total of observed olives) and the rate of egg hatching (number of hatched eggs \times 100 / all observed eggs minus the predated ones) (for more detail on these parameters see Ramos et al., 1987; Ramos and Ramos, 1990). Then, we subjected the data after this transformation to a logistic regression approach in order to compare both parameters and detect differences between managements.

Finally, non-metric multidimensional scaling (NMDS) was used to assess the overall pattern of species composition of the natural enemies. Data used for the NMDS were square-root transformed and subjected to Wisconsin double standardization (Legendre and Gallagher, 2001). The Bray-Curtis dissimilarity distance was used to compute the resemblance matrix amongst sites. Species scores, representing the different natural enemy taxa were added to the final NMDS plot as weighted averages. Based on the NMDS, smooth surfaces were generated with the data of *P. oleae* adult abundance and predated eggs to explore associations between families of natural enemies and *P. oleae*. Smooth surfaces result from fitting thin plate splines in two dimensions using generalized additive models. The function selects the degree of smoothing by generalized cross-validation and interpolates the fitted values on the NMDS plot represented by lines ranking in a gradient (Oksanen et al., 2018) (see Table A3.3 of supplementary data in Appendix; also available at <https://doi.org/10.1016/j.agee.2021.107441>). This method allowed us to indirectly relate different levels of the abundance of predated eggs and adults

of *P. oleae* with the abundance and correspondence of different families of natural enemies.

Analyses were computed in the R software v.3.6.2 (R Development Core Team, 2018). Accordingly, the “lme4” package (Bates et al., 2015) was used to fit GLMM and the “vegan” package (Oksanen et al., 2018) was used to compute NMDS and smooth surfaces. Package lme4 was used because whilst other packages are more mature and better documented, lme4 is fastest, offers built-in facilities for likelihood profiling and parametric bootstrapping and especially it offers tools for crossed designs (Bates, 2010; Bates et al., 2018).

Results

Overall, 6400 olives were observed with a total of 15,412 laid eggs of *P. oleae*. 81% of the eggs were predated, 12.2% hatched, and 6.9% were live eggs. We collected a total of 62,008 adults of *P. oleae* and a total of 4001 natural enemy arthropods, of which 36 families were identified (Table 1). 70.7% of the natural enemy specimens were predators, 26.8% were omnivores, and 2.5% were parasitoids. The most abundant families of predators were: Anthocoridae, Miridae (order Hemiptera); Chrysopidae (order Neuroptera); and Thomisidae (order Araneae). Amongst hymenopterans the most abundant family of parasitoids was the Scelionidae, and Formicidae was the most abundant family of omnivores and of all the natural enemies.

The structure of the arthropod community, i.e., the composition and abundance of arthropod families, is mostly the same between tilled and mowed orchards (Fig. 2). However, six families of natural enemies were present only in one of the two managements, i.e., mowed: Liocranidae, Uloboridae (order Araneae), Nabidae (order Hemiptera), Aeolothripidae (order Thysanoptera); and tilled: Malachiidae (order Coleoptera), Ichneumonidae (order Hymenoptera). Moreover, the abundance of three families of natural enemies was significantly higher in the mowed orchards, Anthocoridae (Wald $\chi^2 = 3.928$, $df = 1$, $p = 0.047$), Miridae (order Hemiptera) (Wald $\chi^2 = 5.247$, $df = 1$, $p = 0.021$), and Scelionidae (order Hymenoptera) (Wald $\chi^2 = 5.071$, $df = 1$, $p = 0.024$) (Fig. 2), as well as the abundance of *P. oleae* adults (Wald $\chi = 4.624$, $df = 1$, $p = 0.031$).

Table 1. Relative abundance (RA), acronyms, presence in orchards: tilled (T) and mowed (M), and trophic guilds of the families of natural enemies ($n = 36$) identified in organic olive orchards. Numbers represent presence (1) and absence (0).

Guild	Order	Family	Acronym	T	M	RA (%)
Omnivores	Dermaptera	Forficulidae	Fo	1	1	1.51
	Hymenoptera	Formicidae	For	1	1	98.49
Parasitoids	Hymenoptera	Braconidae	Bra	1	1	8.49
		Elasmidae	El	1	1	12.26
		Encirtidae	En	1	1	5.66
		Eulophidae	Eu	1	1	3.77
		Ichneumonidae	Ich	1	0	0.94
		Pteromalidae	Pt	1	1	26.42
		Scelionidae	Sc	1	1	42.45
Predators	Araneae	Araneidae	Ar	1	1	1.48
		Corinidae	Co	1	1	0.74
		Linyphiidae	Li	1	1	0.60
		Liochranidae	Lio	0	1	0.07
		Oxyopidae	Ox	1	1	2.41
		Philodromidae	Ph	1	1	2.35
		Salticidae	Sa	1	1	6.61
		Theridiidae	The	1	1	1.17
		Thomisidae	Tho	1	1	19.95
		Uloboridae	Ul	0	1	0.03
	Coleoptera	Cantharidae	Ca	1	1	0.74
		Carabidae	Car	1	1	0.07
		Coccinelidae	Coc	1	1	6.17
		Malachiidae	Ma	1	0	0.07
		Staphylinidae	St	1	1	0.10
		Mantodea	Mantidae	Man	1	1
	Diptera	Asilidae	As	1	1	0.13
		Empididae	Em	1	1	0.64
	Hemiptera	Anthocoridae	An	1	1	11.64
		Lygaeidae	Ly	1	1	0.37
		Miridae	Mi	1	1	31.05
		Nabidae	Na	0	1	0.07
		Reduviidae	Re	1	1	1.11
	Neuroptera	Chrysopidae	Chr	1	1	10.43
		Coniopterygidae	Con	1	1	0.54
	Raphidioptera	Raphidiidae	Ra	1	1	0.13
	Thysanoptera	Acolothripidae	Ae	0	1	0.87

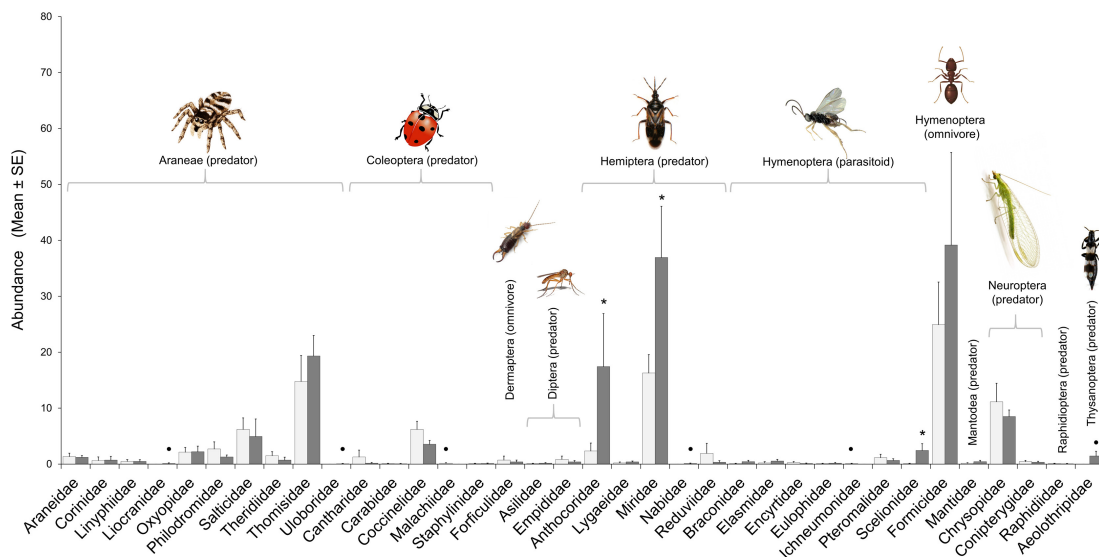


Figure 2. Natural enemy abundance classified by management: tilled (white bars) and mowed (grey bars). Families are grouped by orders and trophic information. An asterisk indicates that a family of natural enemy showed significantly differences between managements. Black points indicate the families that were present in only one of the managements.

GLMM analysis showed that there is a positive relationship between the abundance of natural enemies and the amount of predated eggs in both managements (Fig. 3). Both effects, natural enemy abundance and management, were statistically significant (Table 2). The relationship tended to be high in the mowed orchards and this pattern appeared at the lowest abundance of natural enemies (Fig. 3).

Furthermore, there are differences in the effectiveness of predation of *P. oleae* eggs between managements, i.e., in mowed orchards the potential damage of the pest was significantly higher (Wald $\chi^2 = 8.996$, $df = 1$, $p = 0.002$) but egg hatching was significantly lower (Wald $\chi^2 = 5.295$, $df = 1$, $p = 0.021$) than tilled orchards.

The results of the NMDS, which represents the relationship and structure of the communities of natural enemies and their association with egg predation and the abundance of adults of *P. oleae*, are shown in Fig. 4. Accordingly, the families Araneidae, Linyphiidae, Liocranidae, Oxiopidae, Salticidae, Theridiidae, Thomisidae, Uloboridae (order Araneae); Coccinellidae, Malachiidae, Staphylinidae (order Coleoptera); Anthocoridae, Lygaeidae, Miridae, Nabidae, Reduviidae (order Hemiptera); Braconidae, Elasmidae, Formicidae, Pteromalidae, Scelionidae (order Hymenoptera); Chrysopidae (order Neuroptera); Mantidae (order Mantodea); Raphidiidae

(order Raphidioptera); and Aeolothripidae (order Thysanoptera) were associated with elevated egg predation (Fig. 4a). However, the families Corinidae, Oxiopidae, Salticidae (order Araneae); Cantharidae, Coccinelidae (order Coleoptera); Lygaeidae (order Hemiptera); Encyrtidae, Eulophidae, Ichneumonidae (order Hymenoptera); and Coniopterygidae (order Neuroptera) were associated with a low abundance of *P. oleae* adults (Fig. 4b). In this type of analysis, an association of a family of natural enemies with a high number of predated eggs implies that these taxa could be involved in egg predation (or egg damage), increasing predation rates. Conversely, an association with a low or intermediate abundance of adults of *P. oleae* means that such taxa could be feeding on adults, decreasing their abundance to a lower rate.

Based on the NMDS, trophic status, size, and the morphological features of each family, the families that are more likely to damage the eggs of *P. oleae* are: Coccinelidae, Staphylinidae (order Coleoptera); Anthocoridae, Miridae, Nabidae, Reduviidae (order Hemiptera); Braconidae, Formicidae (order Hymenoptera); Chrysopidae (order Neuroptera) and Aeolothripidae (order Thysanoptera). However, we have ruled out the families that had (1) a low abundance in both managements (Coccinelidae, Staphylinidae, Nabidae, Reduviidae), and (2) no predatory form of feeding (parasitoids: Braconidae). Hence, only Aeolothripidae, Anthocoridae, Chrysopidae, Formicidae, and Miridae are the families that could explain the differences in egg predation between the tilled and mowed orchards.

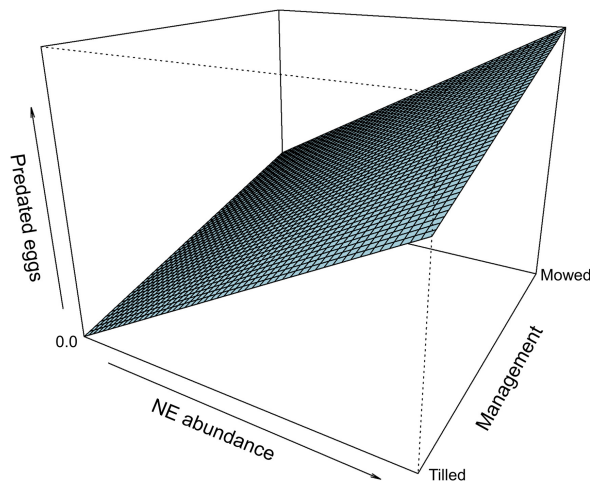


Figure 3. Relation amongst variables according to GLMM analysis: egg predation, the natural enemy (NE) abundance, and management.

Table 2. Fixed effects of the fitted model (GLMM) explaining egg predation: type of management and natural enemy abundance.

Variable	df	Wald χ^2	<i>p</i>
Management (tilled or mowed)	1	4.524	0.033
Natural enemy abundance	1	5.841	0.015

Discussion

In this study, we have assessed the effectiveness of the biological control of *P. oleae* in organic olive orchards in terms of egg predation by natural enemies. As expected, the presence of ground cover within the orchards positively affected the predation of eggs laid by the antophagous generation of *P. oleae*, and thus, egg predation was more effective in mowed orchards than in tilled orchards.

Organic orchards are very balanced and stable systems (Vossen, 2007). The orchards that we measured were very similar in their agricultural practices and in their landscape structure (with the exception of the ground cover management). This was reflected in the composition and abundance of families of natural enemies. Both local and large-scale factors can affect the abundance of natural enemies and pests in olive orchards, such as less pesticide application or microclimate conditions and landscape diversity or patch size, respectively (Boccaccio and Petacchi, 2009; Rodríguez et al., 2009; Ortega and Pascual, 2014; Villa et al., 2016a; 2020; Morente et al., 2018; Álvarez et al., 2019a; 2019b; 2021b). This may explain why the structure of the arthropod community tended not to differ in our study. Nonetheless, it has been shown that the abundance of natural enemies is positively affected by ground cover (Lousão et al., 2007; Cárdenas et al., 2012; Rodríguez et al., 2012; Álvarez et al., 2019a; 2019b). When analysing the relationship between egg predation and natural enemy abundance in both managements, mowed orchards tended to have higher predation as the abundance of natural enemies increased. Interestingly, the highest differences in predated eggs between mowed and tilled orchards appeared especially when the levels of natural enemies were low. This implies that the differences in predation were caused by a subtle, but still higher abundance of natural enemies.

On the other hand, previous studies on olive orchards showed that the presence of ground cover had no effect on the abundance of *P. oleae* adults when tilled and mowed orchards were compared (Paredes et al., 2013b; Paredes et al., 2015a).

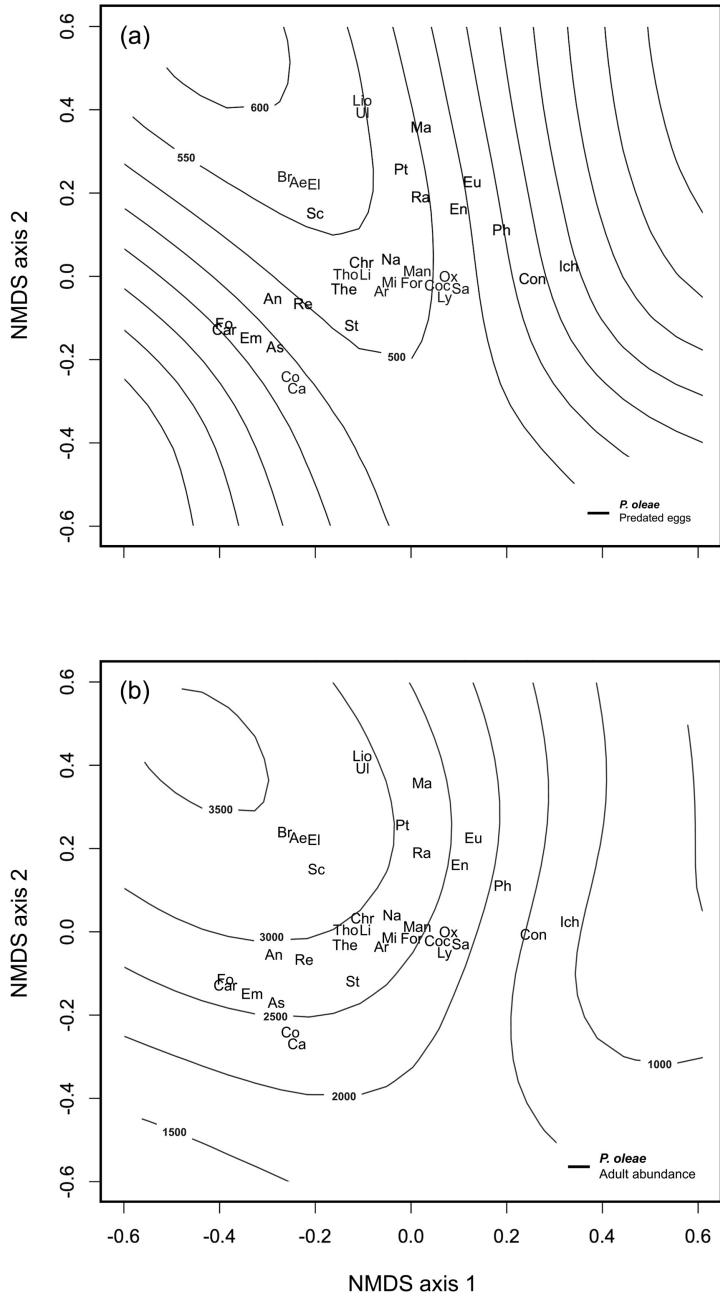


Figure 4. Non-metric multidimensional scaling (NMDS) of the total abundance of natural enemies. Proximity amongst families of natural enemies within the ordination plot indicates that their abundances are positively related. Lines (smooth surfaces) represent different levels, in the form of a gradient, of pre- dated egg counts (A) and adult abundance (B) of *P. oleae*, according to generalized additive models. See family acronyms in Table 1.

Nonetheless, it has been found that certain plant species in the ground cover could promote an increase in the abundance of (Villa et al., 2016c). Our results follow such a tendency, ground cover may increase the abundance of adults of *P. oleae*. Based on the former results one could assume that ground cover does not promote biological control by itself. However, we showed that egg hatching of *P. oleae* is lower in orchards with a ground cover, and thus, less hatching implies that there are potentially less larvae of *P. oleae* that could damage olives. Therefore, we can assume that the effects of the ground cover to control *P. oleae* lead towards the predation of eggs rather than attacking the adults.

Regarding the predators, our results are in agreement with previous studies that have recorded the role of predator heteropterans, such as Anthocoridae and several species of Miridae as major predators of olive pests (Mazomenos et al., 1994; Cantero, 1997; López-Villalta, 1999; Morris et al., 1999; Alvarado et al., 2004; Paredes et al., 2013a; 2015b). The fact that these groups are positively affected by the presence of ground cover suggests their sensitivity to perturbation. However, it has been shown that predator heteropterans are more sensitive to the presence of native adjacent vegetation rather than ground cover, although some species such as *Deraeocoris punctum* (Rambur), have shown the opposite (Paredes et al., 2013a) implying that differences at species level are important. These inconsistencies may be the result of the movement of the natural enemies across habitats within and outside olive orchards. For example, Álvarez et al. (2019a) showed that predators and parasitoids move from ground cover to adjacent vegetation and olive trees, respectively, but omnivores move from adjacent vegetation to ground cover and olive trees, specifically when the ground cover withers. In addition, there is evidence that *Anthocoris nemoralis* (Fabricius) (Plata et al., 2017) and some lacewings (Chrysopidae) (Porcel et al., 2017) move from ground cover to adjacent vegetation.

Lacewing larvae, for example, have been described as one of the main natural enemies that attack *P. oleae* (Bento, 1999; Torres, 2006; Villa et al., 2016b). Lacewing larvae are positively affected by ground cover (Villa et al., 2016b). Interestingly, in our study this group did not differ between the tilled and mowed orchards, although we mainly sampled adults which are very stable geographically (Alcalá-Herrera et al., 2019b). This could be explained by the fact that winged adults have high ranges of movement (Rusch et al., 2010) and it is possible that they move across the region from one orchard to another to lay their eggs. Nevertheless, in our study, lacewings were related with high levels of egg predation, which supports the hypothesis that this group is of great importance in the biological control of *P. oleae*.

Another family that showed interesting patterns was Aeolothripidae. In our study, it showed an important interaction with egg predation, but this family was present only in the mowed orchards. The role of Aeolothripidae as a natural enemy of olive pests has been poorly documented (reviewed by Torres, 2006). It is known that Aeolothripidae attack other Thysanoptera, however, it also has been suggested that some genera of Aeolothripidae can feed on the eggs of lepidopterans (Lewis, 1973). Moreover, some species of European *Aeolothrips* sp. can feed on mites, larvae, and eggs of psyllids and whiteflies, as well as on aphids (Trdan et al., 2005). Thus, the role of Aeolothripidae in the predation of the eggs of *P. oleae* should be investigated more thoroughly.

In the case of the omnivores, it is known that ants are important predators of *P. oleae* (Morris et al., 1999; 2002). Our results showed that ants had the highest abundance within olive orchards, however, we did not find differences in the abundance of ants between mowed and tilled orchards. This is of great importance, because a predator that is not affected by management and has high abundances could be used to enhance local biological control strategies. Several studies have shown *Tapinoma* ants as the most abundant type of ant within olive orchards, sometimes representing more than 50% of the relative abundance amongst omnivores within olive orchards (Morris et al., 1998a; 1998b; 1999; 2002; Morris and Campos, 1999; Redolfi et al., 1999; Pereira et al., 2004; Rodríguez et al., 2005; Santos et al., 2007b; Campos et al., 2011), which makes it one of the strongest candidates for controlling *P. oleae*. Indeed, some species of the *T. nigerrimum* complex are beneficial in olive orchards in the southern area of the Iberian Peninsula (Seifert et al., 2017). Furthermore, it has been found that it is possible to boost the abundance and trophic interactions of *Tapinoma* ants within the canopy of olive trees with mature ground cover (Álvarez et al., 2019b) and less pesticide use (Morente et al., 2018).

In addition, we found that the family Braconidae shows an important association with predators upon egg predation. Only one species of Braconidae is known to parasitize the eggs of *P. oleae*: *Chelonus eleaphilus* Silv (Arambourg, 1986). This species is a poliembryonic parasite, i.e., females oviposit inside the eggs of their prey (Grbic and Strand, 1998; Segoli et al., 2010). This species is one of the most important and specific parasitoids of *P. oleae* in the Mediterranean region. The fact that Braconidae populations respond to ground cover management may be due to their need for flowers to feed on (Nave et al., 2016). On the other hand, in our analysis Elasmidae and Scelionidae showed a similar pattern to Braconidae, but Scelionidae had higher abundances in mowed orchards. Some species of the family

Scelionidae may attack other natural enemies causing intra-guild predation, such as *Telenomus acrobater* Giard, which has been described as parasitizing the eggs of lacewings (Alrouechdi and Panis, 1981; Campos, 1986; Rodríguez et al., 2005).

Finally, it is important to point out that the species composition of natural enemies showed interesting patterns (Fig. 4). The fact that the tendency of the variable predated eggs depends on the tendency of *P. oleae* adult abundance should be taken into account, i.e., the more *P. oleae* adults there are, the more the eggs they can lay, and thus, be predated. This is why the panels in Fig. 4, are very similar. However, the families that are related with the predation on adults are well defined. The spiders are the arthropods that are most likely to predate adults, which is in agreement with previous studies (Paredes et al., 2015b). Interestingly, and according to what we have mentioned, in the NMDS natural enemies assembled in different groups that correspond to their trophic status. Consequently, several assemblages might fulfil complementary functional roles determined by the way they catch prey (Uetz et al., 1999; Straub et al., 2008). For example, it has been found that a single assemblage of natural enemies, such as *A. nemoralis*, *Brachynotocoris* sp., and *Pseudoloxops coccineus* (Meyer Dur), is better correlated with the control of *P. oleae* (Paredes et al., 2015b). The assemblage of these species has been explained as the result of the (complex) life cycle of *P. oleae* (Wilby et al., 2005) and their preference for eggs (Paredes et al., 2015b). In addition, the arachnid families Araneidae and Linyphiidae, which are orb-weaving and sheet-weaving spiders respectively, are most likely to play a role in reducing the adults of *P. oleae* (Paredes et al., 2015b).

Conclusions

A mowing management of the ground cover within olive orchards positively affected the key natural enemies that play an important role predated *P. oleae*, even though arthropod communities were similar between tilled and mowed orchards. Hence, the establishment and maintenance of ground cover in organic olive orchards is of great significance due to its potential to promote the biological control of *P. oleae* by means of egg predation, especially when there is a low abundance of natural enemies. The hypothesis is that an olive orchard with ground cover produces more active and voracious natural enemies, and it may allow the establishment of more and efficient key predators. To the best of our knowledge this is the first time that this type of empirical data has been recorded for olive orchards. The fact that in our study the differences in the biological control of pests were shown by eggs rather than the abundance of adults suggests that the studies on

biological control should focus on specific instars of the development of pests where the biological control is more likely to occur, which is a concern that has already been pointed out for conservation biological control (Karp et al., 2018). Thus, the effect of landscape structure on egg predation of *P. oleae* specifically in olive orchards needs to be investigated more thoroughly.

Authors contributions

H.A.A. and F.R. conceived the ideas. F.R. and M.C. designed fieldwork and F.R., R.J.M., and M.M. conducted fieldwork. H.A.A. performed data analysis and write the manuscript. All authors revised the final version and gave their approval for submission.

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Chapter 4

The biological control of *Prays oleae* in organic olive orchards is enhanced in diversified landscapes with high amounts of scrublands at lower spatial scales

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Abstract

The assumption that more semi-natural habitats within agricultural landscapes increase biological control is controversial and relies on how natural enemies respond to landscape composition and configuration. Recent accounts suggest that the damage and adult abundance of *Prays oleae*, is affected by semi-natural habitats and landscape diversity. So, in this study we assessed which vegetation within semi-natural habitats is the best ecological infrastructure to avoid *P. oleae* pressures and increase biological control at the landscape scale. For this, we collected data from organic olive orchards in four years. Then, we subjected the abundance of *P. oleae* adults, the abundance of natural enemies, and three metrics of natural enemy-pest functionality to a multi-model inference with a multi-scale approach. Our results show that when semi-natural habitats are analysed dividing them into specific cover categories the effects produced on our response variables followed different patterns with higher effects at a small spatial scale, however, the landscape composition and configuration variables produced essentially the same type of effect on the response variables across all spatial scales. Furthermore, the proportion of sparse scrubland in the landscape jointly with the presence of a mowed ground cover is the main factor driving the biological control of *P. oleae* by means of egg predation, but diversified landscapes with dense edges are needed to reduce *P. oleae* adult abundance.

We agree that the synergy between scrublands and ground covers in olive orchards within diversified landscapes is the key factor that helps to control *P. oleae* in a more efficient way by directing the biological control to eggs rather than adults. Our findings can help farmers and technicians to improve the ecological management of olive orchards by promoting the conservation and establishment of diversified semi-natural habitats, with a special interest in scrubland patches, maintaining mowed ground covers within olive orchard landscapes.

Introduction

There is a growing interest in suitable plant species for ecological restoration and ecosystem services within agroecosystems, e.g., to prevent soil erosion, maintain soil fertility and enhance the biological control of insect pests (Oldfield, 2019; Pedrini et al., 2019). Currently, in the European Union policies are implemented with the aim of restoring semi-natural habitats, such as ground cover and adjacent vegetation within vineyards, citrus, almond, and olive orchards (Malavolta and Perdakis, 2018).

From a “biodiversity-ecosystem function” point of view, semi-natural habitats interspersed within the growing area or located at the edges can reinforce microclimate conditions in crops and orchards, and thus provide food and shelter to natural enemies of insect pests (Clemente-Orta and Álvarez, 2019; Tschamtker et al., 2016; Wan et al., 2018a). In regard to biological control, the assumption that more semi-natural habitats in agricultural landscapes increase biological control is controversial and relies on how natural enemies respond to landscape composition (amount and diversity of land cover types) and landscape configuration (spatial arrangement of land cover types). Accordingly, it is paramount to detail and understand the features of the vegetation within semi-natural habitats that affect natural enemies at the local and landscape scale (with information of several years and scales) to achieve farming (yield), conservation, and ecosystem service’s goals.

It has been shown that in the Mediterranean region olive orchards have great potential to boost populations of the natural enemies of olive pests thanks to the presence of semi-natural habitats (Álvarez et al., 2019a; 2021a; Gkissakis et al., 2016; Paredes et al., 2013a). This is due, in part, to the existence of synergistic effects between semi-natural habitats which jointly promote a high abundance of some (but not all) predators of olive pests (Paredes et al., 2013a). Álvarez et al. (2019a) demonstrated such a synergistic

relationship by describing the abundance and movement of natural enemies between different semi-natural habitats and olive orchards. However, the tendency produced by this synergistic relationship is modulated by the complexity of the semi-natural habitats, i.e., habitat complexity (plant richness and plant arrangement and scattering) affects key arthropods that predate olive pests differently, suggesting that each key arthropod taxon responds to their individual needs for plant resources but forming groups modulated by the gradient of complexity (Álvarez et al., 2021b). This pattern is especially seeing in predators and omnivores. Thus, the higher the complexity of a semi-natural habitat, the higher the abundance and richness of a given arthropod community (Álvarez et al., 2021b), which is a pattern found in natural ecosystems (Haddad et al., 2001; Knops et al., 1999).

Álvarez et al. (2019b) pointed out that an important point of view to consider concerning the biological control of olive pests is the maturity of ground covers, which affects the structure and complexity of the trophic network of the olive canopy. They showed that the taxa of herbivores, omnivores, and parasitoids do not change drastically between mature and non-mature covers whilst there is an increase in predator taxa in mature ground covers, which subsequently produced an increase in the vulnerability of herbivores. In other recent study, Álvarez et al. (2021a) showed the role of the ground cover comparing a mowed vs tilled management in organic olive orchards surrounded by natural habitats. They found that there is a high rate of predation in both type of organic orchards, over an 80 %, but whereas in mowed orchards natural enemy taxa and abundance did not essentially differ, and the potential damage of the pest was higher, egg hatching was rather low. Thus, they concluded that mowed orchards were more effective for controlling pests by means of egg predation rather than tilled orchards. This effect was especially significant when there was a low abundance of natural enemies (e.g., at the end of the spring).

Despite the efforts of different authors to assess the effects of ground covers and semi-natural habitats in olive orchards, the number of studies focusing jointly on olive pests, natural enemies, or their interaction at the landscape scale are rather few. In relation to *Prays oleae*, one of the most important olive pests in the region, recent accounts suggest that pest adult abundance and pest damage is sensitive to landscape structure such as the amount of semi-natural habitats, landscape diversity, or several metrics of landscape configuration (Alves et al., 2021, Martínez-Núñez et al., 2020; 2021; Paredes et al., 2019; Villa et al., 2020; 2021). Conversely, studies which focused on natural enemy-pest interactions at the landscape scale have suggested that natural enemies such as *Chrysoperla carnea* complex, *Anthocoris*

nemorialis, or *Tapinoma nigerrimum* complex are positively correlated with the pest (or pest damage) but are affected by landscape structure and field management differently than the pest (Alves et al., 2021; Martínez-Núñez et al., 2021; Paredes et al., 2019). Nonetheless, this information only highlights the need for in-depth knowledge to elucidate which vegetation patches and semi-natural habitats are the best ecological infrastructures to avoid pest pressures and increase natural enemy abundance and biological control at the landscape scale.

Based on the effects previously reported for the overall proportion of semi-natural habitats over pest and natural enemy abundance in olive orchards, and to further extend the knowledge of species–environment relationships in this agroecosystem, in the present study we subjected the abundance of *P. oleae* adults, natural enemies, and three metrics of natural enemy-pest functionality to a novel analysis methodology with a multi-scale approach in the landscape. So, we aimed to respond the following questions: (1) What effects are produced by semi-natural habitats when they are divided into specific cover categories? (2) Is the patch configuration of such categories an important factor in the landscape? and (3) How do these effects vary at different spatial scales of study?

Material and methods

Study area

The study was conducted in the years 2011, 2012, 2013 and 2015 in southern Spain, in the province of Granada. We selected six organic olive orchards based on (1) the absence of ground cover (tillage in late spring: tilled) and (2) the use of mowing techniques during late spring to maintain the ground cover (mowed) (see Table A4.1 of supplementary data in Appendix). All the orchards were located in areas surrounded by extended natural habitats interspersed in an olive-orchard matrix, which includes different management systems, in three different localities (two orchards per locality, north and south): Deifontes (37°19' N and 3°34' W), Granada (Dehesa del Generalife, 37° 10' N and 3° 34' W), and Piñar (37°24' N and 3°29' W) (Fig. 1a).

Agricultural management in these organic orchards did not differ amongst the orchards in the years of study. The distance of planting was 10 × 10 m, and two varieties of olive trees were grown: Pícuál (location of Deifontes and Piñar) and Lucio (location of Granada). The climatic and topographic conditions were typical of the olive orchards in the study area (see Álvarez et al., 2019a; Paredes et al., 2013a).

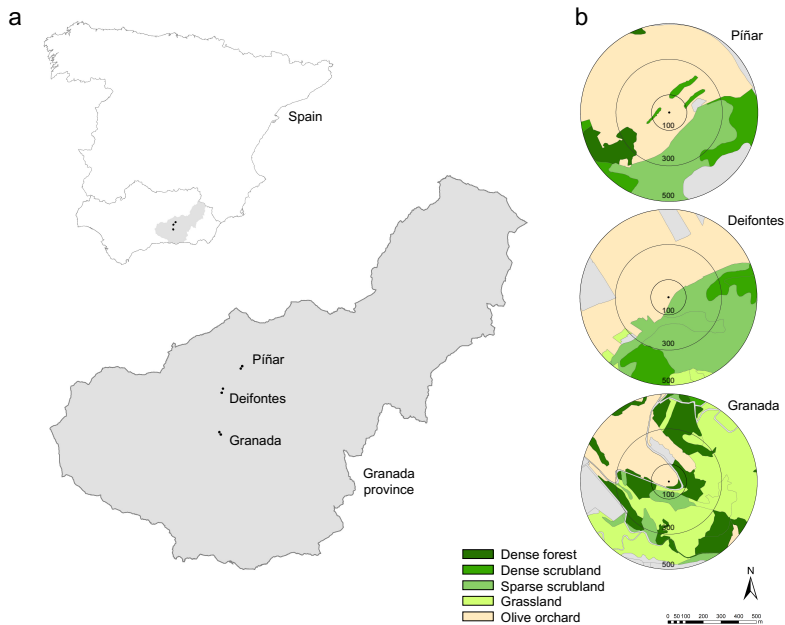


Figure 1. Study area in the south of Spain. a Locations of the sampled landscapes in Andalusia, province of Granada. b Example of land cover categories within buffers at different spatial scales (radii of 100, 300, and 500m) in the studied locations.

Sampling design

Prays oleae adults and eggs

June and July are the months when the anthophagous generation of *P. oleae* laid their eggs on newly growing olives. Firstly, 200 olives were collected from four randomly selected trees (total of 50 olives per tree) in each orchard per month (June and July) and the same tree was never re-sampled. The purpose of this was to examine the eggs laid by *P. oleae*. Secondly, *P. oleae* adults were collected using pheromone traps (2 traps per orchard), which were randomly distributed in each orchard and changed every 10 days. We also used a modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA) to collect adults directly on the olive tree canopy. Adults and eggs of *P. oleae* were stored and identified at the Zaidin Experimental Station (CSIC).

Natural enemies

Adult arthropods were collected twice a month by (1) batting four branches per tree over an entomological net and by (2) using a modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA) (a sample per tree). Olive trees were sampled in randomly selected plots formed by four parallel transects with a separation of 100 m between the transects. Each transect consisted of ten trees of which only five trees were sampled, following a discontinuous sequence, i.e., 20 samples per plot. After being collected, the samples were cooled and transported to the Department of Zoology, University of Granada and the Zaidin Experimental Station (CSIC). The samples were stored individually and maintained at -20°C until the specimens were identified. The arthropods were identified to family level, otherwise specified, and the spider and insect potential natural enemies (NE) that showed high abundances were separated and used for this study. Identification of the NE was based on the records in the entomological collection of the University of Granada and the literature data (see Table A1.1 of supplementary data in Appendix).

Identification of egg damage

The olives were observed with the help of a microscope-stereoscope to record the number of olives with laid eggs of *P. oleae*, and to characterize the appearance of the eggs. Then, we recorded the number of (1) eggs that had hatched and give place to a larva inside the olive (hatched eggs); (2) eggs that had not hatched and were still alive and showed a white to yellowish colour (live eggs); and (3) eggs that had been damaged by predators and of which only the translucent chorion adhering to the fruit remained (predated eggs).

Factors measured at landscape scale

Based on the cover types for Andalusia obtained from the information system of occupation of the Spanish soil database at 1:10 000 (SIOSE, www.siose.com) in ArcGis software, and following the definition of classes in the technical guide of the Andalusian soil vegetation cover and uses map (see forest and natural areas, Junta de Andalucía, 2007), 23 cover types of vegetation were found in the sampled areas.

We took into account the olive orchard and the cover types within natural vegetation and then we grouped the cover types in five cover categories, i.e., dense forest, dense scrubland (with and without forest formation), sparse scrubland (with and without forest formation), grassland

(with and without forest formation), and olive orchard (see Junta de Andalucía, 2007).

Then we extracted, using the software FRAGSTAT (McGarigal et al., 2012), the area percentage of the five cover categories in the landscape and five descriptors of patch features at the landscape scale: (1) the edge density (ED: equals the sum of the lengths in m of all edge segments in the landscape, divided by the total landscape area in m², multiplied by 10,000. It reports edge length on a per unit area basis that facilitates comparison among landscapes of varying size); (2) the perimeter area ratio mean (PARA_MN: equals the ratio of the patch perimeter (m) to area (m²), and equals the sum, across all patches in the landscape (mean). It is a measure of shape complexity without standardization to a simple Euclidean shape (e.g., square), but it is not scale independent); (3) the Shannon diversity index applied to landscapes (SHDI: equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion. It increases as the number of different patch types (i.e., patch richness) increases and/or the proportional distribution of area among patch types becomes more equitable); (4) the aggregation index (AI: equals the number of like adjacencies involving the corresponding class, divided by the maximum possible number of like adjacencies involving the corresponding class, which is achieved when the class is maximally clumped into a single, compact patch; multiplied by 100 to obtain a percentage. It is computed as an area-weighted mean class aggregation index, where each class is weighted by its proportional area in the landscape); and (5) contagion index (CONTAG: equals minus the sum of the proportional abundance of each patch type multiplied by the proportion of adjacencies between cells of that patch type and another patch type, multiplied by the logarithm of the same quantity, summed over each unique adjacency type and each patch type; divided by 2 times the logarithm of the number of patch types; multiplied by 100 to obtain a percentage, i.e., when a single class occupies a very large percentage of the landscape, contagion is high, and vice versa. This index is affected by both the dispersion and interspersion of patch types).

After that, each variable in the landscape surrounding the central point of each sample area within radii of 100 m, 300 m, and 500 m were calculated (Fig. 1b). Finally, the correlations amongst landscape variables were assessed using Spearman rank correlation coefficients to build models.

Data analysis

For comparison purposes the site (orchard) was used as our experimental unit. Thus, we pooled together samples by (1) orchard and (2) months for the four years to avoid pseudo-replication. The orchards were not always the same throughout years, of the six orchards, three were sampled in 2011 (2 tilled and 1 mowed), three in 2012 (1 tilled, 1 mowed, and 1 tilled and mowed), four in 2013 (1 tilled and 3 mowed, of which 1 was new), and three in 2015 (all mowed, of which 1 was new) (see Table A4.1 of supplementary data in Appendix). Monthly samples were considered independently. We used this approach because our experimental unit (orchard) changed throughout the years of study, for example, in some of the re-sampled orchards farmers passed from a tilled to a mowed management. Information of year, site ID, and management in each orchard was used to control for inter-annual variation and site-management variation.

We used as the dependent variables (1) the abundance of *P. oleae* adults, (2) the abundance of NE spiders: Aranidae, Corinidae, Liniphidae, Liochranidae, Oxiopidae, Philodromidae, Salticidae, Therididae, Thomisidae, and Uloboridae, (3) the abundance of NE insects: Anthocoridae, Miridae (Heteroptera), Formicidae (Hymenoptera), and Chrysopidae (Neuroptera). Accordingly, the families of insect and arachnid were selected based on the results of Álvarez et al. (2021a) as the potential NE that are most likely to predate *P. oleae* eggs (i.e., NE insects) and *P. oleae* adults (i.e., NE arachnids). In addition, we used three metrics of NE-pest functionality as dependent variables: (4) the pest damage (potential damage of the pest to the orchard obtained as the number of olives with any kind of eggs laid \times 100 / total of observed olives), (5) the egg hatching (number of hatched eggs \times 100 / all observed eggs minus the predated ones), and (6) the egg predation (rate of predatory activity: number of predated eggs \times 100 / all observed eggs).

To analyse the relationships of NE and pest abundance and the metrics of NE-pest functionality with the landscape variables, firstly we standardized the landscape variables (mean centered and scaled) for each spatial scale (i.e., 100, 300, and 500 m). Secondly, linear mixed models (LMMs, for the normal distribution) and generalized linear mixed models (GLMMs, for the negative binomial distribution) were fitted for each spatial scale. We included per model one of the dependent variables and (1) the landscape variables as fixed factors as independent variables and (2) year, site ID, and management as random factors. Models were analysed separately for the landscape composition variables (cover categories) and landscape configuration variables (descriptors of patch features). Overall, we fitted a total of 36 models. Residuals were graphically inspected with qqplot and histograms to ensure

there was no violation of normality and homoscedasticity assumptions on the models. After that, each of the models were subjected to a multi-model inference, this procedure fits models using all possible combinations of predictors and weights them using the Akaike information criterion (AIC) using the ‘dredge function’.

All analyses were computed in the R software v.4.0.3 (R Developmental Core Team, 2020). We used the lmer function and glmer.nb function of the lme4 and MASS packages to fit LMMs and GLMMs, respectively. Multi-model inference was computed using the MuMIn package.

Results and discussion

Overall, 7 200 olives were observed with a total of 18 831 laid eggs of *P. oleae*. Pest damage was of 76.15 %. However, 82.57 % of the eggs were predated, 11.60 % hatched, and 5.93 % were live eggs. We collected a total of 61 183 adults of *P. oleae* and a total of 3 312 NE of which 930 were arachnids and 2 382 were insects. 20.40 % of the NE insects were predators and 79.60 % were omnivores. The most abundant families of NE arachnids were: Thomisidae, Salticidae, and Oxiopidae, but amongst the NE insects, the most abundant family of predators was Chrysopidae (followed by Anthocoridae), and the most abundant family of omnivores was Formicidae (followed by Miridae). These results show that there is a high amount of egg predation in organic olive orchards, as previous studies have suggested (Álvarez et al., 2021a), and that the most abundant NE in these olive orchards are indeed the taxa that predate olive pests (Álvarez et al., 2021a; Paredes et al., 2019).

Multiple scales for examining cover categories in the landscape

A multi-scale approach is especially useful when the ecological neighborhood of the organism–landscape interaction is unknown (Holland and Yang, 2016). Also, it has been recognized that the problem of the scale at which ecological processes should be considered is critical if we want to produce general predictions, because ecological dynamics are always stochastic at small scales, but variability is conditional on the scale of description (Chave, 2013). Therefore, results from multi-scale studies could be used to guide ecologically sustainable landscape planning by identifying local management practices that are suited to the landscape context (Holland and Yang, 2016).

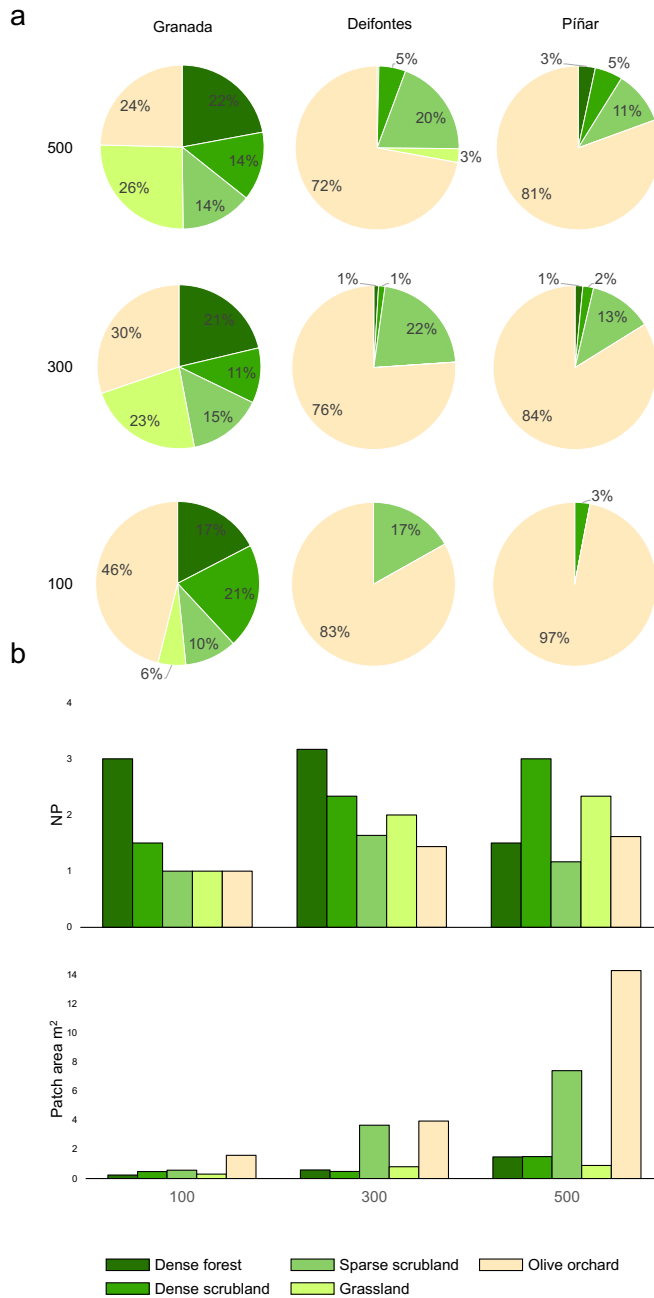


Figure 2. Composition of cover categories and patch features at different spatial scales. a Proportion of cover categories in the studied locations. b Mean patch number (NP) and mean patch area for each cover category.

Thus, our results show that the proportions of the cover categories in the sampled areas varied across the scales used. In the case of Deifontes and Píñar, at 100 m there is a higher proportion of sparse scrubland and dense forest in the landscape, and when the scale increases to 300 and 500 m the proportion of the natural habitats tend to increase, but olive orchards tend to decrease in the landscape. However, in the case of Granada the proportion of the cover categories tend to be similar for each scale, but grassland was particularly present in all scales (Fig. 2a). Similarly, the number of patches and the patch area tend to increase as the spatial scale increase, but this tendency is especially shown by sparse scrubland and olive orchard (Fig. 2b). This pattern can be explained due to the nature of the agricultural matrix in the landscapes of Andalusia, i.e., in this area the plots of olive orchards are distributed in large and plane growing areas, the matrix is composed primarily of olive orchards rather than a mixture of crops, and the patches of natural vegetation are relicts of natural habitats left on the hills (Rega et al., 2018). Moreover, 70% of the Andalusian olive oil sector is organized in cooperatives. Through their technical staff, cooperatives take advantage in the joint management of the orchards (Mozas Moral and Bernal Jurado, 2008), resulting in the homogenization of the landscape in wide zones.

Effects of landscape composition

The landscape composition variables showed effects on the three metrics of NE-Pest functionality (pest damage, egg hatching, and egg predation) mostly at spatial scales across 100 and 300 m, but only dense forest mainly showed effects at spatial scales across 300 and 500 m (Fig. 3). Similarly, for the abundance of *P. oleae* adults, NE insects, and NE arachnids the variables showed general effects at 100 m and to a lesser extent at 300 m. Although, sparse scrubland and grassland also showed effects on NE insects and NE arachnids at 500 m, respectively. Interestingly, dense forest showed effects only on *P. oleae* adult abundance at spatial scales across 300 and 500 m (Fig. 3) (see Table A4.2 of supplementary data in Appendix). This confirms that landscape composition affects *P. oleae* and their NE in olive orchard landscapes, being both dependent on the scale (see Alves et al., 2021; Villa et al., 2020).

Though, the type of effects on pest damage were intrinsically linked to the type of effects on *P. oleae* adult abundance. Almost all landscape composition variables showed negative effects on pest damage with the exception of sparse scrubland. Only the proportion of olive orchard showed negative effects on pest damage but positive effects on *P. oleae* adult abundance. These results are in agreement with previous studies and confirms

the pattern of olive pests, such as *P. oleae*, or *Bactrocera oleae*, responding positively to olive orchards (as specific pests of olive trees) and negatively to semi-natural habitats (Villa et al., 2020; 2021; Paredes et al., 2019; Alves et al., 2021; Martínez-Núñez et al., 2020; Ortega et al., 2016). However, it is interesting that whereas the proportion of sparse scrubland is slightly promoting pest damage and *P. oleae* adult abundance at lower spatial scales, the opposite pattern is showed by the proportion of dense scrubland.

As it can be expected, the effects on egg hatching and egg predation were mutually exclusive (Fig. 3). Different landscape composition variables showed opposite type of effects at the same spatial scales, for example, sparse scrubland and olive orchard had positive effects on egg predation (and negative effects on egg hatching) at 100 m, conversely, dense scrubland and dense forest had negative effects on egg predation at spatial scales across 100 and 300 m and across 300 and 500 m, respectively.

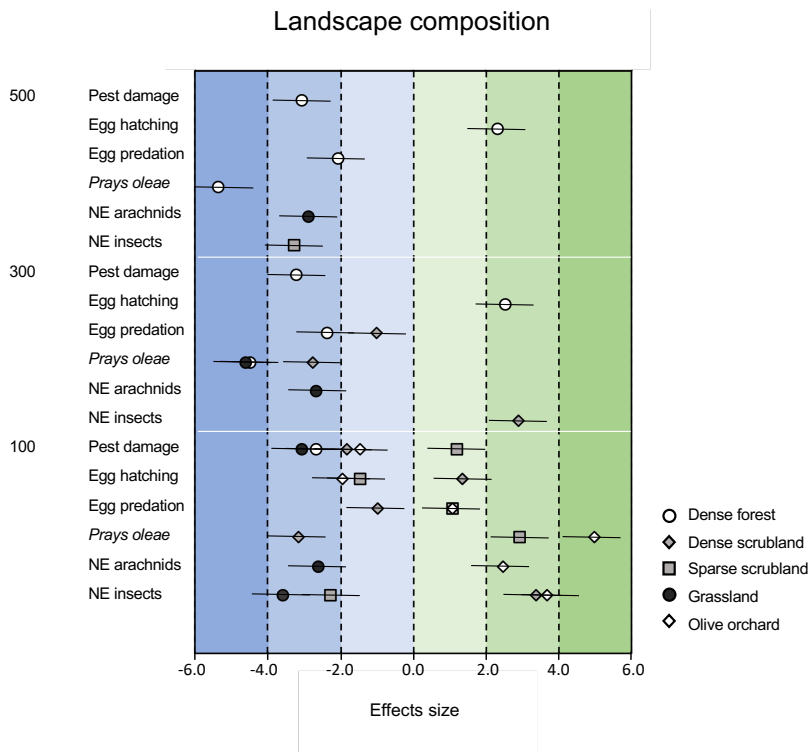


Figure 3. Effect and standard error for the linear mixed models and generalized linear mixed models subjected to a multi-model inference with the five variables of landscape composition (cover categories), fitted at three spatial scales (100, 300, and 500 m). Only significant variables in the best models ($\Delta AIC < 2$) are presented.

On the other hand, grassland showed positive effects and olive orchard showed negative effects on both NE insect and NE arachnids. In addition, dense scrubland showed positive effects on NE insects, but sparse scrubland showed negative effects. Thus, in regard to semi-natural habitats the abundance of NE insects is boosted by dense scrubland and reduced by sparse scrubland and grassland.

Indeed, scrublands stand out for their effects showing a contradictory but elucidating tendency. For example, sparse scrubland whereas increasing *P. oleae* abundance and pest damage, it positively affects egg predation and consequently it reduces egg hatching. Nonetheless, the pattern is mutually exclusive with the abundance of NE insects, which was unexpected (Fig. 3). Conversely, dense scrubland produces the entire opposite results.

The question arises as to why a cover category that had negative effects on NE abundance can produce positive results on egg predation and reduce egg hatching, and vice-versa? This could be explained by a trophic guild approach. According to theory the presence of semi-natural habitats should increase the abundance of NE and at the same time enhance biological control (Bianchi et al., 2006). However, it is now known that this is not a rule, and sometimes semi-natural habitats fail to enhance biological control (amongst other causes) because intraguild predation or the availability of resources (Tscharntke et al., 2016). For example, there is evidence that some birds that benefit from natural habitats can feed on cabbage pest caterpillars, but also on their parasitoids, which increases pest damage and affects yields (Martin et al., 2013). There is also evidence that some omnivore natural enemies (such as the highly abundant ants in our study area) benefit from the resources produced in semi-natural habitats (e.g., adjacent vegetation and ground cover) increasing its abundance and moving across habitats within olive orchards (Álvarez et al., 2019a), which in this case can occasionally release the pest from biological control, increasing egg hatching.

The anterior is in accordance with the results of previous studies that show that *P. oleae* egg predation by NE insects and *B. oleae* pupa predation by NE arachnids are high in organic olive orchards (Álvarez et al., 2021a; Picchi et al., 2017). Therefore, here we show that indeed, a complex landscape increases natural enemy abundance, but its effect on biological control is driven mostly by the amount and composition of one of the cover categories in the landscape (in this case scrublands), which supports (1) the idea that habitat complexity of semi-natural habitats modulates NE abundance (i.e., plant richness and plant arrangement and scattering, Álvarez et al., 2021b)

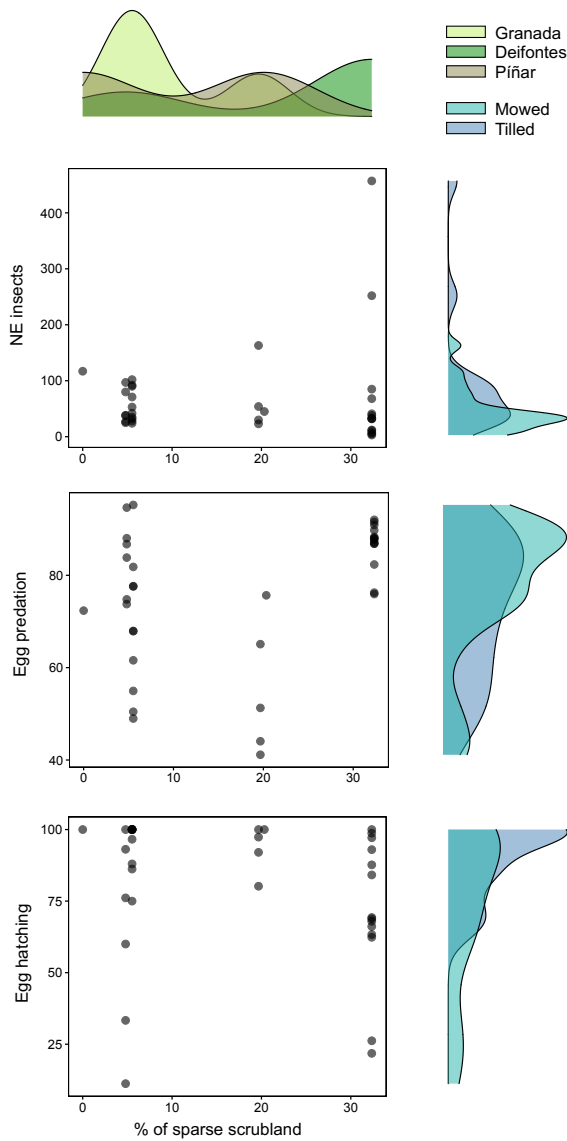


Figure 4. Relationship amongst the proportion of sparse scrubland and natural enemy insects' abundance (NE insects), egg predation, and egg hatching for all years (untransformed data). It is showed the density of the data separating (1) the proportion of scrubland in each sampled location and (2) the management of the ground cover on the orchards, i.e., mowed and tilled.

and (2) the complex habitat hypothesis (Bianchi et al., 2006) and the non-effective natural enemy hypothesis (hypothesis number 1 in Tscharrntke et al., 2016), two of the main hypotheses in biological control theory.

In addition, our data integrate the use of ground cover as mowed or tilled managements (see Table A4.1 of supplementary data in Appendix). We can see that mowed orchards tend to have higher densities on low numbers of NE insects and high percentages of egg predation than tilled orchards (Fig. 4). Conversely, the highest density on egg hatching is present in tilled orchards (Fig. 4). These results are in agreement with previous findings (Álvarez et al., 2021a; 2019b; Morente et al., 2018) that suggests that ground cover positively affect key taxa that play an important role on olive orchards with and without ground cover, and thus, mowed orchards tend to be more effective for controlling *P. oleae* by means of egg predation rather than tilled orchards, especially when there is a low abundance of natural enemies (Álvarez et al., 2021a).

Effects of landscape configuration

Each metric of NE-pest functionality and the abundance of *P. oleae* adults, NE insects, and NE arachnids responded differently to landscape configuration (Fig. 5) (see Table A4.3 of supplementary data in Appendix).

The patch aggregation index (AI) was the variable with more effects, closely followed by edge density (ED). Interestingly, AI had negative effects on all the metrics of NE-pest functionality at all spatial scales, especially at 100 m, however it showed positive effects on the abundance of NE insects and *P. oleae* adults at all spatial scales and at 500 and 300 m, respectively. ED showed positive effects on egg hatching and the abundance of NE insects, at all spatial scales. Moreover, ED showed negative effects on the abundance of *P. oleae* adults at 300 and 500 m (Fig. 5).

In addition, the Shannon diversity index (SHDI) applied to landscapes showed positive effects on the metrics of NE-pest functionality, especially at lower spatial scales (100 and 300 m) whilst it showed negative effects on the abundance of NE insects. Particularly, the perimeter-area ratio mean (PARA_MN) positively affected egg predation at 300 m whilst the contagion index (CONTAG) showed only a negative effect on egg predation at 500 m (Fig. 5).

Based on the anterior, ED needs to be taken into account because whereas it negatively affects *P. oleae* adult abundance, egg hatching tends to be positively affected by it. This is a pattern that is important to olive's yield, i.e., having a low number of adults but a high number of larvae is a bad scenario for olive orchards because a high number of hatched larvae can affect the development of the olive fruit, which is directly related to economic losses (Paredes et al., 2019).

On the other hand, fragmented habitats can lead to disruption of the resources in the different habitats, and predators generally are more vulnerable to fragmentation than their prey (Clemente-Orta and Álvarez, 2019). Our study shows that fragmentation, which can be extracted indirectly from the tendencies in PARA_MN, ED, and AI, produce the same effects on pest damage and egg predation.

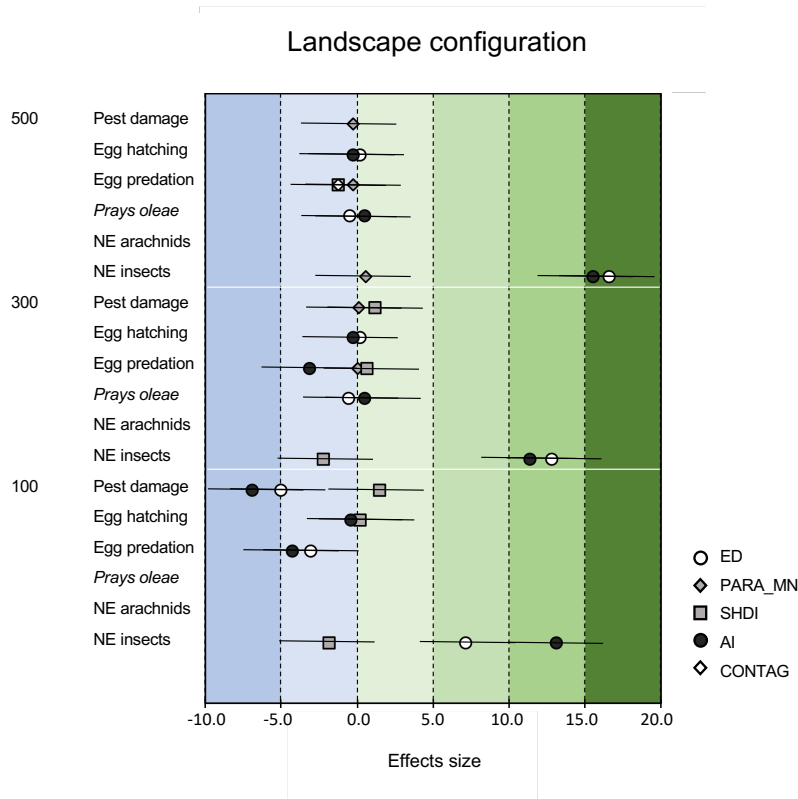


Figure 5. Effect and standard error for the linear mixed models and generalized linear mixed models subjected to a multi-model inference with the five variables of landscape configuration (patch features), fitted at three spatial scales (100, 300, and 500 m). Only significant variables in the best models ($\Delta AIC < 2$) are presented.

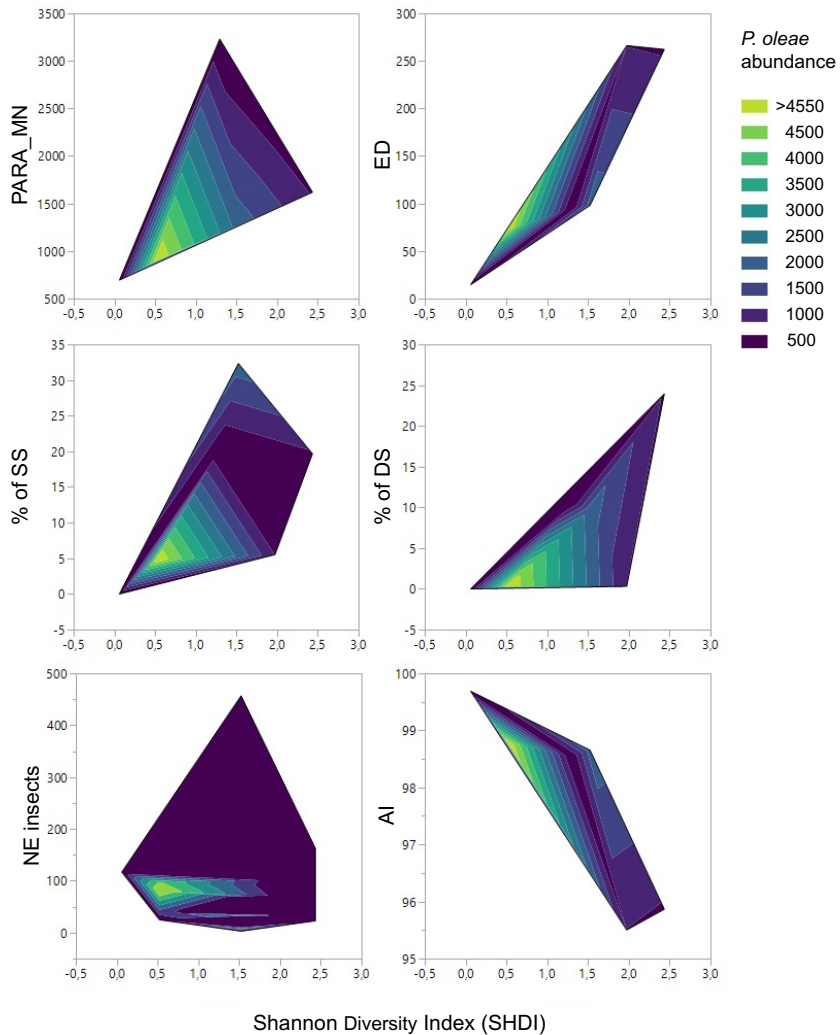


Figure 6. Graphic representation of the interaction of *P. oleae* adult abundance with the landscape diversity and (1) variables of landscape configuration, (2) variables of landscape composition, and (3) natural enemies. The contour plots show the response values and desirable operating conditions. The predictor on the X axis was the Shannon diversity index, and the predictors on the Y axis were as follow: perimeter area ratio (PARA_MN), edge density (ED), aggregation index (AI), proportion of sparse scrubland (SS), proportion of dense scrubland (DS), and natural enemy insects' abundance (NE insects). Contour lines connect points that have the same adjusted response value integrating the data of total abundance of *P. oleae* adults. The form of the aggregate is given by the variable in Y axes.

Finally, if we focus on the response of *P. oleae* adult abundance and its interaction with landscape diversity (SHDI) in relation to (1) patch features (PARA_MN, ED, and AI), (2) the proportion of both sparse scrubland (SS) and dense scrubland (DS), and (3) the abundance of NE insects (Fig. 6), one can see that *P. oleae* adult abundance produced a continuum of abundance that is negatively related with SHDI. Interestingly, high amounts of sparse scrublands within diversified landscapes reduce *P. oleae* adult abundance compared to dense scrublands. Furthermore, NE insects stop the increment of *P. oleae* adult abundance in low to medium diversified landscapes and with low levels of NE insect abundance, which supports the findings of Alvarez et al. (2021a) for the egg predation of *P. oleae*. According to the anterior, the resulting overall pattern suggests that *P. oleae* adult abundance (and thus pest damage) increases in landscapes poorly diversified, with elongated-highly aggregated patches where their margins are not very dense, and/or a single cover type dominates the landscape (Fig. 6).

Conclusions

Our results show for the first time the main drivers of the biological control of *P. oleae* in organic olive orchards by using multi-model inference at different spatial scales. We can conclude that:

1. When semi-natural habitats are analysed dividing them into specific land cover categories the effects produced on the variables of adult abundance and the metrics of NE-pest functionality follow different patterns with higher effects at small spatial scale.
2. Landscape configuration variables (patch features) have more significant effects at bigger spatial scales.
3. The landscape composition and configuration variables produce essentially the same type of effect on the abundance and the metrics of functionality across all spatial scales.
4. *Prays oleae* adult abundance show more effects mainly at bigger spatial scales, and NE abundance at lower spatial scales.
5. The proportion of sparse scrubland in the landscape jointly with the presence of a mowed ground cover is the main factor driving the biological control of *P. oleae*.
6. Diversified landscapes with dense edges reduce the adult abundance of *P. oleae*.

Overall, we can confirm the hypothesis that suggest that an olive orchard with the presence of ground covers surrounded by semi-natural habitats produces more active and voracious natural enemies than their high abundances, and it may allow the establishment of more and efficient key predators (Álvarez et al., 2019b; 2021a). So, the present results can help farmers and technicians to improve the ecological management of olive orchards by promoting the conservation and establishment of diversified semi-natural habitats with the sparse scrublands as a primal ecological infrastructure within olive orchard landscapes, maintaining ground covers with mowing techniques, all to increase the biological control of *P. oleae* by means of egg predation. Nonetheless, to diminish the incidence of *P. oleae* adults in olive orchards it is paramount to make such landscapes more diverse.

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Declarations

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Part Two:

Trophic Interactions

Chapter 5

Maturity of ground covers increases the resilience and presence of natural enemies in the trophic network of olive canopy

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Abstract

The quality of a habitat is related to its lifetime (age) and the disturbances to which it has been exposed. Natural enemies and their interactions in trophic networks can be affected by the maturity of the systems they inhabit. The positive effects of ground covers and adjacent vegetation on natural enemies have been demonstrated in olive groves; however, the effect of the quality of such habitats has been largely neglected. In the present study, we assessed the effects of matureness of ground covers on the arthropod community of the olive canopy, especially the natural enemies. Sampling was made in an organic olive orchard at two periods of time separated by more than 10 years. We analysed the differences in abundance and richness of arthropods in the olive canopy and their interactions with ground cover and adjacent vegetation using trophic networks. Our results suggest that the establishment and maturity of the ground cover inside the olive orchard affected the structure and complexity of the trophic network. The taxa of herbivores, omnivores, and parasitoids did not change drastically while there was an increase in predator taxa between both periods, which subsequently produced an increase in the vulnerability of herbivores. In essence, the taxa of predators increased twice their number maintaining the same proportion of preys per

taxon. According to our analysis, a mature ground cover could provide the trophic network of the olive trees with new efficient taxa to enhance the biological control of pests.

La madurez de las cubiertas vegetales aumenta la presencia de enemigos naturales y la resiliencia de la red trófica de la copa del olivo

Resumen

La calidad de un hábitat está en relación con su tiempo de vida (edad) y las perturbaciones a las que ha sido expuesto. Los enemigos naturales y sus interacciones en las cadenas tróficas se pueden ver afectadas por la madurez de los sistemas que habitan. En el olivar se han evidenciado los efectos positivos que tiene la presencia de las cubiertas vegetales y la vegetación adyacente sobre los enemigos naturales, pero no se han tomado en cuenta los efectos que pueda tener la calidad de dichos hábitats. En el presente trabajo se evaluaron los efectos de la madurez en la cubierta vegetal sobre la comunidad de artrópodos, en especial los enemigos naturales, presentes en la copa del olivo. Los muestreos fueron realizados en el mismo olivar ecológico en dos periodos de tiempo separados por más de 10 años. Las diferencias en la riqueza y abundancia de artrópodos en la copa del olivo, así como sus interrelaciones con la cubierta vegetal y la vegetación adyacente fueron analizadas a partir de la construcción de redes tróficas. Los resultados sugieren que el establecimiento y maduración de la cubierta vegetal en el olivar afecta a la estructura y complejidad de la red trófica de la copa del olivo. El número de taxones de parasitoides, omnívoros y herbívoros no cambia drásticamente, mientras que hay un aumento importante de depredadores entre los dos periodos, lo que produce un crecimiento paralelo en la vulnerabilidad de los herbívoros. En esencia, el número de taxones de depredadores cambia a más del doble manteniendo la misma proporción de número de presas por taxón. Nuestro análisis sugiere que una cubierta vegetal madura provee a la red trófica del olivo de nuevos taxones eficientes para el control biológico de plagas.

Introducción

El olivar es uno de los cultivos perennes de mayor importancia en la región mediterránea, siendo España el primer productor a nivel mundial (FAO, 2017). En la Unión Europea, diferentes políticas están siendo implementadas con el objetivo de restaurar y conservar la vegetación (natural) adyacente y/o los hábitats semi-naturales, junto con el establecimiento y

mantenimiento de cubiertas vegetales en diversos cultivos (Malavolta y Perdakis, 2018).

Recientemente, en el olivar se han evidenciado los efectos positivos que tiene la presencia de las cubiertas vegetales y la vegetación adyacente sobre la abundancia de enemigos naturales, como arácnidos, parasitoides e insectos depredadores (Ruano et al., 2004; Torres, 2006; Rodríguez et al., 2012; Paredes et al., 2013a; Villa et al., 2016a; Álvarez et al., 2018; Morente et al., 2018; Álvarez et al., 2019a). La sinergia entre vegetación adyacente y cubierta vegetal juega un papel importante en el olivar (Álvarez et al., 2019a), estableciendo qué tipo de enemigos naturales pueden encontrarse o sobre la copa de los olivos (Paredes et al., 2013a; 2013b). Aunque algunos estudios sugieren que las cubiertas vegetales no son por sí solas una herramienta efectiva para promover el control biológico y disminuir así la abundancia de las plagas del olivo (Paredes et al., 2013b; 2015a). No obstante, la estructura y complejidad del paisaje junto con el manejo del agroecosistema, afectan la abundancia de diversas plagas en el olivo (Rodríguez et al., 2009; Boccaccio y Petacchi, 2009; Ortega y Pascual, 2014; Villa et al., 2016a; 2016b; Morente et al., 2018; Paredes et al., 2019; Álvarez et al., 2019a), lo que podría estar enmascarando los beneficios que genera una cubierta vegetal dentro del olivar.

La abundancia y riqueza de enemigos naturales en un agroecosistema depende de múltiples factores (Rusch et al., 2010) que están relacionados con la estructura y complejidad del paisaje (Rand et al., 2006; Rusch et al., 2010; Tschardt et al., 2012; 2016; Landis, 2017). Bianchi et al. (2006) han propuesto que paisajes complejos con una proporción alta de parches de hábitats semi-naturales (por ejemplo, bosques o matorrales) con poca fragmentación promueven y aumentan la abundancia de enemigos naturales dentro de un cultivo, reduciendo las poblaciones de plagas. Esta perspectiva se basa en el hecho de que algunos enemigos naturales requieren de hábitats semi-naturales para el desarrollo de uno o varios de sus estadios de vida (Rusch et al., 2010). Así, la cantidad, calidad y/o estructura de dichos hábitats producirá efectos positivos o negativos sobre los enemigos naturales dentro del agroecosistema (Bianchi et al., 2006; Tschardt et al., 2012; 2016).

La calidad de un hábitat está en relación con su tiempo de vida (edad) y las perturbaciones a las que ha sido expuesto, lo que se ve reflejado en la biodiversidad que lo conforma (abundancia y riqueza de especies e interacciones ecológicas) (Colwell et al., 2004; Laurance et al., 2002; Laurance, 2007; Tschardt et al., 2012; Álvarez et al. 2016; 2017a). La vegetación adyacente y las cubiertas vegetales junto con los propios cultivos siguen esta premisa. Así, las comunidades de enemigos naturales y sus

interacciones en la cadena trófica se pueden ver afectadas por la madurez de los sistemas que habitan; una comunidad ecológica en un sistema en fase de transición/colonización tiende a ser diferente en comparación con una comunidad en un sistema bien establecido (Prach y Walker, 2011; Balmford et al., 2012; Karp et al., 2018). Dicho proceso se ve ejemplificado entre agroecosistemas con cultivos anuales y perennes, por ejemplo, en sistemas anuales la comunidad de artrópodos no puede establecerse y tiende a movilizarse y recolonizar distintos cultivos en periodos de tiempos muy cortos, lo que no sucede en los cultivos perennes (Altieri et al., 1991; Perdakis et al., 2011). En sistemas perennes los enemigos naturales pueden establecerse y prosperar con mayor facilidad (Rusch et al., 2010). Esto se podría extrapolar al mantenimiento de la cubierta vegetal; en esencia, una cubierta vegetal joven y recién establecida no aportaría a la copa de los olivos la misma cantidad o tipo de enemigos naturales que una cubierta madura.

Por tal motivo, el presente trabajo tiene como objetivo evaluar los efectos de la madurez de la cubierta vegetal sobre los enemigos naturales y la comunidad de artrópodos presentes en la copa del olivo. Particularmente, se investigaron: (1) las diferencias en la riqueza y abundancia de artrópodos de la copa del olivo, a partir de la construcción de redes tróficas al inicio y al final de un periodo de 12 años y (2) las interrelaciones que tienen los artrópodos de la copa del olivo con la cubierta vegetal, así como con la vegetación adyacente. El presente estudio se basa en la teoría de redes tróficas (Strogatz, 2001), debido a que es considerada la mejor forma de estudiar los procesos ecológicos que involucran los roles de las especies y la influencia de la biodiversidad sobre la función ecosistémica (Thompson et al., 2012) y que ha mostrado resultados prometedores en el estudio del olivar (Morente et al., 2018).

Material y métodos

El estudio se llevó a cabo en los años 2003 y 2015 en un olivar ecológico de regadío situado a las faldas de una colina ocupada por vegetación natural, donde dominan encinas, almendros, tomillares, jaras y aulagas. La finca se encuentra ubicada en la localidad de Deifontes (37°19'N; 3°34'W), provincia de Granada, España (Fig. 1). Las condiciones climáticas en la región fueron: en 2003, 16.7°C temperatura media anual (33.8°C media máxima y 15.8°C media mínima en junio) y 384.8 mm precipitación media anual; y en 2015, 16.2°C temperatura media anual (33.0°C media máxima y 13.3°C media mínima en junio) y 245.63 mm precipitación media anual.

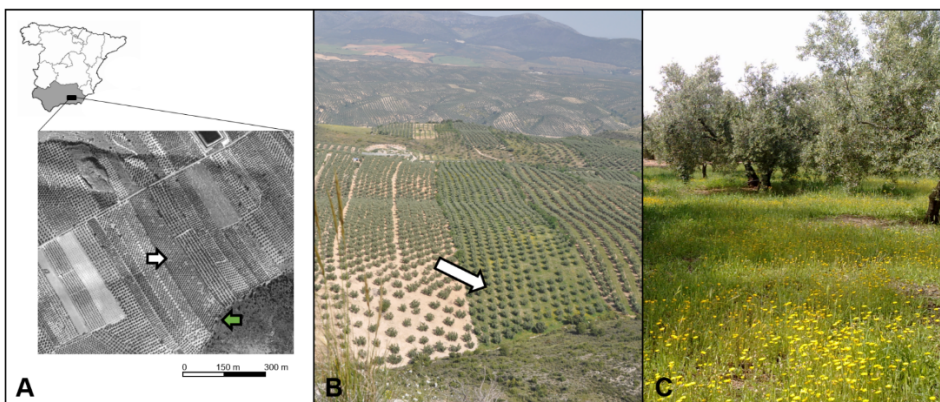


Figura 1. Olivar ecológico (finca experimental). Deifontes, provincia de Granada, Andalucía, España (A); la flecha blanca indica la finca ecológica y la flecha verde el margen con la vegetación (natural espontánea) adyacente (sistema semi-natural). Panorámica del valle y la finca ecológica (B); la flecha blanca indica la finca ecológica. Aspecto de la cubierta vegetal dentro de la finca (C).

Los olivos utilizados son de la variedad Picual, con una edad aproximada de 25 a 50 años y plantados con un espaciado de 8×8 m en una pendiente de 11° . El sistema de manejo del cultivo está basado en el sistema de regulación natural (sensu Pajarón Sotomayor, 2006), el cual es un cultivo ecológico que favorece la regulación natural de plagas y la fertilidad natural (entre otros factores) lo que asegura la productividad y rentabilidad futura de las explotaciones, y no solamente sustituye los productos químicos de síntesis utilizados en otros manejos por productos autorizados en el reglamento de agricultura ecológica. Así, durante las fechas de muestreo no se aplicó ni *Bacillus thuringiensis* (Bacillales: Bacillaceae) ni agroquímicos permitidos en agricultura ecológica. La principal diferencia en el cultivo desde 2003 hasta 2015 ha sido el establecimiento y maduración de la cubierta vegetal. En 2003 la cubierta recibía una grave perturbación anual con arado superficial durante el mes de abril, mientras que en 2015 la cubierta fue manejada mediante uno o varios segados entre abril y julio (proceso llevado a cabo desde 2005).

La recogida de artrópodos se realizó en junio de ambos años, uno de los meses con mayor abundancia de artrópodos en el olivar (Ruano et al., 2004). Para la copa del olivo, en 2003 se tomaron muestras mediante el método de vareo en 20 árboles seleccionados aleatoriamente. Se realizaron cinco golpes por rama en un total de cuatro ramas por árbol (orientadas

según los puntos cardinales) sobre una red entomológica de 50 cm de diámetro (Ruano et al., 2004). En 2015 se muestrearon bloques de olivos seleccionados aleatoriamente, cinco en el borde del cultivo (junto a la vegetación adyacente) y cinco en el centro. En cada bloque se escogieron aleatoriamente cuatro olivos, y en cada árbol se tomó una muestra que consistía en la succión de una superficie de 50 × 50 cm² de la copa del olivo (30 segundos) con un aspirador entomológico CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA). En la cubierta vegetal y la vegetación adyacente, los muestreos se realizaron sobre las plantas más reconocibles y abundantes (procedimiento hecho sólo en el año 2015). Dependiendo de la disponibilidad y siguiendo el mismo método de aspirado que en la copa del olivo, se muestrearon aleatoriamente 20 plantas por especie (especies en vegetación adyacente: *Cistus albidus*, *Prunus dulcis*, *Quercus rotundifolia*, *Retama sphaerocarpa*, *Rosmarinus officinalis*, *Thymus mastichina*, *Thymus zygis gracilis* y *Ulex parviflorus*. Especies en cubierta vegetal: *Anacyclus radiatus*, *Centaurea melitensis*, *Diplotaxis catholica*, *Erodium cicutarium*, *Leontodon longirostris* y *Senecio vulgaris*), esto permite estandarizar las muestras para comparar diferentes tipos de plantas (herbáceas, arbustos y/o árboles). Las muestras se refrigeraron en campo y se conservaron a -20°C hasta su identificación. Posteriormente cada muestra se limpió de restos vegetales y se procedió a la identificación taxonómica de los artrópodos recogidos. Éstos se preservaron en una solución de alcohol etílico al 70 %. Se hizo el esfuerzo de identificación a nivel de especie en aquellos grupos taxonómicos que incluían más de un gremio trófico. Considerando que el método de muestreo utilizado en 2003 es diferente al usado en 2015, se llevó a cabo la construcción de las curvas de acumulación de especies (Colwell y Coddington, 1994) para asegurarnos de que el cambio de protocolo no tuvo un efecto en los resultados obtenidos en la colecta. Para ello, se usó el número de muestra como la variable que refleja el esfuerzo de muestreo y la abundancia de cada especie recolectada. Para evaluar la eficiencia de los muestreos se calcularon los índices de riqueza de especies no paramétricos basados en la abundancia ACE y Chao 1 (Gotelli y Colwell, 2011) y se calculó el porcentaje de similitud entre los datos reales y los de los índices. El análisis se llevó a cabo a través del software EstimateS v.9 (Colwell, 2013).

Redes tróficas y cálculo de sus descriptores

Se construyó una red trófica cualitativa por año de muestreo (2003 y 2015) a partir del protocolo propuesto por Goldwasser y Roughgarden (1993). Las redes se construyeron considerando las relaciones de depredación, parasitismo y canibalismo. La identificación de las presas y huéspedes de los

depredadores y parasitoides incluidos en las redes se realizó con base en los datos extraídos de la bibliografía existente (ver Tabla A5.1 en Apéndice, también disponible en <https://doi.org/10.7818/ECOS.1779>). Además, se ha utilizado el concepto de especie trófica de Cohen et al. (2012) (grupos funcionales de taxones que comparten los mismos depredadores y presas) con el objetivo de reducir el sesgo metodológico derivado de la identificación taxonómica de algunos nodos a diferentes niveles. Las redes tróficas han sido dibujadas con el software Pajek v. 1.18 (Batagelj y Mrvar, 2003).

Tras la construcción de la red trófica se procedió al cálculo de cuatro descriptores de la red: (1) densidad de enlaces (LDq'), o proporción de enlaces por nodo, (2) conectancia (Cq'), que hace referencia al número de enlaces realizados frente a los enlaces potencialmente posibles, (3) generalidad (Gq'), o número medio de presas por depredador y (4) vulnerabilidad (Vq'), relacionada con el número medio de depredadores por presa. Los descriptores se estimaron a partir de una matriz de depredación especie por especie (S-by-S, Bersier et al., 2002):

$$a = [a_{ij}]$$

donde la relación de depredación o parasitismo de la especie j hacia la i se definió como $a_{ij} = 1$ mientras que el resto de relaciones se definieron como $a_{ij} = 0$.

Análisis de correspondencia

Para establecer la interrelación que pudiera existir entre los artrópodos de la copa del olivo y la cubierta vegetal, así como la vegetación adyacente, se analizó la correspondencia entre cada tipo de vegetación (olivo, cubierta vegetal del olivar y vegetación adyacente) y todos los taxones por medio de un análisis de correspondencia (Greenacre, 2013). Uno de los objetivos del análisis de correspondencia es establecer la relación entre dos variables nominales en un espacio dimensional reducido, mientras se describe al mismo tiempo la relación entre las categorías que conforman dichas variables (Legendre y Gallagher, 2001; Greenacre, 2013). Para llevar a cabo el análisis se introdujeron datos de la presencia de los taxones en cada uno de los tipos de vegetación. Previo al análisis, el conteo de la abundancia de cada taxón se utilizó para ponderar los datos. El análisis de correspondencia se llevó a cabo con el software SPSS v19 (IBM Corp., 2010).

Resultados

En la red trófica de la copa del olivo, se registraron en junio de 2003, 33 taxones que incluyeron seis depredadores, dos omnívoros, nueve parasitoides y 16 herbívoros. En junio de 2015 la riqueza de taxones fue superior, registrándose 44 taxones distribuidos en 14 depredadores, cinco omnívoros, siete parasitoides y 18 herbívoros (Tabla 1). A pesar de haber utilizado métodos de muestreo diferentes en cada año, los índices ACE y Chao 1 obtenidos a partir de las curvas de acumulación de especies indican que el cambio de tipo de muestreo no supone un sesgo importante en los resultados obtenidos para la construcción de las redes tróficas cualitativas. Así, los taxones recolectados en la copa del olivar en 2003 representan el 82.33% de la riqueza respecto al índice ACE mientras que en 2015 representa el 84.04%. Del mismo modo, la riqueza obtenida en 2003 representa el 88.63% de la riqueza total en relación con índice Chao 1 y en 2015 el 77.82 % (ver curvas de acumulación en Fig. 2).

En lo referente a los descriptores de la red trófica, se observó un cambio en algunos de ellos entre los años 2003 y 2015 (Tabla 2). Así, la densidad de enlaces por nodo, fue mayor en 2015 que en 2003 (Fig. 3; ver Tabla A5.2 en Apéndice, también disponible en <https://doi.org/10.7818/ECOS.1779>). Del mismo modo, la vulnerabilidad de las presas fue mayor en 2015, sin embargo, la conectancia y la generalidad presentaron valores similares entre los dos años (Tabla 2).

Los resultados del análisis de correspondencia muestran que, de los 44 taxones pertenecientes a la red trófica de 2015, 28 permanecen ligados exclusivamente a la copa de olivo, de los cuales 27 presentan una misma correspondencia (ver posición del asterisco en la Fig. 4). Por otro lado, 16 taxones tienen interrelación con la vegetación adyacente y la cubierta vegetal: dos omnívoros, tres depredadores y dos herbívoros están ligados a la vegetación adyacente, y tres omnívoros, tres depredadores y tres herbívoros están ligados a la cubierta vegetal (Fig. 4). Más aun, nueve de esos 16 taxones son nuevos integrantes de la red trófica del olivo que no aparecen en la red de 2003.

Discusión

Nuestros resultados apoyan la hipótesis de que la presencia de cubiertas vegetales en el olivar ecológico aumenta la diversidad de especies de artrópodos. Lo que en nuestro caso de estudio favorece el establecimiento de enemigos naturales, pudiendo aumentar el control natural de las plagas del cultivo (Simões et al., 2014).

Tabla 1. Grupos taxonómicos y abundancia relativa (AR) de especies en la red trófica de la copa del olivo en agroecosistemas con cubierta vegetal joven (año 2003) y madura (año 2015). Se muestran los acrónimos (Acr) de los taxones estudiados que se utilizan en las Fig. 3 y 4.

2003			2015			
Taxa		Acr	AR (%)	Taxa	Acr	AR (%)
Depredadores						
Coleoptera	Staphylinidae	Staph	0,10	Araneae	Araneidae	Ara 0,20
Hemiptera	<i>Brachynotocoris ferrerii</i>	Bferr	0,72		<i>Loxocles</i> sp.	Loxo 0,20
	<i>Daraecoris punctum</i>	Dpunc	0,41		Oxyopidae	Oxy 0,10
Neuroptera	<i>Notochrysa</i> sp. (Larva) + <i>Chrysopidia</i> sp. (larva)	Neur	0,61		Philodromidae	Phil 0,61
					Salticidae	Sal 0,10
					Thomisidae	Thom 0,72
				Coleoptera	Malachiidae	Mal 0,10
				Diptera	Cecidomyiidae	Ceci 0,61
				Hemiptera	<i>Anthocoris nemoralis</i>	Anem 0,51
					<i>Brachynotocoris ferrerii</i>	Bferr 0,10
					<i>Daraecoris punctum</i>	Dpunc 0,10
					<i>Dicyphus</i> sp.	Dicy 0,10
					<i>Pseudoloxops coccineus</i>	Peocc 0,20
				Neuroptera	<i>Chrysoperla carnea</i> s.l. (larva)	Chrys (larva) 0,41
				Thysanoptera	<i>Aeolothrips</i> sp.	Aeolo 0,51
Omnívoros						
Hymenoptera	<i>Crematogaster auberti</i>	Cauber	0,10	Coleoptera	Dasytidae	Dasy 0,20
	<i>Tapinoma ibericum</i>	Tibe	0,10	Hymenoptera	<i>Crematogaster auberti</i>	Cauber 0,72
			<i>Plagiolepis pygmaea</i>		Ppig 0,92	
			<i>Tapinoma ibericum</i>		Tibe 0,41	
Parasitoides						
Hymenoptera	Braconidae	Brac	0,51	Hymenoptera	Aphelinidae	Aph 0,10
	Chalcididae	Chalc	0,20		Cynipidae	Cyn 0,10
	Diapriidae	Diapr	0,20		Elasmidae	Elas 0,10
	Elasmidae	Elas	0,31		Encyrtidae	Enc 0,31
	Encyrtidae	Enc	8,60		Mymaridae	Mym 0,10
	Eulophidae	Eul	0,20		Pteromalidae	Pte 0,20
	Ichneumonidae	Ichn	0,20		Scelionidae	Scel 0,31
	Platygastridae	Plat	0,10			
	Pteromalidae	Pte	0,72			

Herbívoros								
Coleoptera	Cerambycidae	Ceram	0,10	Coleoptera	Curculionidae	Curc	0,20	
	Chrysomelidae	Chrysom	0,10		Diptera	Bibionidae	Bib	0,10
	Dermestidae	Der	0,10			Bombyliidae	Bom	0,10
Diptera	Sciaridae	Scia	1,02		Sciaridae	Scia	0,10	
Hemiptera	Aphididae	Aphi	0,20		Tephritidae	Teph	0,20	
	Cicadomorpha + Fulgoromorpha	Cic	0,31	Hemiptera	Aphididae	Aphi	0,31	
	<i>Euphyllura olivina</i>	Eoli	47,49		Cicadomorpha + Fulgoromorpha	Cic	1,74	
	Lygaeidae	Lyg	0,10		Coccidae	Cocc	0,10	
	<i>Saissetia oleae</i>	Sole	0,61		<i>Euphyllura olivina</i>	Eoli	14,12	
Lepidoptera	-	Lep	0,61		Lygaeidae	Lyg	0,10	
	<i>Prays oleae</i>	Pole	5,42		Miridae	Miri	0,20	
Psocoptera		Psoc	0,51		Rhopalidae	Rhop	0,20	
Thysanoptera	Thripidae	Thrip	0,31		<i>Saissetia oleae</i>	Sole	0,31	
				Lepidoptera	-	Lep	0,20	
					<i>Prays oleae</i>	Pole	2,25	
				Thysanoptera	<i>Liothrips oleae</i>	Lole	0,10	
					Phlaeothripidae	Phlaco	0,20	
					Thripidae	Thrip	0,51	

Tabla 2. Descriptores de la red trófica de la copa del olivo en agroecosistemas con cubierta vegetal joven (año 2003) y madura (año 2015). Densidad de enlaces (LD'q), conectancia (C'q), generalidad (G'q) y vulnerabilidad (V'q).

Año	LD'q	C'q	G'q	V'q
2003	5,76	0,20	11,13	6,42
2015	9,47	0,22	11,36	14,84

Contrariamente, algunos trabajos recientes a escala de paisaje sugieren que la cubierta vegetal tiene poco efecto sobre los enemigos naturales y la abundancia de las plagas del olivo (Paredes et al., 2013b; 2015a; Karp et al., 2018). Consideramos que estos resultados se pueden explicar teniendo en cuenta la madurez. Por ejemplo, se sabe que un agroecosistema necesita un tiempo de adaptación y estabilización a partir de la implementación de una metodología ecológica para llegar a un punto óptimo (Dabbert y Madden, 1986; Hill y MacRae, 1996; Lamine y Bellon, 2009).

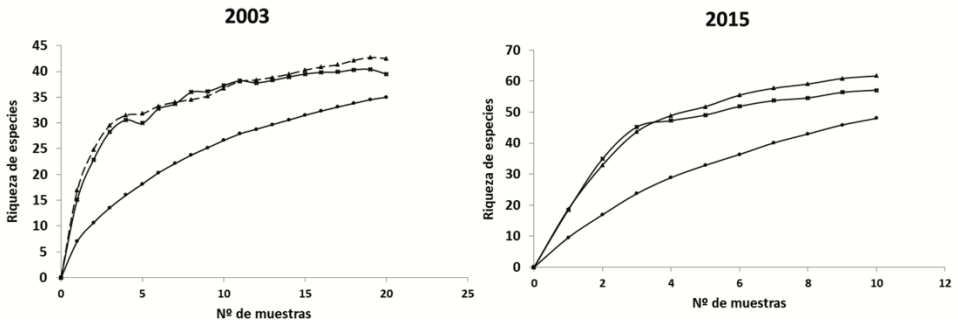


Figura 2. Curvas de acumulación de especies en la copa del olivar estudiado con cubierta vegetal joven (año 2003) y madura (año 2015). Estimadores no paramétricos: Chao1 (cruz), ACE (triángulo).

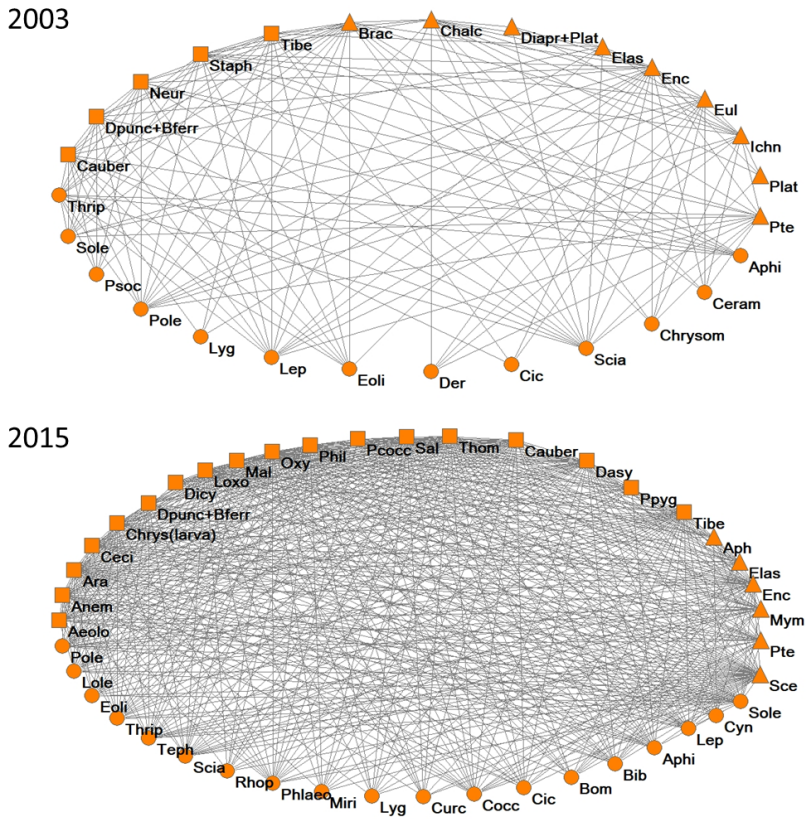


Figura 3. Red trófica registrada en la copa del olivar estudiado con cubierta vegetal joven (año 2003) y madura (año 2015). Se muestran taxones depredadores y omnívoros (cuadrados), parasitoides (triángulos) y herbívoros (círculos).

Aunado a esto, se ha demostrado que márgenes maduros de vegetación entre cultivos mantienen una distribución más uniforme en la abundancia de enemigos naturales que márgenes jóvenes (Burgio et al., 2006). En nuestro caso de estudio, la maduración de una cubierta vegetal dentro del cultivo acompañada de la eliminación de la aplicación de agroquímicos en el mismo, ha podido favorecer el establecimiento de diferentes especies de artrópodos depredadores que, no sólo están ligados a las cubiertas o zonas de vegetación adyacente, sino que pasan a formar parte de la red trófica de la copa del olivo por lo que aportan funcionalidad a ese estrato.

Por otro lado, los resultados de nuestro análisis apuntan a que el establecimiento y maduración de la cubierta vegetal afecta a la estructura y complejidad de la red trófica de los artrópodos de la copa del olivo. De este modo, el aumento de depredadores entre los años 2003 y 2015 produce un aumento paralelo en la vulnerabilidad de los herbívoros, mientras que la generalidad de la red (no. de presas por depredador) se mantiene constante en el tiempo; es decir, el número de taxones de depredadores cambia a más del doble manteniendo la misma proporción de número de presas por taxón depredador.

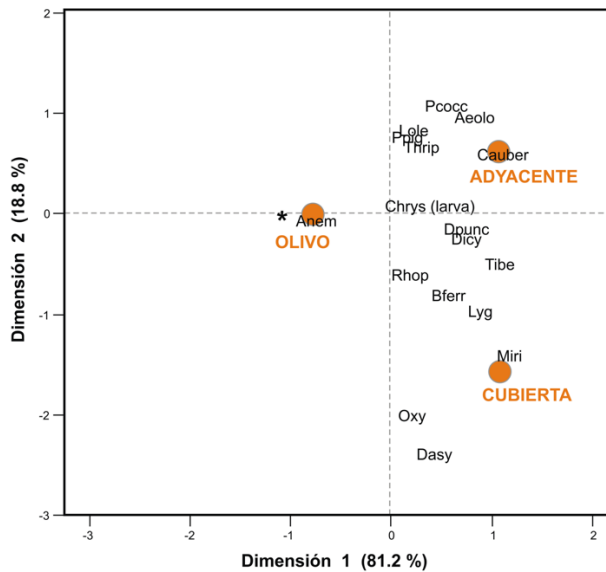


Figura 4. Plano bidimensional del análisis de correspondencia entre los taxones presentes en la copa del olivo en el olivar estudiado y los diferentes tipos de vegetación para el año 2015. Se muestran 17 taxones con correspondencias diferentes. El asterisco indica el mismo sitio de correspondencia que mantienen los 27 taxones restantes (ver tabla 1).

Este resultado indica que la presión de depredación sobre los herbívoros del olivar aumenta de manera considerable a pesar de que el número de taxones de herbívoros no cambia notablemente. Consecuentemente, la densidad de enlaces se ve afectada de manera positiva por el incremento de las relaciones que se establecen en la red trófica, dando lugar a una red más compleja. Así también, dicha complejidad en la red trófica en 2015 se ve reflejada en la presencia de taxones que proporcionan servicios ecosistémicos y que pueden generar un control biológico de plagas, como es el caso de los hemípteros depredadores *Anthocoris nemoralis* y *Pseudoloxops coccineus*. Dichos taxones han sido descritos, en conjunto con *Brachynotocoris ferreri* y el género *Tapinoma* entre los grupos de depredadores más efectivos para controlar a *Prays oleae* y *Euphyllura olivina* (Paredes et al., 2015b). De manera interesante, en nuestro estudio *B. ferreri*, *P. coccineus* y *Tapinoma ibericum* son provistos por la cubierta vegetal y la vegetación adyacente (Fig. 4).

Por otro lado, la conectancia no se ve afectada por la presencia de la cubierta vegetal madura en el olivar. El carácter generalista de la mayoría de depredadores y parasitoides en el olivar (Cárdenas et al., 2006; Gonçalves y Pereira, 2012) puede dar lugar a un aumento del número de enlaces de manera paralela al aumento de riqueza de taxones, impidiendo que cambie la conectancia. Este resultado es similar al obtenido por Morente et al. (2018) con relación al uso de insecticidas en el olivar. Así, el mantenimiento de la conectancia al aumentar la riqueza del sistema es indicativo de la robustez del mismo ante la pérdida de especies (Dunne et al., 2002; Morente et al., 2018).

En general, el papel que juega la cubierta vegetal dentro del olivar se ve reflejado en la capacidad de la misma para aportar nuevos grupos de enemigos naturales a la copa del olivo (Fig. 3). La vegetación adyacente también provee de enemigos naturales a la copa del olivo (Fig. 3), como ya lo habían registrado Jiménez-Muñoz et al. (2017) y Álvarez et al. (2018) para el sitio de estudio. Sin embargo, nuestros datos apuntan a que la cubierta vegetal aporta más grupos de enemigos naturales que la vegetación adyacente, lo que está en relación con la alta abundancia de artrópodos que se pueden encontrar en ella (Álvarez et al., 2018; 2019a). Esto es posiblemente el resultado de un efecto de desbordamiento o efecto de masas (spillover) (Rusch et al., 2010; Tschardt et al., 2012; 2016). El desbordamiento de enemigos naturales desde un hábitat semi-natural hacia un cultivo resulta, principalmente, del aumento de la abundancia de dichos organismos en el hábitat semi-natural, lo que lleva a muchos individuos a invadir otras áreas, así como la dispersión de los enemigos naturales hacia áreas cercanas debido al aumento en la abundancia de presas (Shmida y Wilson, 1985; Tschardt

et al., 2012). Dicha tendencia puede ser explicada desde la perspectiva de la “distribución complementaria del recurso” (Ries y Sisk, 2004; Ries et al., 2004) dadas las características de nuestra zona de estudio. Por ejemplo, una distribución complementaria del recurso se refiere a un escenario donde dos hábitats cercanos contienen recursos completamente diferentes (en cantidad y calidad), pero los cuales se complementan entre sí (Dunning et al., 1992; McCollin, 1998; Fagan et al., 1999). Asumiendo que la cubierta vegetal es un sistema completamente diferente a la vegetación adyacente y al olivo, en estructura y calidad, entonces los recursos en la cubierta vegetal atraen a los enemigos naturales los cuales aumentan su abundancia produciendo un desbordamiento hacia la copa del olivo, (aunque en ciertos grupos de enemigos naturales se producen patrones contradictorios dentro de los olivares, por ejemplo las arañas, ver Picchi et al., 2016; Benhadi-Marín et al., 2019). Así, en el momento en que las plagas del olivo tienden a aumentar en abundancia, los enemigos naturales pueden depredarlas, ya sea en su fase adulta, en su fase juvenil o su fase de huevo. Particularmente, una tendencia a resaltar es que los enemigos naturales en una red trófica más compleja y resiliente pueden reducir la abundancia de adultos plaga per se, sin embargo, es posible que ayuden más bien, a que éstas no aumenten a niveles contraproducentes para la producción del cultivo, atacando estadios más vulnerables como los huevos o los juveniles. Este hecho tendrá que ser estudiado con mayor detalle en estudios a largo plazo sobre los hábitats semi-naturales y el cultivo.

Conclusión

Los agroecosistemas de olivo con manejo ecológico, en los que (1) no se usa ningún tipo de plaguicidas o agroquímico, (2) se mantienen cubiertas vegetales maduras y (3) se conservan hábitats semi-naturales adyacentes, resultan prometedores para promover el control biológico de las plagas del olivo y aumentar la resiliencia del sistema. En general, nuestro caso de estudio muestra que una cubierta vegetal madura permite a diversos depredadores y parasitoides establecerse en la copa del olivo, al menos de forma temporal, y posiblemente controlar la abundancia de las plagas cuando ésta aumenta en el cultivo. Este hecho debe ser estudiado con detenimiento en futuros trabajos, puesto que implica la incorporación de datos de estructura espacial y temporalidad al estudio de las cubiertas vegetales. Finalmente, basándonos en estos resultados, recomendamos el mantenimiento hasta la madurez de las cubiertas vegetales y el aumento de la vegetación natural adyacente de forma conjunta para potenciar la presencia de organismos benéficos en el cultivo del olivo.

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Chapter 6

Elucidating the trophic role of *Tapinoma ibericum* (Hymenoptera: Formicidae) as potential predator of olive pests

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Abstract

Ants play a key role improving the structure and function of local communities. They interact with plants, herbivores, predators, and parasitoids, and are able to change their trophic role in space and time. Unfortunately, these features make difficult to establish the net trophic role of ants in agroecosystems. Here we aim to determine the isotopic enrichment and tissue incorporation rates in ants of the *T. nigerrimum* complex by experimentally disentangle their diet within olive orchards using stable isotopes analysis, and thus, assess their current ecological function and whether they can be considered as beneficial insects. We compared the isotopic signature of ants feeding on (1) natural diets, (2) experimental diets in the laboratory across a gradient of time, and (3) natural diets of ants inhabiting natural habitats and olive orchards that had different agricultural managements. Then, we contrasted the results with ant foraging surveys. Our results showed that, (1) two species of the *T. nigerrimum* complex may inhabit the zone, *T. ibericum* and *T. nigerrimum*, but only *T. ibericum* is inhabiting olive orchards; (2) ants within olive orchards did not produce the patterns showed by experimental hyper-predators; (3) the isotopic signature did not vary

according to field management; and (4) the diet of ants in nature varies greatly according to resource availability, which may be reflected on isotopic signature variability. Therefore, *T. ibericum* is possibly the species that can potentially contribute to control olive pests without being a hyper-predator. The information presented here could be used by farmers and technicians to enhance local biological control planning and/or strategies in olive orchards.

Introduction

Ants are an important proportion of the arthropod fauna in many terrestrial ecosystems that play a key role improving the structure and function of local communities (Hölldobler and Wilson, 1990; Ottonetti et al., 2008). The positive effect of ants in agriculture is known since ancient times (380 years A.D. (Van Mele, 2008)), i.e., ants consume large numbers of pest insects, disturb pests during feeding and oviposition, and increase soil quality and nutrients (Choate and Drummond, 2011). However, ants are involved in different mutualistic interactions affecting arthropod herbivores and eventually plant health (Calbuig et al., 2015), making difficult to conclude their positive or negative effects on the host plants (Rosumek et al., 2009). Moreover, ants interact with plants, herbivores, predators, and parasitoids (Vandermeer et al., 2002); they are able to change their trophic role in space and time (Mooney and Tillberg, 2005); and most of them have a wide diet, being the majority of ant species omnivores (Ottonetti et al., 2008), which hinders the study of their nutritional ecology (Feldhaar et al., 2009). For all that, the net trophic role of ants in agroecosystems is difficult to establish (Vandermeer et al., 2002; Tillberg et al., 2006; Ottonetti et al., 2008). Also, nestmates could share different food by trophallaxis (Børgesen, 2000), making difficult to assess the trophic ecology for a whole colony (Tillberg et al., 2006) or the ecological impact of different colonies.

In olive orchards ants are abundant, especially in the soil. One of the most abundant species in these orchards in the Iberian Peninsula had been identified as *Tapinoma nigerrimum*, (Nylander, 1856) (Ruano et al., 2004; Santos et al., 2007b; Campos et al., 2011). The *T. nigerrimum* complex is widely distributed in the circum-Mediterranean region, being very abundant in west and central Europe and the north of Africa (Seifert et al., 2017), being a common inhabitant of crops in this region (Mansour et al., 2012). Recently, the taxonomic position of this complex of species has been deeply studied, founding four species (Seifert et al., 2017) that can be identified only by high-resolution methods of Numeric Morphology-Based Alpha-Taxonomy

(NUMOBAT) in which Nest Centroid Clustering plays a central role (Seifert et al., 2014). In its natural habitats along the Iberian Peninsula, the *T. nigerrimum* complex has been described as omnivore, consuming honeydew secretions, seeds, and occasionally other insects (Cerdá et al., 1989). However, it has been recorded that *T. nigerrimum s.l.* in olive orchards behaves as a dominant ant species (Morris et al., 1998a; Redolfi et al., 2003; Pereira et al., 2004) that sometimes act as an herbivore and other as a predator consumer of olive pests, but even of other natural enemies (Morris et al., 1998b; Pereira et al., 2004).

Stable isotopes analysis (SIA) has acquired an important role in ecology, having the potential to simultaneously capture complex interactions, including trophic omnivory, and track energy or mass flow through ecological communities (Post, 2002). Based in the premise “you are what you eat”, the ratio of stable isotopes (SI) of nitrogen ^{15}N is used to estimate the trophic position of each species, and carbon ^{13}C is used to evaluate the ultimate source of carbon for an organism, i.e., the diet (Post, 2002). In general, both stable isotope ratios suffer an enrichment in the tissues of the consumers with respect to their diet, due to the elimination of the lighter ^{12}C isotope by breathing and ^{14}N isotope by urine excretion (Ponsard and Arditì, 2000, but see Spence et al., 2005). Studying natural abundance of SI permits to evaluate trophic relationships, estimate animal diets (Santi-Júnior et al., 2018), and assess species interactions (Caut et al., 2006), under a number of methodological considerations (Quinby et al., 2020). One of them is to know the isotopic enrichment rate for the interacting species, which may change in different groups of animals (Spence et al., 2005; Quinby et al., 2020), and the necessary time needed for isotopes to be incorporated in animal tissues (Franssen et al., 2017). Both factors are fundamental to be accounted in trophic interaction studies by SIA (Quinby et al., 2020).

In this study we experimentally disentangle the diet of *T. nigerrimum* complex in olive orchards using SIA. We aim to determine the isotopic enrichment and tissue incorporation rates in ants of the *T. nigerrimum* complex, these data can help to know the current ecological function of these ants in agroecosystems, and whether they can be considered as beneficial insects. We used colonies of the *T. nigerrimum* complex from olive orchards in a sole location to perform a diet experiment in the laboratory, in which worker ants were fed with different types of food across a gradient of time. For that, we analysed and compared natural and experimental diets. In addition, we investigated whether there were differences in the natural diet of nests inhabiting a natural habitat and olive orchards that had different agricultural

managements in different locations. Our experimental data was also confronted with a direct foraging sampling survey in nests of *T. nigerrimum s.l.*

Material and methods

Study area and sampling

The study was conducted in 2010 and 2011 in the province of Granada, southern Spain. Climatic conditions in the region were: for the year 2010, 15°C mean annual temperature, 27.55°C – 11.1°C mean maximum and minimum temperatures from April to July, and 565.12 mm mean annual precipitation; and for the year 2011, 16°C mean annual temperature, 29.52°C – 13.47°C mean maximum and minimum temperatures from April to July, and 368.82 mm mean annual precipitation (a slightly hot and dry year than the former). With respect to pest incidence (i.e., *Prays oleae*, one of the most important pest of olive trees), the highest occurrence of adults/trap/day occurred between June 14th and 21st in both years, and the percentage of adults/trap/day was higher in 2011 (49 %) than in 2010 (34.7 %). The percentage of flowers with larvae (easy to consume by herbivore predators) was higher in 2010 (8.9 %) than in 2011 (1.7 %) (RAIF, 2010; 2011).

Firstly, we collected partly 12 nests inhabiting olive orchards (locality: Arenales; April 2010), taking around 1000 workers alive to rear them in the laboratory. Secondly, we collected samples of workers (100 ants per nest approximately) of 93 nests in 6 localities: Arenales, Colomera, Dehesa del Generalife, Deifontes, Pinos Puente, and Sierra Nevada and at different times, coincident with the laboratory experiment (Fig. 1, Table 1). The nests were selected from two different types of habitats, i.e., natural shrubby habitats at the Sierra Nevada national park and olive orchards with different agricultural managements across the region: organic, conventional, or integrated (Table 1) (see Table A6.1 of supplementary data in Appendix).

Ants in this study were collected weather permitting on April, June, and July, which are months of high arthropod abundance in olive orchards (Ruano et al., 2004; Santos et al., 2007b). Also, the samplings of June and July (t2, t3 and t4) were coincident with the highest presence of *P. oleae*, in the most harmful phase to the yield (Ramos et al., 1998). We used an electrical entomological aspirator (Entomopraxis D702) to collect ants. Nests were considered different when they were separated by more than 20 m. The number of nests per locality varied according to availability (Table 1). Samples were stored individually and maintained at –20°C until prepared for analyses. Some specimens from olive orchards and natural habitats were identified by NUMOBAT technique (see Seifert et al., 2017).

Table 1. Study areas and type of habitats in which *Tapinoma* nests were collected, in Andalusia, Spain.

Species	Locality	Sampling points	Nests <i>n</i>	Type of habitat	Description of the habitat
<i>T. ibericum</i>	Dehesa	2	38	Organic olive orchard	Shallow ploughed April, natural vegetation patches and edges, rained fed
	Deifontes	2	30	-	Cover crop present, mowed April-July, drop irrigated
	Arenales	2	18	Integrated olive orchard	Ploughed, no cover crop, sporadic flood irrigation
	Pinos Puente	1	3	-	Not ploughed, herbicide application, cover crop stripes, rained fed
	Colomera	2	8	Conventional olive orchard	Not ploughed, herbicide application, cover crop stripes, drop irrigation
<i>T. nigerrimum</i>	Sierra Nevada	2	6	Native ecosystem	Shrubby natural habitat

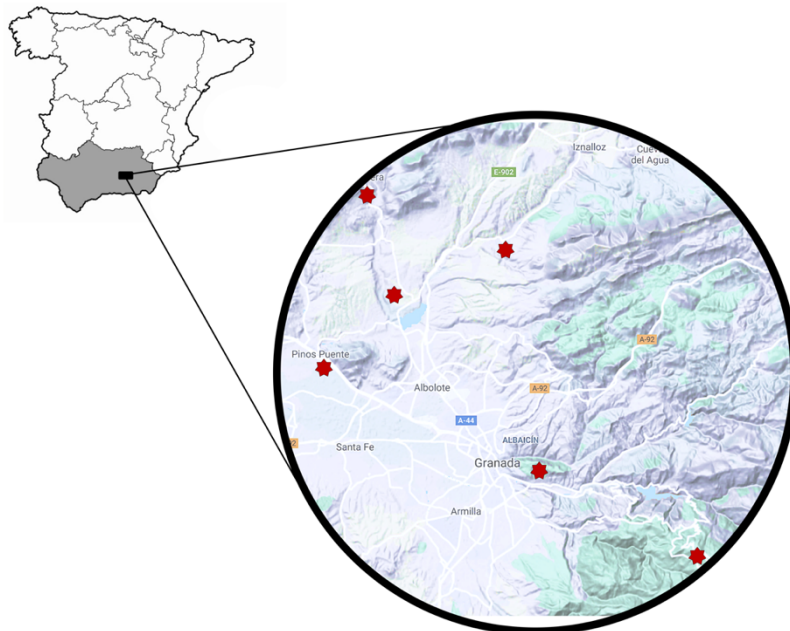


Figure 1. Location of the study areas in southern Spain.

Experimental protocol and rearing

As in the area of the study the main insect pest that damages olives is the olive moth *P. oleae* (RAIF, 2018), which is widely distributed in the circum-Mediterranean region (Tzanakakis, 2006), and in order to determine the trophic status of the species in the *T. nigerrimum* complex and whether or not they are beneficial insects that predate *P. oleae*, we performed an experiment in which we reared worker ants, feeding them with 4 types of food, i.e., a basal diet (mixture of honey and yeast), and different species of insects available in the olive farms: *Aphis craccivora* (Hemiptera: Aphididae) (herbivore of cover crop plants), larvae of *P. oleae* (Lepidoptera: Praydidae) (herbivore consumer of olive fruits in June and July), and larvae of *Chrysoperla carnea s.l.* (Neuroptera: Chrysopidae) (generalist predator of other insects including *P. oleae*, Corrales and Campos, 2004).

Diets were obtained and supplied to the ants in different manners. The honey and yeast were bought at local markets and were supplied ad libitum in small squares of waxed-paper and filter-paper (see Fig. A6.1 of supplementary data in Appendix). Larvae of *C. carnea* were bought from the biofabric BIOBEST (Sistemas Biológicos S.L.). *P. oleae* larvae and *A. craccivora* (aphids) were obtained from the field. We collected larvae of *P. oleae* directly from the canopy of olive trees because it cannot be bred in captivity. The phase of comparison amongst diets begun when these larvae were available in the field (17 June). Aphids were collected in the cover crop of the olive farms. For this, we tilled alfalfa plants then plants were clean with water in a bucket to separate the aphids, and finally, the remaining water was passed through a filter to extract the aphids. All insects were maintained at -20°C in the laboratory until to be offered to the nests included in each treatment group. The food was supplied ad libitum to each nest.

The experimental protocol was performed as follows. Twelve nests were transported to the laboratory after being collected in the field (olive orchards, locality: Arenales, April). Each nest was introduced in an individual plastic container then nests were maintained in a climatic chamber under controlled climatic conditions: 24°C ($\pm 2^{\circ}\text{C}$) mean temperature, 60 % (± 5 %) relative humidity, and 12 hours of light:dark period. All nests were fed with a mixture of honey and yeast ad libitum over two months since the beginning of the experiment (t_0), trying to standardize the base-line isotopic signature of all the nests and maintain them until *P. oleae* larvae were available in the field (June). Then, the nests were separated in four groups randomly distributed, i.e., one group for one type of food, and were fed ad libitum with the assigned diet. Samples (20 workers approximately) were periodically collected and some individuals (100) from every nest analysed in five different times: after

field collection (t0, 23 April); after the beginning of the experiment: 55 days later (t1, 17 June); 73 days (t2, 5 July); 83 days (t3, 15 July); and 93 days (t4, 26 July) (Table 2). Samples were stored individually and maintained at -20°C until the specimens were prepared for analyses. The ant samples obtained from the field at different times permitted us to compare the isotopic signatures obtained in the experiment with those of natural samples collected in different olive farms.

Stable isotopes analysis

The individuals of each sample were dried and pulverized manually in a mortar until it was reached 0.4 mg of the resulting powder, then the sample was encapsulated in tin tubes Eurovector 5x9 mm. Stable isotopes were analysed in two steps: (1) the capsules were introduced in a gas chromatographer EUROVECTOR EURO EA 3000 which volatilize the sample, thereupon, (2) the gases were passed throughout a column into a continuous flux mass spectrometer IRMS ISOPRIME Elemental Analyzer. Analyses were conducted in the Laboratory of stable isotopes (LIE, Scientific Instrumentation Centre, University of Granada). The isotope composition of N and C was expressed using the δ notation relative to international standards (atmospheric N_2 and caseine, respectively) that were reported per mil (‰) on the relative δ -scale and in reference to them. Standards were analysed every 10 samples to ensure the measurements were acceptable in terms of repeatability, and to correct any possible deviations in measurements. Variability was accepted as valid under 0.2 ‰ values.

Foraging sampling surveys

40 nests pertaining to 4 different olive orchards (Deifontes) were sampled in spring-summer 2011, recording (1) data of trail activity (entering workers), i.e., number of workers entering the nest with a prey in 5 minutes/trail/day surveys, after testing that non-charged-with-prey ants regurgitated honeydew (50 ants), ants entering the nest without prey were considered as honeydew transporter and (2) the number and nature of the prey (abundance) carried by ant workers in each trail in 60 minutes/trail/day. The number of sampled trails depended on the availability of active nests. Finally, we recorded the abundance and variety of prey in all ant-trails.

Table 2. Nests used in the diet experiment. It shows the different diet treatments used and the number of nests used per treatment per time.

Type of diet	Nests n			
	t1	t2	t3	t4
Honey-yeast	12	2	2	2
<i>A. craccivora</i>	/	3	3	3
<i>C. camea</i>	/	3	3	3
<i>P. oleae</i>	/	3	3	2

Data analysis

We analysed the trophic status of the *T. nigerrimum* complex by comparing, firstly, the overall signature of the experimental diets including the natural signature of the diet in all nests ($n = 12$, locality: Arenales, all times), for which 2 linear mixed models (LMMs) were fitted using stable isotope signature ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) as the dependent variable and diet as a factor. To control for pseudo-replication and avoid the non-balanced data obtained, we included time as a random effect. Secondly, we fitted 2 linear mixed models to compare the signature of the experimental diets across experimental times (as repeated measures), for which we used stable isotope signature ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) as the dependent variable, and diet, time, and the interaction diet-time as fixed factors. To control for pseudo-replication, we included nest ID as a random effect. As the interaction diet-time was not significant (see results), further differences between groups were inspected without it.

To determine whether the area and/or the agricultural management affects ant diet, we focused on the natural signature of ants and thus, all isotopic samples from all nests collected in the field were used ($n = 103$, nests from the 6 localities) (Table 1). We fitted several linear models using stable isotope signature ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) as the dependent variable and area or management as factors (separately).

All analyses were computed in the R software v 4.0.5 (R Developmental Core Team, 2021). For each model, we tested if there were significant differences using the F -test with the ANOVA function of car package. Further differences between the groups in each model were tested using the Tukey (contrasts) *post hoc* test. LMMs and Tukey *post hoc* tests were computed using the lme4 package and the multcomp package, respectively.

Results

Overall, a total of 103 samples of ant nests were collected. Between them, two species of the *Tapinoma nigerrimum* complex were identified by NUMOBAT technique: *Tapinoma ibericum* Santschi, 1925, and *Tapinoma nigerrimum* (Nylander, 1856). However, *T. ibericum* was only found in the olive orchards samples, and conversely *T. nigerrimum* in the shrubby natural habitats of Sierra Nevada national park (6 nests, Table 1).

Differences in diet

The isotopic signature of *T. ibericum* ants differed amongst diets in our experiment. Thus, the LMM analysis on overall isotopic signatures of the ants fed with the different diets showed significant differences in the $\delta^{15}\text{N}$ signature ($F_{4,53} = 6.461$, $p = 0.001$). Only ants consuming predators (*C. carnea*) had a significant different concentration of $\delta^{15}\text{N}$ when compared with the rest of the treatments and the natural signature of the ants in the olive farms (Tukey *post hoc* test, $p < 0.01$). Specially, the concentration of $\delta^{15}\text{N}$ of ants consuming predators was significantly higher ($7.3\text{‰} \pm 0.4$; Fig. 2), which does not match with the natural signature of *T. ibericum* ($4.7\text{‰} \pm 1.8$). The rest of treatments have a concentration of $\delta^{15}\text{N}$ not significantly different with the natural signature of the ants (Fig. 2). On the other hand, LMM analysis showed that there are also significative differences in the $\delta^{13}\text{C}$ signature ($F_{4,53} = 6.33$, $p = 0.001$). The natural signature of the diet had different concentration of $\delta^{13}\text{C}$ than the signature of ants fed with *A. craccivora* (Tukey *post hoc* test, $p = 0.032$) (herbivore), *C. carnea* ($p = 0.001$), and the mixture of honey and yeast ($p = 0.001$) (Fig. 2). However, only the natural signature of the diet was similar to the ants fed with *P. oleae* (herbivore) (Fig. 2).

From the detailed temporal analysis of isotopic experimental changes, it can be seen how after 39 days of eating their experimental diet (days between t1 to t4), the ants changed their isotopic signature for both isotopes. the temporal $\delta^{15}\text{N}$ enrichment ratio was of 2.1‰ between the herbivore consumers ($5.2 \text{‰} \pm 0.8$) and the predator consumers ($7.3\text{‰} \pm 0.4$) (Fig. 3) (see Table A6.2 of supplementary data in Appendix). Nevertheless, the value $\delta^{15}\text{N}$ should not arrive to their maximum, due the $\delta^{15}\text{N}$ value of their diet is higher (*C. carnea*, $\delta^{15}\text{N}=7.85\text{‰}$). Moreover, $\delta^{13}\text{C}$ increased a mean of -0.2 ‰ from the herbivore consumers ($-24.6\text{‰} \pm 0.4$) to the predator consumers ($-24.4\text{‰} \pm 0.6$) (Fig. 4) (see Table A6.2 of supplementary data in Appendix).

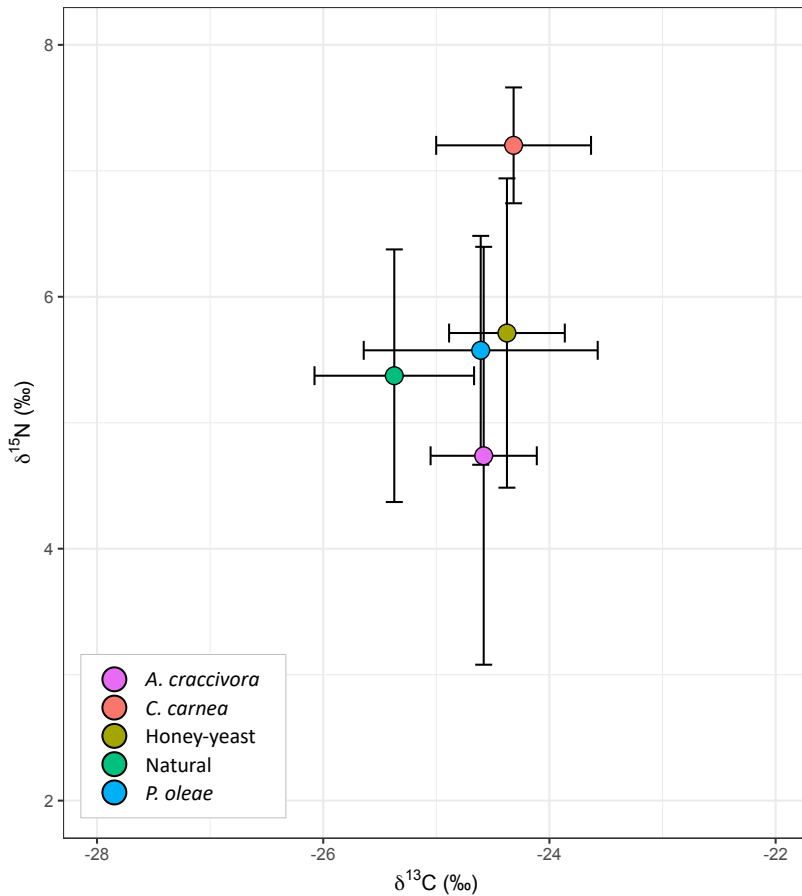


Figure 2. Overall isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of natural and experimental diets of *Tapinoma ibericum*.

Figures 3 and 4 show the changes in the rate of enrichment of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures, respectively, through time (t) amongst predatory diets. Essentially, they represent the pattern that an ant consuming herbivores should follow vs a hypothetical hyper-predator. The LMM analysis comparing the signatures of different diets across experimental times, showed that for the $\delta^{15}\text{N}$ only the effect of the diet is significant ($F_{3,21} = 4.50, p = 0.013$) and the interaction diet-time was not ($F_{4,18} = 0.79, p = 0.545$).

Moreover, only ants fed with *C. carnea* had different $\delta^{15}\text{N}$ compared with ants fed with *A. craccivora* (Tukey *post hoc* test, $p = 0.001$) and *P. oleae* ($p =$

0.010). On the other hand, for the $\delta^{13}\text{C}$ signature, neither the effect of time and diet nor the interaction diet-time were significant.

Accordingly, throughout time, ants fed with *C. carnea*, i.e., the hyper-predators, increased their $\delta^{15}\text{N}$ signature, the increase tended to follow a continuous rate. Conversely, ants fed with herbivores decreased their $\delta^{15}\text{N}$ signature. The difference in the $\delta^{15}\text{N}$ signature between *C. carnea* diet with *A. craccivora* and *P. oleae* started to be clear since the t2 experimental time just one week after the pass to a strict predatory diet. However, they become evident at t3 and continue to separate until reaching t4. These results suggest that *T. ibericum* needs at least 20 days to integrate to its tissue the $\delta^{15}\text{N}$ of the diet that is consuming to be detectable.

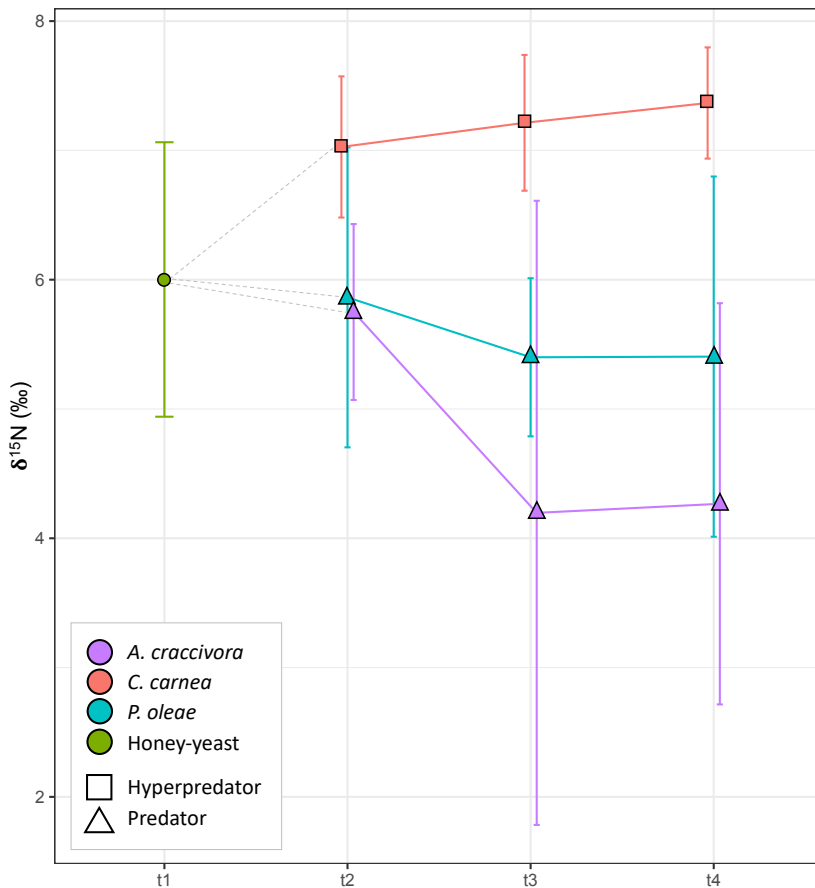


Figure 3. Isotopic signature and enrichment ($\delta^{15}\text{N}$) of experimental diets of *Tapinoma ibericum*, throughout experimental times.

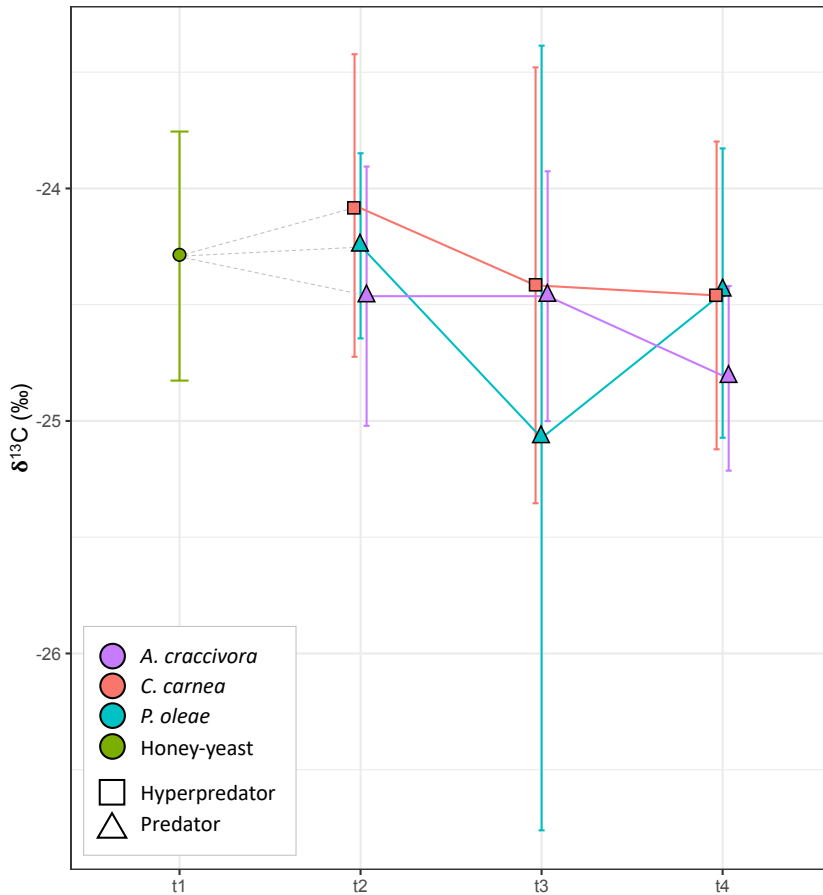


Figure 4. Isotopic signature and enrichment ($\delta^{13}\text{C}$) of experimental diets of *Tapinoma ibericum*, throughout experimental times.

Differences amongst areas and managements

Study area had an effect on ant isotopic signature (natural signature). The $\delta^{15}\text{N}$ signature differed significantly amongst study areas ($F_{5,97} = 3.521$, $p = 0.005$), however, only Dehesa del Generalife had a higher signature than Pinos Puente (Tukey *post hoc* test, $p = 0.039$) and Sierra Nevada ($p = 0.025$). This suggests that the trophic profile of *T. ibericum* ants inhabiting olive orchards is similar in most of the locations despite the different management (manure methods) in each olive orchards (Fig. 5). Conversely, *T. nigerrimum*, which inhabits only shrubby habitats at Sierra Nevada, have a different

isotopic profile, only this species had different concentration of $\delta^{13}\text{C}$ when compared with the rest of the areas ($F_{5,97} = 13.804$, $p = 0.001$; Tukey *post hoc* test, $p < 0.001$), i.e., the concentration of $\delta^{13}\text{C}$ is much lower. This suggests that *T. nigerrimum* had a different type of diet than *T. ibericum*, i.e., a different isotopic baseline might contribute to this difference. Furthermore, contrary to the results showed by study areas, the agricultural management did not show any significant difference on ant isotopic signature (Fig. 5).

Foraging surveys

A total of 369 preys were recorded in all the 40 ant-trails (mean \pm SD = 15.98 ± 10.06) (results based on the 60 minutes/trail/day surveys). We found 14 groups of arthropods as preys of which 34 % were herbivores, 3.29 % olive pests, and 1.41 % natural enemies, we also found miscellaneous, larvae, and animal rests (Table 3). Interestingly, the most abundant group of preys were dead ants (23 %), aphids (21.13 %), miscellaneous rests (21.13 %), and animal rests (19.72 %). Moreover, according to the data of ant activity in trails (i.e., 5 minutes/trail/day) the 4 % of all ants recorded in this type of survey ($n = 5\,443$) carried a prey.

Discussion

Stable isotopes analysis showed that *Tapinoma ibericum* has an overall isotopic signature compatible with a frequently consumer of herbivores and of *Prays oleae*. Indeed, the isotopic signature of *T. nigerrimum* is very different than that of *T. ibericum* probably due to important baseline differences in both habitats. Both species are omnivores (Seifert et al., 2017) but based on our analysis the former resembles more to an herbivore that can consume occasionally other herbivores (such as aphids, see Fig. 3 and 4). It is known that the ants of the *T. nigerrimum* complex act as facultative predators (Cerdá et al., 1989; Morris et al., 1998a; 1998b; Seifert et al., 2017), so this feature could be boosted by the type of habitats they inhabit and the fluctuant availability of different sources. In contrast, *T. ibericum* appears to match better with a $\delta^{15}\text{N}$ profile of an herbivore-predator but, interestingly, it did not match with the profile of a hyper-predator (see Fig. 3 and 4). In fact, their $\delta^{13}\text{C}$ natural profile is compatible with the profile of ants submitted to experimental diet based in *P. oleae* larvae.

With respect to the enrichment ratio during the diet experiment, $\delta^{13}\text{C}$ increase -0.2 % and $\delta^{15}\text{N}$ 2.1% between herbivore and predator consumers in 39 days, but they did not surpass the signature of the different diets.

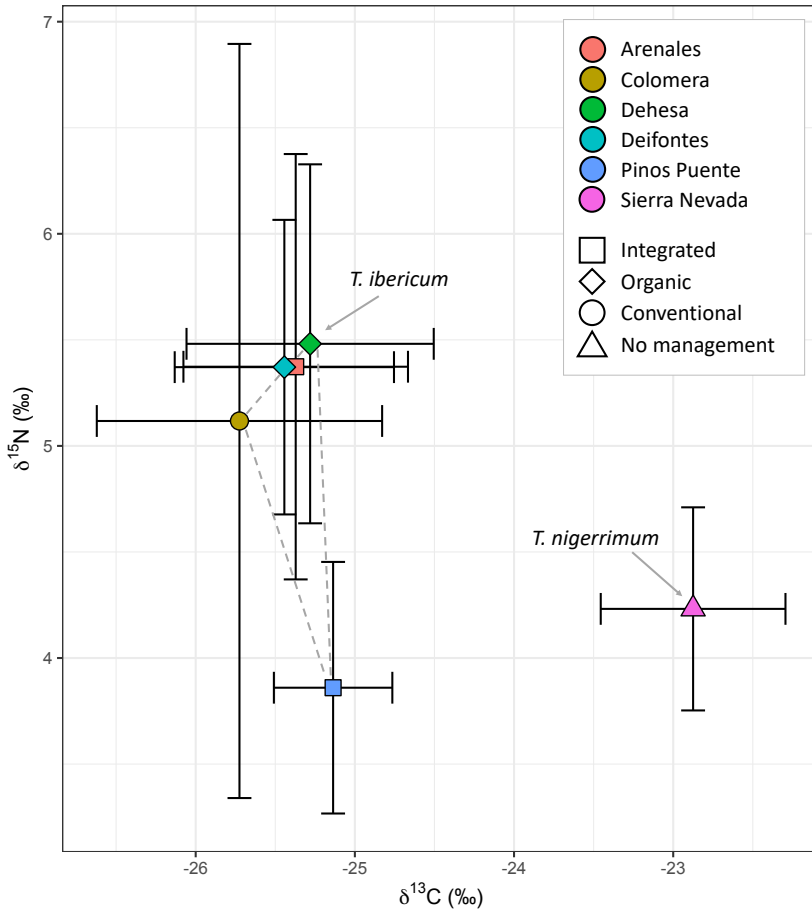


Figure 5. Overall isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of natural diets of *Tapinoma ibericum* and *Tapinoma nigerrimum*, from the different localities.

Another useful information for forthcoming SIA studies is that changes in diet begin to be detectable after 20 days of feeding in a particular diet.

Foraging surveys confirmed the varied diet of *T. ibericum* in olive orchards and its importance in the control of herbivores, including olive pests, although the year 2011 had a lower level of anthophagous *P. oleae* larvae available for *T. ibericum*. Our results allow to establish the enrichment ratio during the diet experiment, thus $\delta^{13}\text{C}$ increase a 0.2 ‰ and $\delta^{15}\text{N}$ a 2.1‰ between herbivore and predator consumers in 39 days, but they did not surpass the signature of the different diets. Another useful information for next SIA studies is that changes in diet begin to be detectable after 20 days.

Table 3. Abundance (relative abundance: RA) and variety of prey in ant-trails of *Tapinoma ibericum*, based on 60 minutes/trail/day surveys.

Order	Family/Species	RA (%)
Araneae		0.63
Hemiptera	Aphididae	21.13
	Cicadomorpha	2.82
	<i>Euphillura olivina</i>	3.13
	Heteroptera	1.10
Collembola		3.60
Coleoptera		0.78
Diptera		0.63
Embioptera		0.31
Hymenoptera	Formicidae	23.00
	Others	0.78
Lepidoptera		0.16
Neuroptera		0.47
Psocoptera		0.16
	Larvae (miscellaneous)	0.47
	Remains (animals)	19.72
	Remains (miscellaneous)	21.13

An interesting aspect revealed by our study is the common consumption of corpses of other ants (even individuals of the same species) by *T. ibericum*. This fact was impossible to control during the diet experiment and it could be responsible of a part of the variability found in SIA results for each diet. Interestingly, this variability was lower for ants fed with insects obtained from bio-factories where insects are reared with controlled diets (*C. carnea s.l.*) than for ants fed with natural insects collected from the field (*A. craccivora* and *P. oleae*).

Several studies pointed out that the olive moth *P. oleae* was consumed by *T. nigerrimum s.l.*, (Morris et al., 1999; 2002). This could be due to the fact that *P. oleae* have its highest abundances between May and July (Paredes et al., 2013; Villa et al., 2016). It is possible that before such a period of time *T. ibericum* might be feeding on the honeydew of herbaceous plants, and when the abundance of a pest increases, they turn to feeding on such a source of food (Morris et al., 1999; 2002). Hence, *T. ibericum* have got to invade the olive trees in order to feed on *P. oleae* because olive pests are highly associated with olive trees (Paredes et al., 2013; Álvarez et al., 2019a). In relation to this, Álvarez et al. (2019a) showed recently that ants living next and within organic

olive orchards tend to move to the ground cover and the olive trees mainly when the ground cover started to wither, which corresponds with the time that *P. oleae* lays the eggs on young olive fruits (Ramos et al., 1978). Furthermore, the abundance and trophic interactions of *Tapinoma* ants within the canopy of olive trees can be boosted by mature ground covers and less pesticide use (Álvarez et al., 2019b; Morente et al., 2018).

On the other hand, our results showed that *T. nigerrimum* seems to inhabit conserved natural ecosystems, which support the previous findings by Seifert et al. (2017) separating *T. ibericum* from *T. nigerrimum*. For example, our results suggest that in the region of the study *T. ibericum* is the species that inhabits olive orchards, which feeds on the same type of food no matter the type of agricultural management and manure applied in the different olive orchards (Fig. 5). This is of great importance, because a predator that is not affected by management could be used to enhance local biological control planning and strategies.

Several studies have shown *T. nigerrimum s.l.* as the most abundant ant within olive orchards, sometimes representing more than 50 percent of the relative abundance amongst omnivores (Morris et al., 1998a; 1998b; 1999; 2002; Morris and Campos, 1999; Redolfi et al., 1999; Pereira et al., 2004; Rodriguez et al., 2005; Santos et al., 2007b; Campos et al., 2011), which makes it one of the strongest candidates for potential control *P. oleae*. However, while negative effects showed on previous studies are likely to be caused by other species of the *T. nigerrimum* complex rather than *T. ibericum*, in the Iberian Peninsula the latter had the potential to feed on another important predator, the lacewing *C. carnea* (Morris et al., 1998b). Our analyses showed that in the field *T. ibericum* feed on *P. oleae* rather than *C. carnea*, and thus, this clarifies its role as a natural enemy. Nevertheless, the high variability showed by isotopic signatures is pointing to a varied omnivorous diet in the nature. Although, it is important to point out that there could be antagonistic interactions with other predators of *P. oleae* but such interactions can be appeased by less insecticide use (Morente et al., 2018) and modulated by ground covers (Álvarez et al., 2019a; 2019b; 2021a; 2021b). Thus, as suggested by Mansour et al. (2017), even when there could be negative effects, ants should not be excluded from agroecosystems because the exclusion of a predator may alter the nature and intensity of predatory, competitive, and mutualistic interactions amongst natural enemies (Píñol et al., 2012).

Overall, our results support the previous assumptions that the referred *T. nigerrimum s.l.* is beneficial for olive orchards in the south-centre of the Iberian Peninsula. Of the two species identified here, *T. ibericum* is possibly the species that can potentially contribute to control *P. oleae* without being a

hyper-predator in all types of olive orchards. However, trophic interactions based on stable isotopes analysis and direct observations amongst ants and pests in olive orchards should be investigated more thoroughly.

Acknowledgements

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Part Three:

Global Climate Change

Chapter 7

Metabolism and endogamy: effects of a global warming scenario produce trade-offs and constrains on survival and functional traits in a Mediterranean predator

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Abstract

To adapt to changes in temperature, animals tend to invest more energy in heat tolerance to improve survival, which in turn brings concurrent costs upon plastic key traits that are related to fitness. Although, what if global warming produced a genetic bottleneck on populations that may be reflected in the potential to deal with thermal extremes? As metabolism entails all transformations of materials and energy into various life structures and functions, theory predicts that the allometric relationship between metabolic rate and body mass will follow the $3/4$ power law with an independent influence of body size and temperature on metabolic rates. We assessed within population genetic variance produced by endogamy in the (a) functional traits, (b) metabolic rate allometries, and (c) larvae survival of the green lacewing *Chrysoperla pallida* (a natural enemy predator), through a series of experiments at different temperatures based on the A1B scenario of global warming. We demonstrated that an exogamic line, but not an endogamic line, will express phenotypic plasticity in metabolic rates and scaling, and thus, a down-regulation in their metabolism. So, endogamy is reducing the potential of thermal plasticity when individuals are subjected to thermal stress during ontogeny. Moreover, in order to improve survival due to the effect of larger body sizes, mandible size is constrained, and under thermal extremes, larger individuals tend to develop smaller mandibles, which is also constrained by the effect of metabolic rates in the endogamic line. These results did not

follow the predictions of the metabolic theory of ecology and indicate how substantial phenotypic and genetic variation can be dealt with thermal extremes in ectotherm natural enemies, and thus, highlight the pressures produced by such a global warming scenario that could ultimately lead to maladaptation and may deleteriously affect biological control.

Introduction

Ambient temperature plays a major role in the regulation of physiological functions in insects, such as metabolism, growth, or reproduction, which can affect traits involved in behaviour, life span, or survival (Harvey et al., 2020; Colinet et al., 2015; Kingsolver et al., 2015; González-Tokman et al., 2020). Then, predicting how animal populations will respond to warming temperatures is amongst the most pressing challenges in current ecology.

Insects have evolved strategies that let them to adapt to warmer conditions (Salman et al., 2019), however, exposure to conditions that may impose immense physiological stresses can lead to maladaptation in insect populations compromising their ability to deal with thermal extremes (Colinet et al., 2015), which can lead to the local extinction of populations (Brady et al., 2019). Though, if insects show narrow “thermal safety margins” (the optimal temperature for an insect species), implying that those insects have lower physiological flexibility to adjust to new temperatures (Kingsolver et al., 2013; Sgrò et al., 2016), their survival will be ultimately compromised.

On the other hand, metabolism entails all transformations of materials and energy into various life structures and functions (Brown et al., 2004; Glazier, 2005), and thus, metabolic rate has received much attention in regard to thermal tolerance and temperature rising (Fossen et al., 2019). The allometric relationship of metabolic rate with body mass is of great significance. Allometry refers to the scaling relationship between a given trait and body size, given the equation $y = \beta x^\alpha$, where y is the size of the trait of interest and x refers to body size (Bonduriansky, 2007; Álvarez et al., 2013a; 2013b; Álvarez et al., 2017b; Vera-Cano et al., 2017). A common assertion has been that the allometric slope of this relationship, β , is invariant following the “3/4-power law” (Brown et al., 2004). However, for organisms with high activity and a metabolism that is constrained by the surface area available, the slope should be close to a 2/3 tendency (following the surface/volume ratio) (Glazier, 2010). Moreover, it has been showed that within natural temperature ranges, the metabolic rate increases exponentially with

temperature for a given body size, but temperature is a major source of variation in the slope, and thus, its effect on the slope varies considerably, which depends on the type of organism (Glazier, 2005; Fossen et al., 2019).

Whereas inter and intra-specific variation in the scaling relationship of metabolic rate and body mass is well known, studies assessing within population genetic variation on the slope are rare (Fossen et al., 2019). This is of great importance because knowing the evolutionary potential of the plasticity of the slope will let us predict the ability of populations to adapt to changes in temperature, and therefore global warming. Recently, Fossen et al. (2019) showed that genotype by environment interactions can generate genetic variation in the ontogenetic allometric slope of animals, experiencing directional changes in temperature during growth, so the slope can evolve despite having limited genetic variation at constant temperatures.

While the anterior has been tested on animal models (e.g., the aquatic crustacean *Daphnia magna*), no attention has been paid to the natural enemies of insect herbivores (agricultural pests) (Harvey et al., 2020), which are of great economic importance. For example, it is known that the sensitivity of species to high temperatures increases with trophic level (Voigt et al., 2003), so the predators of pests could undergo higher pressures than their prey when subjected to thermal extremes (Harvey et al., 2020), which can lead to severe yield and habitat losses in zones where climate change may impact severely, e.g., the Mediterranean basin (Ponti et al., 2014; Duque-Lazo and Navarro-Cerrillo, 2017).

In this study we assessed within population genetic variance produced by endogamy in the (a) functional traits, (b) metabolic rate allometries, and (c) larvae survival of the Mediterranean green lacewing *Chrysoperla pallida* Henry et al., 2002, which belongs to the *C. carnea* complex (*C. carnea* s.l.). This complex comprises about 20 cryptic species distributed throughout the Northern Hemisphere (with some tropical-African representatives) (Henry et al., 2002). The larvae of green lacewings are voracious predator insects, so members of this complex are widely used as biocontrol agents in agricultural lands and greenhouses. We performed an experiment at three different temperatures imitating the summer natural conditions in which Mediterranean lacewings inhabit, based on the A1B scenario of 1.8°C of increasing warming temperature of the United Nations, to estimate the effects of temperature rising on a transgenerational thermal acclimated population. So, we aimed to respond the following questions:

- (1) are thermal extremes modifying the metabolic rates of green lacewings larvae?

- (2) are green lacewing larvae maintaining or modifying their metabolism under thermal extremes, and if so, will there be counteracting costs to deal with this?
- (3) is survival of green lacewing larvae inherently affected by thermal extremes and metabolism?

Material and methods

Study organism

The green lacewing *Chrysoperla pallida* is a valid species (Price et al., 2015) widely distributed in central Europe, but it exhibited a meridional and Mediterranean bias, occurring in an area bounded by Portugal and Spain to the west, England to the north, and Greece, Hungary, Georgia, and Iran to the south and east. It is limited to elevations below 1500 m and not found in northern Europe or Asia (Henry et al., 2002; Price et al., 2015; Monserrat, 2016). The genus *Chrysoperla* is morphologically identified by the posterior position of a transversal vein with respect to the oval cell in the forewing, but *C. pallida* is identified by the absence of pigmentation in the gradate series of the forewing (Fig. 1d), the form of the pretarsal claw, the pigmentation of the genal area in the head, and specifically by the pigmentation of the abdominal setae (blond), maxillary stipes (slight), and the shape of the genital lip (short and narrow) (Monserrant, 2016) (Fig. 1c). Also, *C. pallida* larvae lacked the antero-medial and frontal spots on the head (Henry et al., 2002) (Fig. 1b). The species inhabit trees and tall shrubs at the edges of forests or areas of human activity, and has been recognized to colonize urban areas (Henry et al., 2002; Price et al., 2015; Monserrat, 2016) and greenhouses (Rodríguez et al., 2019). Moreover, *C. pallida* has been identified as the species used as a biocontrol agent (jointly with *C. mutata* with the name *C. carnea s.l.*) by commercial companies in Mediterranean areas (Rodríguez et al., 2019).

Specimen collection

We collected lacewing adults directly (weather permitting) with the help of entomological nets between 2200 and 2400 h in the locality of Granada, Andalusia, Spain. Specimen collection started in late spring (May) and continued until the end of summer (October) in the years 2019 and 2020. Lacewing adults were placed individually in plastic petri dishes and transported to the Department of Zoology in the University of Granada.

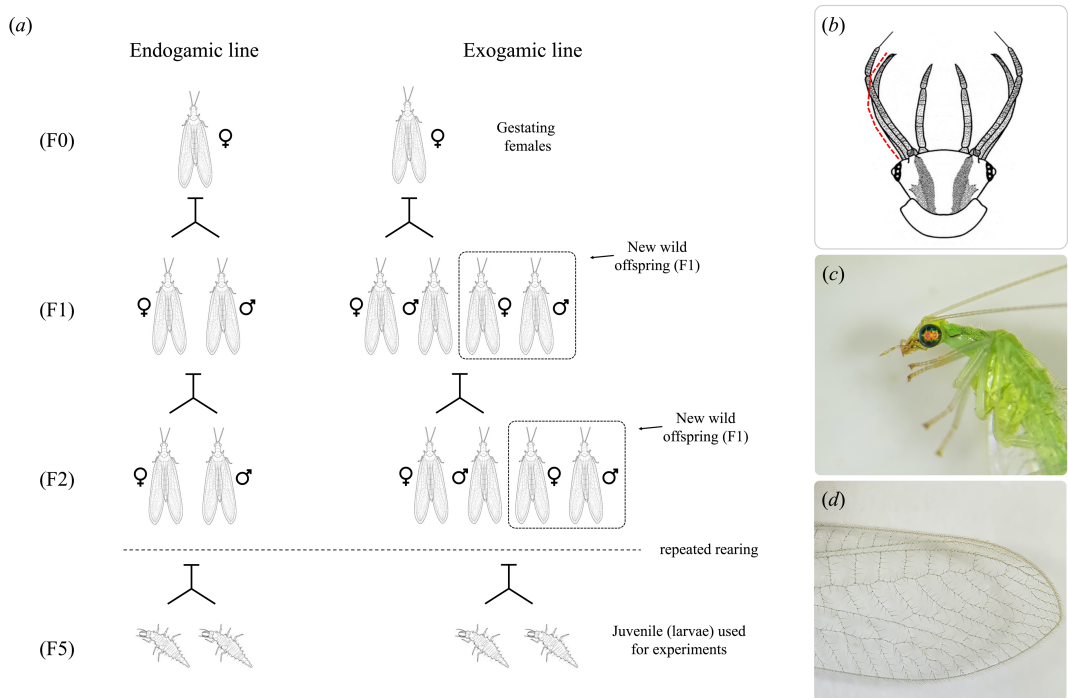


Figure 1. Morphological traits and rearing of *Chrysoperla pallida*. (a) Transgenerational rearing scheme of the stock colony to produce two genetic lines: exogamic and endogamic. (b) Head of *C. pallida* larva, the red line shows the segmented measurement of mandible length. (c) Head, thorax, and (d) wings of *C. pallida* adults.

We identified *C. pallida* specimens following Monserrat (2016), but we were able to identify lacewings alive by gently holding the lacewing from the posterior end of the four wings jointly, preventing that the legs touched any surface, and gently manipulating the specimen to see morphological traits under a stereomicroscope (SMZ1000 Nikon, Japan). We separated the specimens by sex because sexually mature females and males of *C. pallida* are easily identified by the form and size of the abdomen. After identification, *C. pallida* adults were returned to individual petri dishes and prepared for rearing. The rest of the lacewings that were identified other than *C. pallida* were set free.

Specimen rearing

The stock colony of *C. pallida* was reared in the laboratory (Fig. A7.1 of supplementary data in Appendix) in a climatic-chamber with controlled

conditions: 12:12 h light:dark photoperiod, 25:20°C ($\pm 0.5^\circ\text{C}$) max:min temperature period, and 60 % relative humidity. Specimens were maintained in 1 L plastic boxes with petri-dishes as food containers and 5 ml glass tubes (with cotton taps) to supply fresh water. Adults were fed with pellets of bee pollen and larvae were fed with fresh eggs of *Ephesia kuehniella*.

As we planned to produce two genetic lines, (1) a natural line (exogamic: sexually recombined with genetically unrelated individuals) and (2) an endogamic line (sexually recombined with genetically related individuals), the first *C. pallida* adult females were numbered and placed individually in the 1 L plastic boxes as F0 gestating females. Newly hatched F1 larvae were gently removed using a brush, placed individually in plastic Petri dishes (5.5 cm in diameter, 1.8 cm height), and reared until adult emergence, then, F1 adults were separated by sex. For the endogamic line all adult male and female sons of a single F0 female were introduced together in a plastic box. For the exogamic line the sons of one F0 female and the sons of a different F0 female were introduced together in another plastic box. This procedure was repeated to produce following generations for the two genetic lines. To maintain the heterogeneity of the exogamic line new F0 females were collected throughout the sampled period (years 2019-2020) and reared individually so their F1 sons could be introduced within each new generation (Fig. 1a).

Metabolic rate measurements

Standard metabolic rate (hereafter metabolic rate) was estimated as the rate of CO₂ production ($\dot{M}\text{CO}_2$) using flow-through respirometry. CO₂ concentration was measured using a non-dispersive CO₂/H₂O analyser (PP-Systems, U.S.A.), which was used with the default CO₂ calibration concentration of 2000 ppm. The system integrates a built-in sampling air pump that operates at a flow rate of 350 ml min⁻¹ and an auto-zero feature that ensures warm-up, long term stability, and accuracy. This feature operates using an absorber column which contains a CO₂ scrubbing desiccant. The system periodically switches the flow of gas from the analyser through this absorber column to check the analyser zero and automatically corrects for sample cell contamination, source aging, detector sensitivity, and changes in electronics. All gases circulated in 3 mm inner-diameter plastic tubing and gasses passed through an in-line filter fitted with a 3-micron PTFE hydrophobic filter before entering the analyser. The tubing was connected to an open-flow chamber, which was a transparent tube with an inner top in a conical shape custom-made from Plexiglass (9 cm length, 2.5 cm diameter, 1.5 cm tube connector). The transparent chamber allowed us to observe *C.*

pallida larvae movements and activity to ensure CO₂ was produced during a resting behaviour. The open flow chamber was set inside an incubator with refrigeration (CIR-S 70 IngClimas, Spain) to maintain a constant experimental temperature during measurements. The analyser was set next to the incubator to allow the air passed in few centimetres of tubing to reduce the delay between the occurrence of a CO₂ burst and its detection. We estimated this delay in preliminary measurements by (1) quickly opening and closing the entrance of the chamber and by (2) introducing a larva to the chamber, wait until the larva rests and moving the plastic chamber to make the larva move again. There was an average of 3 s before the resulting peak in CO₂ concentration. Measurement period lasted an average of 45 min (approximately 1000 records). If the larvae did not rest in a given measurement, we repeated it until we recorded the CO₂ production of the resting behaviour.

Data were collected using the Transfer Software (v 1.05; PP-Systems). CO₂ production (\dot{M}_{CO_2}) was estimated from the lowest record when the decline in CO₂ concentration became linear in two moments: (1) when the chamber was empty (incurrent air) and (2) when a larva inside the chamber was resting (excurrent air). The records of incurrent air were made periodically during the experiments in a given day. If there were no accumulation in CO₂ in incurrent air due to human activity in the laboratory, the CO₂ concentration of incurrent air records resulted from the average of all measurements.

Raw measures (ppm) were converted to molar rates of CO₂ production (\dot{M}_{CO_2}) using the flow rate (350 ml min⁻¹) and the Ideal Gas Law: $\dot{M}_{CO_2} = P \times FR (F_{iCO_2} \times F_{eCO_2}) / R \times T$, where \dot{M}_{CO_2} is the rate of CO₂ production (mol min⁻¹), F_{eCO_2} is the fractional CO₂ concentration in excurrent air, F_{iCO_2} is the fractional CO₂ concentration in incurrent air, FR is the flow rate (0.35 l min⁻¹), P is pressure (1 atm), R is the gas constant (0.08206 l atm K⁻¹ mol⁻¹) and T is the experimental temperature (K).

Experimental design and measurements

Temperature maximums were established based on the average of monthly mean maximum temperatures of summer months in the sampling area, for the three years previous to the experiment, i.e., 2016, 2017, 2018. This temperature was 37°C, and thus the A1B scenario of 1.8°C of warming temperature of the United Nations was set from this temperature. We also established a low maximum temperature experiment of 26°C, based on average of monthly mean maximum temperatures of spring. Then, three

experiments were carried out (subsequently) in a Memmert cooled incubator with refrigeration (ICP 600 Memmert, Germany) for the resulting three experimental temperatures: 26, 37, and 38.8°C. We used the programming function of the incubator to imitate the abiotic conditions of summer in the Mediterranean areas where *C. pallida* may live, so for the three experiments we set the following parameters equally: a minimum temperature of 20°C; a 14:10 h light:dark photoperiod; and a 50 % of relative humidity. Then we programmed the incubator to generate a 24 h cycle of four consecutive stages of temperatures, the first stage was a 10 h period of augmentative temperature starting at the minimum temperature and slowly reaching the maximum temperature, the second stage was a 4 h period of static maximum temperature, the third stage was an 8 h period of diminishing temperature slowly reaching the minimum temperature, and the fourth stage was a 2 h period of static minimum temperature (Fig. A7.2 of supplementary data in Appendix).

Newly hatched larvae of the stook colony, reared for a minimum of five generations, were gently removed, individualized in petri dishes, and used for the experiments. Larvae inside petri dishes from the two genetic lines were placed in the same plate inside the ICP incubator. We reared the larvae in the experiments similar to the stook colony, but we fed the larvae specifically with 6.5 mg of *E. kuehniella* eggs in temperature-specific days of separation (see results). Larvae were reared in experimental conditions for a minimum of 6 days and a maximum of 17 days (but 21 days at 26°C) previous to carried out the metabolic rate measurements. Immediately after metabolic rate measurements were done, the larvae were weighted and photographed under a stereomicroscope when the larvae were relaxed. The mandible length of the larvae (left mandible) was measured from photographs as a morphological functional trait. Curved measurements of the mandible were made by curved segmented lines (5 lines separated by 6 points) over the posterior edge of the mandible from the base next the articulation, to the distal point (ImageJ v. 1.53a) (Fig. 1). Survival of each larva under the three experimental temperatures was recorded. We estimated larvae survival as the successful pass of a larvae to the cocoon stage (pupa). We used 20 larvae per genetic line per temperature, resulting in a total sample size of 120 measurements. The experiments and measurements were conducted over 8 months from July 2020 to February 2021.

Data analysis

To estimate the overall effect of warming temperatures of the A1B scenario on *C. pallida* larvae, firstly, we fitted linear mixed models (LMMs)

assessing the effect of the type of genetic line, for which we included the metabolic rate (MR; $\dot{M}CO_2$ of each experimental temperature), body mass (BM; mg), and mandible length (ML; mm) as response variables. For each LMM the temperature (T; categorical) and the type of genetic line (categorical) were the predictor variables and the days of experimental rearing before measurement (numerical) was a random effect. Secondly, we fitted LMMs in the same form but separately for each genetic line.

In addition, to estimate the variance in the intercepts and slopes of the allometric relationship between MR and BM, and between ML and BM at different experimental temperatures, we fitted linear models (LMs) as ANCOVAs with the log-transformed data of MR, BM, and ML to compare OLS regressions. Firstly, two LMs were fitted including as the response variables MR and ML, respectively, and the predictor variables were the interaction of body mass with temperature (BM×T) and the type of genetic line (categorical). Secondly, we fitted LMs in the same form but separately for each genetic line. The slope with SE, and lower and upper CI values were extracted.

Finally, to estimate the effects of warming temperatures of the A1B scenario on the survival of *C. pallida* larvae and its relationship with MR, BM, and ML in each genetic line, firstly, we assessed which of our variables was the most important variable that could explain larvae survival. For this, we fitted a generalized linear mixed model (GLMM) as a global model including the data of survival (binary; 1= alive, 0= death) as the response variable. The predictor variables were MR, BM, ML, T, and the type of genetic line. The days of experimental rearing before measurement (numerical) was a random effect. The binomial family with log-link tendency was used in this GLMM. Then, the model was subjected to a multi-model inference, this novel procedure fits models using all possible combinations of predictors and weights them using the Akaike information criterion (AIC) with $\Delta AIC < 2$. Secondly, each combination amongst MR, BM, and ML, with the three experimental temperatures, and for each genetic line, was subjected to a logistic regression approach (GLMs) in order to assess the probability of survival. The resulting significant logistic regressions were used to assess the effects of the interactions BM×MR and BM×ML on survival.

All analyses were computed in the R software v.4.0.3 (R Developmental Core Team, 2020). We used the default functions to run LMs, GLMs, and logistic regressions; the function lmer in the package lme4 to run LMMs and the package car to run ANOVAs. Further differences within each model were tested using the package emmeans. The multi-model inference was computed using the dredge function in the MuMIn package.

Results

Overall effects of experimental temperatures

The MR, BM, and ML of green lacewing larvae showed significant differences amongst experimental temperatures (figure 2), however, the effect of the genetic line was only significant for the MR ($F_{1, 106} = 6.79, p = 0.010$).

Differences amongst experimental temperatures for both the exogamic line ($F_{2, 16} = 86.39, p = 0.001$) and the endogamic line ($F_{2, 46} = 63.50, p = 0.001$) showed that MR increased drastically from 26 to 37°C (*post hoc* test: $p = 0.001$). Conversely, from 37 to 38.8°C the difference of 1.8°C decreased MR, reaching and tending to reach the levels showed at 26°C for the endogamic line ($p = 0.072$) and the exogamic line ($p = 0.001$), respectively (Fig. 2).

BM tends to increase as temperature increase; however, significant differences were showed only by the endogamic line ($F_{2, 55} = 13.02, p = 0.001$). The differences amongst temperatures were driven by BM at 38.8°C (*post hoc* test: $p = 0.001$) (Fig. 2).

ML responded somewhat differently between the exogamic line ($F_{2, 47} = 3.95, p = 0.025$) and the endogamic line ($F_{2, 54} = 3.59, p = 0.034$), i.e., the mandibles barely increased as temperature increase, but for the later, mandible size tend to decrease from 37 to 38.8°. The differences amongst temperatures were showed between 26 and 38.8°C for the exogamic line (*post hoc* test: $p = 0.018$), but between 26 and 37°C for the endogamic line ($p = 0.036$) (Fig. 2).

Allometric relationships

In the first LMM the allometric slope of the MR was significative ($F_{1, 113} = 14.61, p = 0.001$) as well as the effect of the temperatures ($F_{2, 113} = 257, p = 0.001$), i.e., the MR tend to decrease with BM (Table 1). Moreover, significant differences were found amongst the slopes for the exogamic line, which was driven by the difference between 26 and 38.8°C (Tukey *post hoc* test: $p = 0.042$), but not for the endogamic line (Fig. 3). Nonetheless, the effect of the type of genetic line was not significative.

Each temperature-specific slope did not follow a 3/4 power law tendency, especially at 26°C the slopes in the exogamic and endogamic lines followed a 2/3 tendency (Table 1). Then the rest of the slopes tend to decrease as temperature increase, which was a tendency more drastic for the exogamic line (Fig. 3).

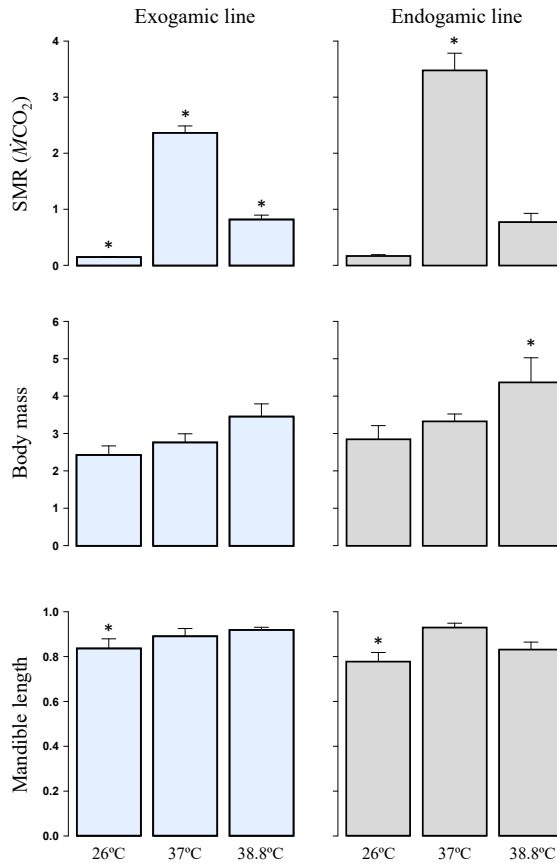


Figure 2. Overall effects of increasing temperature, according to the A1B scenario, on standard metabolic rate (SMR), body mass, and mandible length in both genetic lines (exogamic and endogamic) of *Chrysoperla pallida* larvae. Asterisks represent significant differences amongst temperatures based on post hoc tests, $p < 0.05$.

On the other hand, in the second LMM the allometric slope of the ML was significant ($F_{1, 113} = 98.7, p = 0.001$) as well as the effect of the temperatures ($F_{2, 113} = 3.63, p = 0.029$). The ML was isometric but tended to follow a negative allometry tendency, i.e., the relative size of the mandible decreases with body size (Table 1). Contrary to the MR, the type of genetic line showed significant effects on the allometric relationship of ML with BM ($F_{1, 113} = 7.11, p = 0.008$). Significant differences were found amongst the slopes only for the exogamic line, which was driven by the slope at 38.8°C (Tukey *post hoc* test: 38.8 vs 26°C, $p = 0.001$; 38.8 vs 27°C, $p = 0.001$).

Table 1. Allometric slopes with SE and lower and upper CI for log-transformed data of standard metabolic rate (SMR) and mandible length (ML) of two genetic lines (exogamic and endogamic) from a population of *Chrysoperla pallida* at different temperatures (T).

Genetic line	T (°C)	SMR: Slope (± SE)	Lower CI - Upper CI	ML: Slope (± SE)	Lower CI - Upper CI
Exogamic	26	0.635 ± 0.19	0.260 - 1.011	0.371 ± 0.06	0.253 - 0.490
	37	0.015 ± 0.19	- 0.376 - 0.407	0.329 ± 0.06	0.206 - 0.453
	38.8	- 0.084 ± 0.22	- 0.528 - 0.360	- 0.018 ± 0.07	- 0.159 - 0.121
Endogamic	26	0.507 ± 0.21	0.080 - 0.933	0.289 ± 0.04	0.200 - 0.379
	37	0.243 ± 0.50	- 0.761 - 1.247	0.068 ± 0.10	- 0.142 - 0.278
	38.8	0.382 ± 0.20	- 0.028 - 0.792	0.190 ± 0.04	0.105 - 0.276

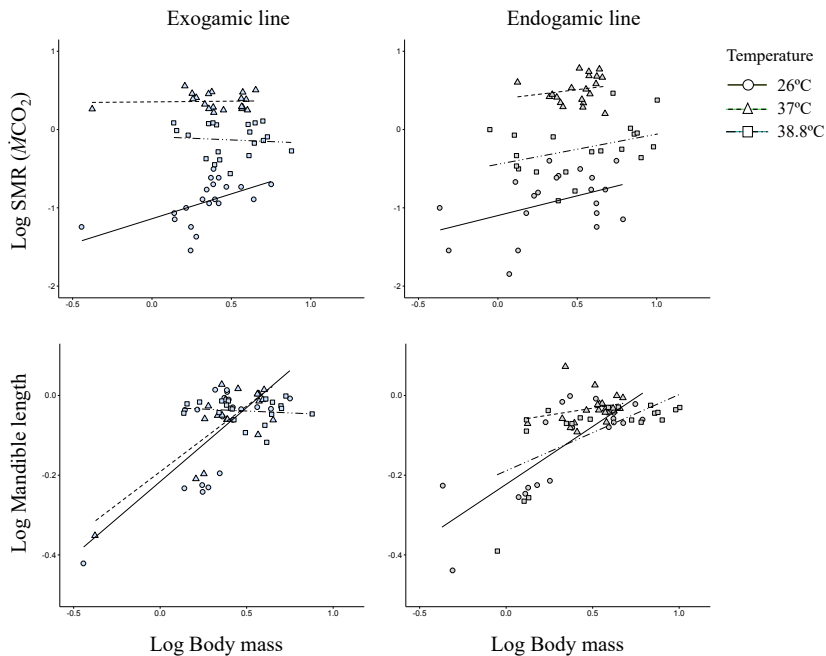


Figure 3. Allometric relationship of the standard metabolic rate (SMR) and mandible length with body mass for both genetic lines (exogamic and endogamic) of *Chrysoperla pallida* larvae at three different temperatures.

Table 2. Multi-model inference statistics of five variables that affect larvae survival in a population of *Chrysoperla pallida* measured in the global warming change experiments. Estimates show the type of effect produced (positive or negative), and the model's n and sum of weights tell information about the level of importance of each variable over 31 possible model combinations, especially the model's n show the number of models in which a variable was present.

Variables	n model	Sum of weights	Estimate	z value	p value
Body mass	5	1.00	0.592	3.36	0.001
Metabolic rate	3	0.55	-0.237	1.62	0.106
Temperature	1	0.24	-1.014	1.98	0.048
Mandible length	1	0.13	-0.931	0.62	0.535
Genetic Line	1	0.12	0.230	0.55	0.579

This suggests that the negative allometry of the mandible was strongest at 38.8°C (Fig. 3).

Larvae survival

The multi-model inference produced 31 possible model combinations. Based on the sum of weights and the number of models where variables were present, variables were listed from most to least important as: (1) BM, (2) MR, (3) T, (4) ML, and (5) the type of genetic line. However, only the effect of BM and T were significative, being the former positive and the later negative (Table 2).

According to the multi-model inference, we inspected the pattern followed by the relation between survival and BM across temperatures showed by logistic regressions (Fig. 4). In the case of the exogamic line, individuals with larger sizes were more likely to survive at all temperatures, this effect tend to be strongest as temperature increase, being the numbers of death-individuals larger at 38.8°C (small individuals) (Fig. 4). Although, in the case of the endogamic line, at 26°C there was a weaker effect in the form of a negative relationship, so individuals with larger sizes were somewhat less likely to survive. Conversely, at 38.8°C there was a strong effect in the opposite direction (Fig. 4).

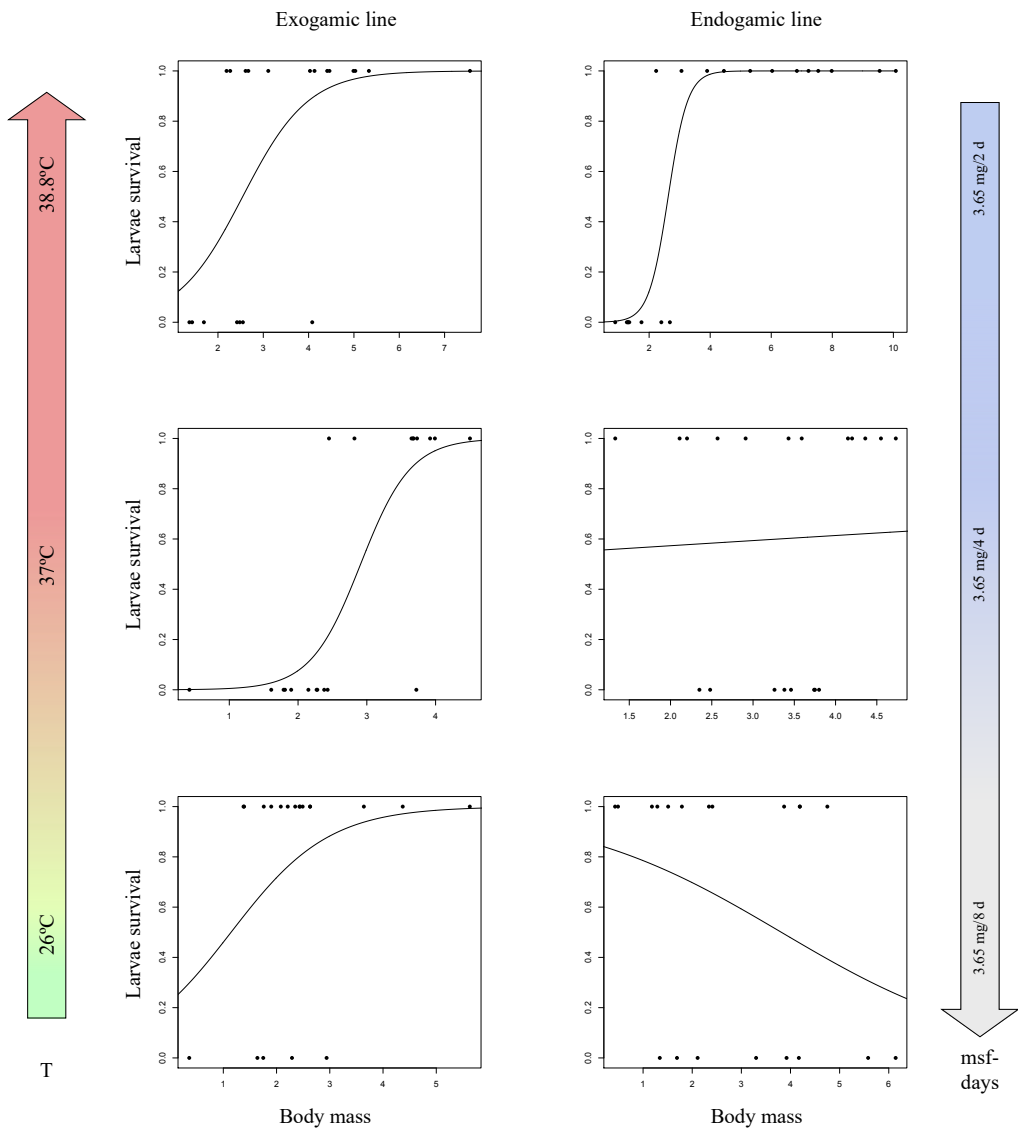


Figure 4. Probability of survival based on the relation between body mass and larvae survival of *Chrysoperla pallida* at three different temperatures. Left arrow shows the summer temperature (T) in a normal range (26 to 37°C) and the resulting temperature according to the A1B scenario (38.8°C). Right arrow shows the minimum-separation-of-feeding-days (msf-days) to prevent the death of larvae.

Finally, the effects of the interactions $BM \times MR$ and $BM \times ML$ over larvae survival were graphically inspected at 38.8°C , i.e., $BM \times ML$ for the exogamic line and $BM \times ML$ and $BM \times MR$ for the endogamic line. The results showed that under the A1B scenario of 1.8°C increasing temperature larger individuals with small mandibles survived more than small individuals with large mandibles (see Fig. 5a and 5b for the exogamic line and endogamic line, respectively), however, for the endogamic line there was a strongest effect on BM and a weaker effect on ML (i.e., large to medium individuals with large mandibles are more likely to survive than very small individuals with large mandibles) (Fig. 5b). In addition, only for the endogamic line, larger males tend to survive more at lower metabolic rates (Fig. 5c).

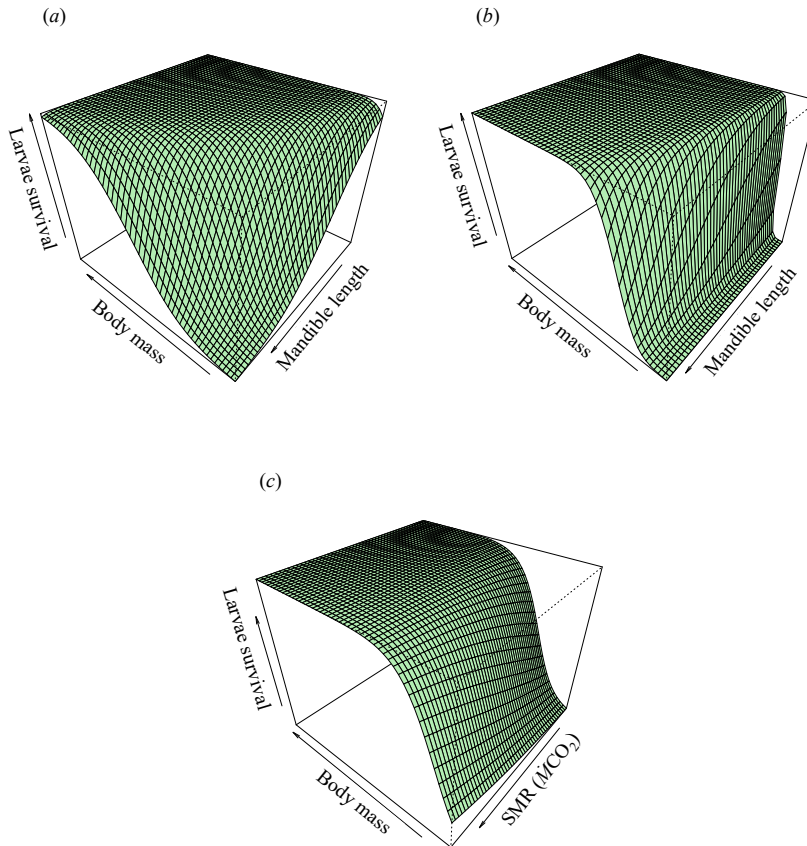


Figure 5. Interaction amongst survival, body mass, and functional traits of *Chrysoperla pallida* larvae at 38.8°C based on significant probabilities. (a) Relationship with mandible length as the functional trait in the exogamic line and (b) the endogamic line. (c) Relationship with standard metabolic rate (SMR) as the functional trait in the endogamic line.

Further effects of temperature rising

Additionally, we recorded that the minimum-separation-of-feeding-days to prevent the death of larvae were: 6.5 mg/8 days at 26°C; 6.5 mg/4 days at 37°C; and 6.5 mg/2 days at 38.8°C, i.e., whereas temperature increase, the need for resources (food) also increased reducing the days between feedings (Fig. 4). This was reflected on the developmental time of the larvae, which pass from a mean of 15 days at 26°C to 7 days at 37 and 38.8°C to see the first cocoon.

Moreover, we recorded that the larvae changed its behaviour as temperature increased, i.e., larvae at 37°C move really fast inside petri dishes than the larvae at 26°C, which had movements that seem more natural, however, at 38.8°C larvae stop moving specially in the hours of maximum temperature. Interestingly, larvae at 38.8°C changed their colour from brown-to-black to a strong yellow-to-brownish (Fig. 6). This suggest that larvae started to be thermal stressed at 37°C and really stressed at 38.8°C, possibly reaching the species thermal safety margins.

Discussion

Metabolic rates and allometric scaling

In this study we have found that temperature rising of 1.8°C surpassing summer maximums, based on the A1B scenario of the United Nations, affects the Mediterranean predator *Chrysoperla pallida*, a green lacewing of economic importance. Particularly, we wanted to assess how within population genetic variance produced by endogamy on transgenerational thermal acclimated individuals will respond under such a scenario.

Our analyses showed that under normal conditions a temperature rising from 26 to 37°C (Mediterranean region) will elevate the MR of this species, however, an increasement of 1.8°C in the summer maximum temperatures over a constant period of time not only reduced the MR of *C. pallida* larvae but produced a more extreme tendency in the endogamic line than the exogamic line. In addition, we showed that larvae at 38.8°C reduced physical activity and even changed their colour, which resemble an aestivation behaviour, whereas they did not stop feeding, so individuals tend to be bigger. A reduction in metabolism could be a response to thermal extremes in this species, for example, it is known that insects respond in different ways to thermal stress, i.e., adaptations to warming include temporal shifts from periods of activity to quiescence via diapause and/or aestivation (Bale et al., 2002; Masaki, 1980; Salman et al., 2019); increasement or reduction of the physical activity (Hemmings and Andrew, 2017); seek for

cooler microclimates where it is experienced less thermal stress (Hemmings and Andrew, 2017); development of better heat tolerance (Kingslover et al., 2013); and physiological flexibility to adjust to thermal extremes within a season (Collinet et al., 2015); amongst others. So, the increasement in temperature produced in our experiment could lead this species to reach its thermal safety margin and adjust their physiology to this scenario of stress.

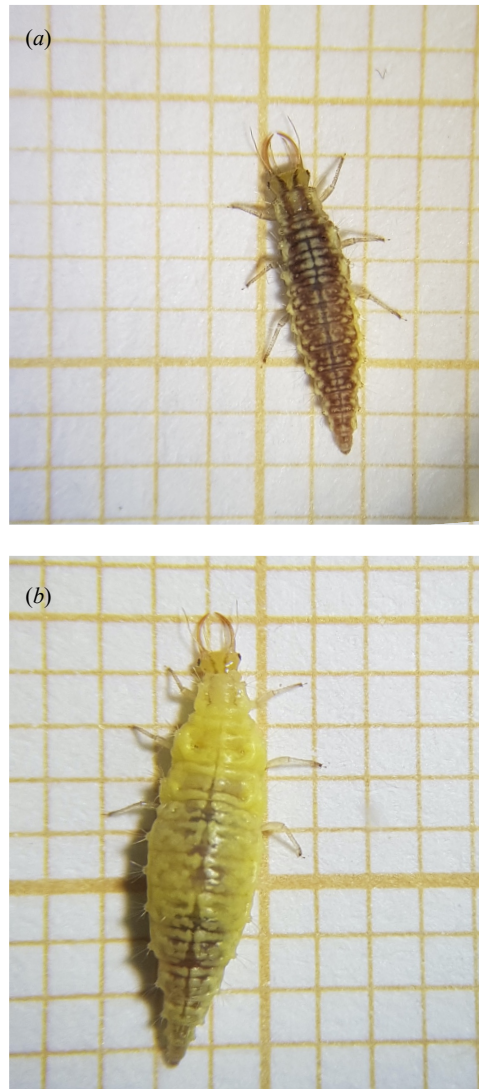


Figure 6. Phenotypic differences produced by rising temperatures on the larvae of *Chrysoperla pallida* reared at different temperatures according to the A1B scenario. Appearance of 3rd instar larvae, (a) reared at normal temperatures from 26 to 37°C and (b) reared at 38.8°C.

Though, is *C. pallida* larvae regulating their metabolism throughout development? What we have found is that only the exogamic line, showed phenotypic plasticity in metabolic scaling, and thus, a down-regulation in their metabolism (Fig. 3). This was reflected in the allometric slopes across temperatures, as it decreased with increasing temperature (when compared to our lowest maximum, 26°C). However, the allometric slopes of the endogamic line were parallel across temperatures. Up and down-regulation is a process that is explained by the “acclimation hypothesis for temperature dependence” (Kjelland et al., 2017; Fossen et al., 2019) whereby organisms attempt to reduce the direct effects of temperature that sub-optimally reduce or increase their metabolism, i.e., ectotherms that grow in cold environments will up-regulate metabolism (e.g., steeper allometric slopes). Conversely, ectotherms in hot environments will down-regulate metabolism (e.g., flatter allometric slopes) (Glazier, 2018). One would expect that this acclimation occurs throughout ontogeny, even if ectotherms are born and reared at a constant temperature for multiple generations. However, if there are no acclimation processes, the allometric slopes should be parallel across temperatures, as was the case of the endogamic line.

Indeed, the allometric slope between MR and BM will vary across different genotypes if individuals are experiencing directional changes in temperature during ontogeny (Fossen et al., 2019), which explains the differences in the pattern of the slope across temperatures between our two genetic lines. Especially, it is known that juvenile life stages are more sensitive to thermal extremes and thermal stress than adult ones (Harvey et al., 2020). Furthermore, it is possible that, at the fifth generation it could be started to generate a genetic bottleneck (very low genetic variance) in the population and animals in our endogamic line could lost the ability to up or down-regulate their metabolism (loss of plasticity) when subjected to thermal stress during ontogeny, suggesting that the slope (and its thermal plasticity) may have a limited potential for evolving over short time scales under such circumstances (Hansen, 2015; Fossen et al., 2019).

On the other hand, in the case of ML, a morphological functional trait, we have found that it expressed a proportional growth with BM. However, for the exogamic line this tendency was expressed only under normal conditions of temperature i.e., from 26 to 37°C, but at 38.8°C it expressed a great negative allometry. As this trait is needed for feeding, allometric theory predicts that it should not express any form of exaggeration but maintain an isometric tendency in the slopes i.e., a proportional growth with body size (Bonduriansky, 2007; Voje, 2016). Such a change, from isometry to negative allometry in a morphological functional trait, suggests a constraint produced

by metabolism, as the slope at 38.8°C follows the pattern showed by MR. It also suggests that this trait could be genetically linked to how MR is expressed, as allometric slopes of traits that may be functionally linked to metabolic rates often appear genetically constrained (Pélabon et al., 2014), a pattern previously known in ectotherms (Pélabon et al., 2014; Voje et al., 2014) that should be investigated more thoroughly.

Larvae survival

Our analyses showed that temperature rising of 1.8°C surpassing summer maximums, based on the A1B scenario of the United Nations, affected negatively the survival of the larvae of green lacewing *C. pallida*. It is known that amongst main life history traits, survival has the widest range of thermal sensitivity, nearly followed by development, and reproduction with the narrowest thermal sensitivity (Ma et al., 2015), but thermal extremes experienced by egg, larval, or pupal stages can decrease survival, rather than thermal extremes experienced by adults (Zhang et al., 2015). We found that BM is the main factor that drives the survival of *C. pallida* larvae, i.e., mortality is positively correlated with temperature rising, being the larvae with larger body sizes the ones with higher possibilities of surviving (Fig. 4). Nonetheless, the endogamic line showed to be more sensible to thermal extremes and the changes in temperature, which were reflected in drastically changing patterns of response from surviving smaller sizes to larger sizes as temperature increases (Fig. 4). Also, in our experiments, increasing temperatures reduced larvae development so larvae reached their fastest development of 6 days at 37°C, and they could not develop faster than that at 38.8°C. The anterior could be explained due to changes in body size induced by thermal extremes. Enhanced metabolism and fast development are induced by high developmental temperatures, which commonly produces small individuals via selection for smaller body sizes (CaraDonna et al., 2018; Foster et al., 2012; Tseng et al., 2018). However, the selective advantage of smaller sizes might become disadvantageous under repeated exposure to thermal extremes, which in turn can produce larger individuals (Gardner et al., 2011; Sentis et al., 2017; Xing et al., 2014). Moreover, it is known (body size hypothesis, Ma et al., 2021) that the smaller early life stages are subject to faster increases in body temperature and water loss and that larger larvae are more heat tolerant.

Nevertheless, insects can exploit the thermal diversity of their microhabitats to avoid thermal extremes (Ma et al., 2021; Harvey et al., 2020). Indeed, it is possible that larvae can exploit a behavioural thermoregulation across the complex mosaic of microclimates that is

produced by living and non-living objects in the environment, seeking better places to avoid thermal extremes, which could explain the patterns in larvae movements at 37°C. For example, different microhabitats filter and/or buffer atmospheric conditions differently, there is a difference of >5°C in microclimate temperature amongst grassland, heathland, or deciduous woodland (Suggitt et al., 2011). Also, it has been showed that heterogeneity on the surface of apple leaves can produce difference in temperature of 6 to 12°C (Saudreau et al., 2017), and temperature in the ground bellow hot rocks can be up to 9°C lower in deserts (Pike et al., 2012). Although, this possibility has been hindered by the type of enclosure in which individual larvae were reared in our experiment, and thus, under such a circumstance larvae exploited behavioural and physiological thermoregulation in the form of aestivation, reducing physical activity and decreasing MR (see above).

On the other hand, we found trade-offs amongst BM, ML, and MR, which consequently affected survival. Our results showed that, in order to improve survival due to the effect of larger body sizes, mandible size is constrained and, under thermal extremes, larger individuals tend to develop smaller mandibles, which was expressed similarly by both genetic lines (Fig. 5). However, for the endogamic line the effect of MR was important and larger males tend to survive more at lower metabolic rates (Fig. 5). Accordingly, variation in thermal sensitivity of different traits may contribute to buffering heat stress in insects via phenotypic plasticity (Gunderson and Stillman, 2015; Hoffmann et al., 2013; Kellermann and Sgrò, 2018; vanHeerwaarden et al., 2016), as we have already showed for MR allometries. However, phenotypic plasticity as a strategy to cope with environmental variation has a (quantitatively) limited scope to increase significantly heat tolerance. As temperature surpasses the optimum for development, insects tend to invest more energy in heat tolerance to improve survival, which in turn brings concurrent costs in other plastic traits that are related to fitness (vanHeerwaarden et al., 2016; Esperk et al., 2016; Loeschcke and Hoffmann, 2007). Though, for the larvae of the green lacewing *C. pallida*, we agree that phenotypic plasticity is an important strategy to deal with thermal extremes in exogamic individuals when conditions hinder the possibilities of exploiting behavioural thermoregulation, however, this strategy will be expressed deficiently by genetically compromised individuals (e.g., the endogamic line).

Overall, our results do not follow some of the predictions made by the metabolic theory of ecology (MTE; Brown et al., 2004). Firstly, the allometric slopes that we observed were lower than the predicted $\beta = 3/4$, and secondly, the occurrence of phenotypic plasticity in metabolic scaling contradicts the

assumption of an independent influence of body size and temperature on metabolic rate. In addition, the existence of trade-offs produced by phenotypic plasticity in order to improve larvae survival showed the pressures produced by thermal extremes on this Mediterranean predator, such a pattern could be a tendency in lacewings, which are globally used as natural enemy agents. This tendency could ultimately lead to maladaptation, which may deleteriously affect biological control of pests under global warming.

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General Discussion

As trophic relationships are a product of evolutionary and phylogenetic relationships between predators and prey, these relationships give form to ecosystems and explain ecosystem evolution via competition for resources (e.g., the Lotka-Volterra based models, Sprott, 2004) with climate playing an important role determining the abundance and distribution of organisms (Thompson et al., 2012). However, in human-manged ecosystems, such as an agroecosystem, the anterior is true but highly simplified and mediated by human activity and management. So, as all ecosystems interact with each other, when there are managed ecosystems near to semi-natural ecosystems organisms respond positively or negatively depending on resource availability or environmental conditions (Ries et al., 2004; Tschardtke et al., 2012).

The first part of this thesis addresses the patterns of response in the abundance of natural enemies produced by the presence of semi-natural habitats and its effect on ecosystem function within olive orchards. In the chapter 1 and 2 it was found that the natural enemies are inhabiting semi-natural habitats (ground cover and natural adjacent vegetation) and, when analysed as trophic guilds they move from such semi-natural habitats to the olive canopy due to ground cover life span and the specific resource needs of each trophic guild, but when analysed by family level focusing on key natural enemies, specific patterns are expressed based on the attraction to plant species (which is due to resource needs) and the structure and complexity of plants and/or plant functional groups within semi-natural habitats, meaning that, semi-natural habitats are bankers of natural enemies and its presence increase their abundance following patterns of habitat complexity. However, as seen in chapter 3, whereas biological control is positively affected by the presence and maintenance of semi-natural habitats, it is produced by voracious and efficient individuals rather than their high abundances within the olive canopy, which focus on the attack on eggs rather than adults. This is explained by the cross-habitat spillover hypothesis, which suggests that changes in resource availability and the trophic structure of one ecosystem can cascade to a nearby ecosystem. Organisms may “move” between distinct habitats, which includes dispersal or foraging, so the transferred organisms and materials may enhance prey availability or nutrient density that promote predation pressures affecting the food chain structure (Tschardtke et al., 2012).

For our case, it was only studied the effects of biological control on one species of specialist herbivore, the olive moth *Prays oleae*. Chapter 3 and 4 showed that the key predators that predate the eggs of *P. oleae* are anthocorids, aeolothrips, chrysopids, formicids, and predatory mirids. These key predators are effective within low numbers and across olive landscapes biological control is enhanced by high amounts of shrublands within diversified landscapes. Moreover, high amounts of shrublands may negatively (sparse scrubland) or positively (dense scrubland) affect *P. oleae* adult abundance and damage. Thus, we can accept that the higher the abundance of natural enemies in semi-natural habitats, the higher the “presence” of natural enemies into the olive orchard and the olive canopy, but only at specific months according to natural enemy trophic function and landscape structure.

The findings reported in the first part of this thesis support (1) the complex-habitat hypothesis: complex low-fragmented landscapes with a high proportion of semi-natural habitats boost the populations of natural enemies within agroecosystems and enhance biological control (Bianchi et al., 2006); (2) the non-effective natural enemy hypothesis: herbivore density is driven by factors other than biocontrol such as crop area and/or intraguild predation (amongst others) (Tscharntke et al., 2016); (3) the habitat composition hypothesis: plant species richness and plant composition (functional groups) influence differently insect abundance (Haddad et al., 2001). Moreover, the findings also suggested a new research hypothesis within biological control theory, the more-effective natural enemy hypothesis: semi-natural habitats produce rather more active and voracious natural enemies within crops than their high abundances (Álvarez et al., 2021a).

On the other hand, recent accounts urge to reconcile the structure of trophic relationships across food chains with ecosystem function (Thompson et al., 2012). It has been suggested several challenges for the matter, the second part of this thesis focus on two of them: the effects of temporal variability on trophic networks and the relation of individual traits (adaptive behaviour) to ecological functions, which remain poorly understood (Thompson et al., 2012). Chapter 5 addresses the first challenge directing the temporal variability to the maturity of a semi-natural habitat: the ground cover within organic olive orchards. It was found that the maturity of the ground cover, over a decade, affected the structure and complexity of the olive canopy trophic network, i.e., the predator taxa increase twice their number with a same proportion of preys per taxon (the vulnerability of prey herbivores increases) whereas the generality of the network is maintained (herbivores, omnivores, and parasitoids were not affected). The reasons explaining why only the number of predator taxa are positively affected can

be provided by ecological theory in the process of how an ecosystem is formed. For example, local populations of organisms occur in spatially discrete patches where they undergo periodic recruitment (colonization) and mortality (extinction) (Levins, 1969). When a new habitat is rising in an available area by means of vegetal succession, time is needed for generalists and specialists to colonize or re-colonize such an area. For animals, generalists could never outperform specialists due to the inherent extra costs of being able to accommodate multiple prey types or variable environments i.e., the “jack-of-all-trades is master of none” (principle of allocation, Levins, 1968; Pianka, 1978). This is true when conditions are optimal, however, when conditions vary and are unpredictable, such as in human mediated ecosystems, generalists may outperform specialists (Richmond et al., 2005). Thus, in the specific case of olive orchards, the first colonizers predators may thrive in the former periods, however, as vegetal succession goes on within semi-natural habitats, more generalist and specialist predators (or hyper-predators) will start colonizing the area and compete for preys into the olive canopy whilst herbivores may only increase in abundance. If the metapopulation can be established throughout time, this may ultimately increase ecosystem services (Collinge, 2000) such as biological control.

By its part, the second challenge, i.e., the relation of individual traits to ecological functions, is addressed in chapter 6 assessing if principal omnivores may change their trophic status and become hyper-predators (adaptive behaviour) and therefore a non-beneficial organism for biological control. The anterior was achieved experimentally (laboratory rearing) and in-field using stable isotopes analysis on ant populations. It was found that, (1) ants within olive orchards do not produce the patterns showed by experimental hyper-predators; (2) only one species is inhabiting olive orchards; (3) the isotopic signature do not vary according to field management (but it may); and (4) the diet of ants varies greatly according to resource availability, which is reflected on isotopic signature variability. Foraging adaptability is an important feature within trophic networks across food chains (Thompson et al., 2012; Kondoh, 2003). A consumers' adaptive behaviour, which switches the food choice in response to qualitative and quantitative resource change, is paramount to stabilize complex trophic networks (Kondoh, 2003). Commonly, consumers cannot consume different resource simultaneously because of the spatial or temporal distribution of preys, the strategy used to capture or hunt different prey, and the sensory strains for discriminating between preys (Stephens and Krebs, 1987; Bernays and Funk, 1999). So, consumers switch foraging behaviour at individual level allocating their effort among possible resources and feeding on the most profitable prey at that

moment. This is why, the densities of consumers in agroecosystems follow the dynamics of herbivores populations, because of the availability of resource (preys). Indeed, our findings showed that great part of the variability in the isotopic signature is due to the variety of food within omnivore diet plus the changes in foraging behaviours based on prey and/or vegetal resource availability. These type of organisms are important to produce stability on ecosystems, thus, without adaptive foragers, food chain complexity may destabilizes community composition (Kondoh, 2003).

Finally, the third part of this thesis tries to address the effects of global climate change on biological control. As in the previous part, the goal is to address the relation of individual traits to ecological functioning. However, considering the possible changes in global temperature patterns, a major concern has raised which focus on the increasing intensity of thermal extremes that is pushing many insect species to or beyond their thermal adaptive limits, so knowing the evolutionary potential of the thermal plasticity of functional traits is paramount to make predictions concerning the ability of populations to adapt to these changes (Fossen et al., 2019). So, in chapter 7 it was assessed the effects produced by increasing temperatures on the functional traits, metabolic rate allometries, and survival of a Mediterranean predator green lacewing, based on the United Nation's A1B scenario of climate change. Such scenario predicts an increasement of 1.8°C on mean temperature for the year 2050. So, to show how this could affect such natural enemy it was produced transgenerational thermal acclimated populations of exogamic and endogamic individuals. It was found that phenotypic plasticity in metabolic rate is a key feature for this species to buffer the effects of thermal extremes when no behavioural thermoregulation can be used to exploit the thermal diversity of their microhabitats (Ma et al., 2021; Harvey et al., 2020). Accordingly, endogamy reduces the potential of thermal plasticity when predator individuals are subjected to thermal stress during ontogeny. The occurrence of phenotypic plasticity in metabolic scaling contradicts the assumption of an independent influence of body size and temperature on metabolic rate (Fossen et al., 2019; Kielland et al., 2017), which is related to down regulation of metabolism (Kielland et al., 2017; Glazier, 2015) based on allometric slopes lower than the predicted 3/4 power law (Brown et al., 2004). In addition, as suggested by previous studies on other species (vanHeerwaarden et al., 2016; Esperk et al., 2016; Loeschcke and Hoffmann, 2007), green lacewing larvae tend to invest more energy in heat tolerance to improve survival, which in turn brings concurrent costs in other plastic traits that are related to fitness. The anterior supports the idea that higher trophic levels are sensitive to continuous events of thermal extremes (Harvey et al.,

2020; Thompson et al., 2012; Ma et al., 2021), and that the metabolic rate slope (and its thermal plasticity) may have a limited potential for evolving over short time scales under such circumstances (Hansen, 2015).

General Conclusions

- (1) Semi-natural habitats (i.e., ground cover and natural adjacent vegetation, and consequently the plant species within them) contribute to the establishment of different guilds of natural enemies, thus positively affecting the abundance and movement of natural enemies into organic olive orchards. The results demonstrate the synergistic relationship between ground cover and natural adjacent vegetation, which is modulated by the ground cover life span.
- (2) Key family (arthropod) abundance is affected by habitat complexity, i.e., the highest the complexity in a habitat the highest the abundances of natural enemies and pollinators. However, these beneficial arthropods are influenced differently by plant richness and plant arrangement and scattering. Whereas eight plant species have the potential to boost the abundance of key natural enemies and pollinators in ground cover and semi-natural habitats, high levels of complexity are paramount to produce positive results.
- (3) The establishment and mowed management of a ground cover in organic olive orchards positively affects key predator families and promotes the biological control of *Prays oleae* by means of egg predation, especially when there is a low abundance of natural enemies. An olive orchard with ground cover produces more active and voracious natural enemies, allowing the establishment of efficient key predators into the olive canopy.
- (4) Landscape composition and configuration affects (1) key natural enemy abundance and predation, and (2) *P. oleae* abundance and damage: (a) when semi-natural habitats are analysed dividing them into specific land cover categories it produces higher effects at small spatial scale; (b) landscape configuration variables (patch features) have more significant effects at bigger spatial scales; (c) the landscape composition and configuration variables produce essentially the same type of effect across spatial scales; (d) *P. oleae* adult abundance show more effects at bigger spatial scales but natural enemy abundance at lower spatial scales; (e) the proportion of sparse scrubland in the landscape jointly with the presence of a mowed ground cover is the main factor driving the biological control of *P. oleae*; and (f) diversified landscapes with dense edges reduce the adult abundance of *P. oleae*.

- (5) The maturity of the ground cover within the olive orchard affects the structure and complexity of the olive canopy trophic network, i.e., when a ground cover is mature predator taxa increase twice their number with a same proportion of preys per taxon (the vulnerability of prey herbivores increases) whereas the generality of the network is maintained (herbivores, omnivores, and parasitoids are not affected). Accordingly, the maturity of a ground cover jointly with the lack of pesticides, promotes the establishment of key taxa that are related with natural habitats to form part of the olive canopy trophic network.
- (6) Within olive orchards, the trophic role of (*T. ibericum*) ants expresses a predator isotopic profile rather than being a hyper-predator, which may contribute to control olive herbivores. Their isotopic signature is not affected by field management and their diet varies greatly according to resource availability. Overall, ants can be considered a beneficial insect (e.g., the Iberian Peninsula).
- (7) Under the AIB scenario of global warming, exogamic individuals of green lacewings (predator larvae) express phenotypic plasticity in metabolic rates and scaling, and thus, a down-regulation in their metabolism. Endogamy reduces the potential of thermal plasticity when predator individuals are subjected to thermal stress during ontogeny. Moreover, in order to improve survival due to the effect of larger body sizes mandible size is constrained, and under thermal extremes larger individuals tend to develop smaller mandibles, which for the endogamic individuals it is also constrained by the effect of metabolic rates. Thus, global climate change may affect the development and adaptability of natural enemies via phenotypic plasticity, which can ultimately lead to maladaptation and may deleteriously affect biological control.

Conclusiones Generales

- (1) Los hábitats semi-naturales (en esencia, la cubierta vegetal y la vegetación adyacente, y por consiguiente, las especies de plantas dentro de estas) contribuyen al establecimiento de diferentes gremios de enemigos naturales, afectando así positivamente la abundancia y movimiento de los enemigos naturales dentro de los olivares orgánicos. Los resultados demuestran la relación de sinergia entre la cubierta vegetal y la vegetación adyacente, la cuál es modulada por el tiempo de vida de la cubierta vegetal.
- (2) La abundancia de familias clave (artrópodos) es afectada por la complejidad del hábitat, es decir, a mayor complejidad en un hábitat, mayor la abundancia de enemigos naturales y polinizadores. Sin embargo, dichos artrópodos benéficos son influenciados de manera diferente por la riqueza de plantas y por el arreglo y dispersión de las mismas. Mientras que nueve especies de plantas tienen el potencial de impulsar la abundancia de enemigos naturales y polinizadores clave en la cubierta vegetal y los hábitats semi-naturales, altos niveles de complejidad son esenciales para producir resultados positivos.
- (3) El establecimiento y segado de la cubierta vegetal en olivares ecológicos afecta positivamente a familias clave de depredadores y promueve el control biológico de *Prays oleae* por medio de la depredación de huevos, en especial cuando existe una baja abundancia de enemigos naturales. Un olivar con cubierta vegetal produce enemigos naturales más activos y voraces, permitiendo el establecimiento de eficientes depredadores clave dentro de la copa del olivo.
- (4) La composición y configuración del paisaje afecta a (1) la abundancia y depredación producida por enemigos naturales clave, y (2) la abundancia y daño producido por *P. oleae*: (a) cuando los hábitats semi-naturales son analizados dividiéndolos en categorías específicas se producen grandes efectos a escalas espaciales pequeñas; (b) las variables de configuración del paisaje (características del parche) tienen mayores efectos significativos a escalas espaciales grandes; (c) las variables de composición y configuración producen, en esencia, los mismos tipos de efectos para todas las escalas espaciales; (d) la abundancia de adultos de *P. oleae* muestra mayores efectos a escalas espaciales grandes, pero la abundancia de enemigos naturales lo hace a escalas espaciales

pequeñas; (e) la proporción de matorral disperso en el paisaje en conjunto con la presencia de una cubierta vegetal segada es el factor principal que dirige el control biológico de *P. oleae*; y (f) paisajes diversificados con bordes densos reducen la abundancia de adultos de *P. oleae*.

- (5) La madurez de la cubierta vegetal dentro del olivar afecta la estructura y complejidad de la red trófica de la copa del olivo, en esencia, cuando una cubierta vegetal es madura los taxones de depredadores incrementan al doble su número, con una misma proporción de presas por taxón (la vulnerabilidad de los herbívoros presa aumenta) a la vez que la generalidad de la red se mantiene (los depredadores, herbívoros y parasitoides no se ven afectados). Respectivamente, la madurez de una cubierta vegetal, en conjunto con la ausencia de productos fitosanitarios, promueve el establecimiento de taxones clave relacionados con los hábitats naturales para formar parte de la red trófica de la copa del olivo.
- (6) Dentro de los olivares, el rol trófico de las hormigas (*T. ibericum*) expresa un perfil isotópico de un depredador en lugar de un hiperdepredador, lo cual puede contribuir en el control de los herbívoros del olivo. Su huella isotópica no se ve afectada por el manejo del campo y su dieta varía fuertemente según la disponibilidad del recurso. En general, las hormigas pueden considerarse un insecto benéfico (por ejemplo, para la península Ibérica).
- (7) Bajo el escenario de cambio climático A1B, los individuos exogámicos de crisopas (larvas depredadoras) expresan plasticidad fenotípica en sus tasas metabólicas y escalamiento, y consecuentemente, una regulación a la baja en su metabolismo. La endogamia reduce el potencial de la plasticidad térmica cuando los individuos depredadores son sujetos a estrés térmico durante su ontogenia. Más aún, con el fin de mejorar la supervivencia debido a el efecto de tamaños corporales grandes, el tamaño de la mandíbula se ve limitado y bajo eventos térmicos extremos individuos grandes tienden a desarrollar mandíbulas pequeñas, lo que para los individuos endogámicos se ve también limitado por el efecto de la tasa metabólica. Por consiguiente, el cambio climático global puede afectar el desarrollo y la adaptabilidad de los enemigos naturales a través de la plasticidad fenotípica, lo cuál puede en última instancia llevar a una falta de adaptación y afectar de manera perjudicial al control biológico.

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Appendix

Chapter 1 Supplementary data

Semi-natural habitat complexity affects abundance and movement of natural enemies in organic olive orchards



Fig. A1.1. Organic olive orchards and field composition in the localities of Deifontes (A, C) and Iznalloz (B, D). Landscape view of the orchards and the patches of adjacent vegetation (A, B), arrows indicate de place of the patch. View of the ground cover within olive orchards (C, D) (used from Álvarez et al., 2019a).

Table A1.1. Taxa and guild information of the different arthropods present in olive orchards and semi-natural habitats.

Name		Guild	Literature
Arachnida			
Araneae	Amaurobiidae	Predator	Paredes et al., 2015; Morente et al., 2018
	Araneidae	Predator	Foelix, 2011
	Corinnidae	Predator	Chen et al., 2010
	Dyctinidae	Predator	Foelix, 2011
	Linyphiidae	Predator	Foelix, 2011
	Liocranidae	Predator	Alp et al., 2013
	Mimetidae	Predator	Foelix, 2011
	Oxyopidae	Predator	Turner, 1979; Morente et al., 2018
	Philodromidae	Predator	Guseinov, 2002; Morente et al., 2018
	Salticidae	Predator	Paredes et al., 2015; Morente et al., 2018
	Sicariidae	Predator	Foelix, 2011
	Theridiidae	Predator	Hódar & Sánchez- Piñero, 2002
	Thomisidae	Predator	Paredes et al., 2015; Morente et al., 2018
	Uloboridae	Predator	Foelix, 2011
Zodaridae	Predator	Pekár, 2004; Morente et al., 2018	
Insecta			
Coleoptera	Alleculidae	Neutral arthropod	Chinery 1988; Morente et al., 2018
	Anthicidae	Neutral arthropod	Zaharadník 1990; Morente et al., 2018
	Apionidae	Neutral arthropod	Van Driesche and Bellows, 2001
	Cantharidae	Predator	Flint et al., 1998; Morente et al., 2018
	Carabidae	Predator	Forsythe, 1982
	Catopidae	Neutral arthropod	Blas-Esteban, 1979
	Chrysomelidae	Neutral arthropod	Mirzoeva, 2000; Morente et al., 2018
	Cleridae	Predator	Löbl and Smetana, 2007
	Coccinellidae	Predator	Evans, 2009; Hodek, 1973; Magro and Hempitünne, 1999; Morente et al., 2018

	Curculionidae	Neutral arthropod	Chinery, 1988; Morente et al., 2018
	Dasytidae	Predator	Branco et al., 2011
	Dermestidae	Neutral arthropod	Schroeder, 2002
	Elateridae	Predator	de la Vega et al., 2012
	Malachiidae	Predator	Sabelis and Van Rijn, 1997
	Monotomidae	Neutral arthropod	Bousquet, 2002
	Mycetophagidae	Neutral arthropod	Young, 2002
	Nitidulidae	Neutral arthropod	Habeck, 2002
	Phalacridae	Neutral arthropod	Thompson, 1958; Morente et al., 2018
	Ptinidae	Neutral arthropod	Philips, 2002
	Scarabaeidae	Neutral arthropod	Ratcliffe et al., 2002
	Staphylinidae	Predator	Arnett et al., 2002; Morente et al., 2018
Blattodea	Blattellidae	Neutral arthropod	Gullan and Cranston, 2010
Dermaptera	Forficulidae	Omnivore	Cañellas et al., 2005
Diptera	Agromyzidae	Neutral arthropod	Gil-Ortiz et al., 2010
	Asilidae	Predator	Carles-Tolrá, 2016
	Bibionidae	Neutral arthropod	Amorim, 1997; Morente et al., 2018
	Bombyliidae	Neutral arthropod	Boesi et al., 2009
	Calliphoridae	Neutral arthropod	Baz et al., 2007
	Camillidae	Neutral arthropod	Barraclough, 1992
	Cecidomyiidae	Neutral arthropod	Skuhrová, 2006
	Ceratopogonidae	Neutral arthropod	González, 2015
	Chamaemyiidae	Predator	Gaimari and Turner, 1996
	Chironomidae	Neutral arthropod	Burt et al., 1986
	Chloropidae	Neutral arthropod	Tracewski et al., 1984; Morente et al., 2018
	Dolichopodidae	Predator	Morente et al., 2018
	Empididae	Neutral arthropod	Downes and Smith, 1969
	Heleomyzidae	Neutral arthropod	Rotheray, 2012
	Limoniidae	Neutral arthropod	Reusch and Oosterbroek, 1997
	Muscidae	Neutral arthropod	Moon, 2019
	Opomyzidae	Neutral arthropod	Vockeroth, 1961
	Phoridae	Neutral arthropod	Alcaine-Colet, 2015
	Sciaridae	Neutral arthropod	Mansilla et al., 2001; Morente et al., 2018

Hemiptera	Tephritidae	Neutral arthropod	Hendrichs and Hendrichs, 1990
	Anthocoridae	Predator	Morris et al., 1999; Morente et al., 2018
	Aphididae	Neutral arthropod	Vickerman and Wratten, 1979; Morente et al., 2018
	Berytidae	Neutral arthropod	Wheeler and Schaefer, 1982; Morente et al., 2018
	Coccidae	Neutral arthropod	Alvarado, 2004; Morente et al., 2018
	Cydnidae	Neutral arthropod	Mayorga-Martínez and Cervantes-Peredo, 2006
	Fulgoromorpha	Neutral arthropod	Wilson, 2005; Morente et al., 2018
	Geocoridae	Predator	Tillman and Mullinix, 2003
	Lygaeidae	Predator (facultative)	Burdfield-Steel and Shuker, 2014
	Miridae	Predator	Paredes et al., 2013; Morente et al., 2018
	Nabidae	Predator	Cabello et al., 2009
	Pentatomidae	Neutral arthropod	Ni et al., 2010; Panizzi et al., 2000
	Psyllidae	Neutral arthropod	Alvarado, 2004; Morente et al., 2018
	Reduviidae	Predator	McMahan, 1983
Hymenoptera	Rhopalidae	Neutral arthropod	Brown and Norris, 2004; Pall and Coscarón, 2012
	Tingidae	Neutral arthropod	Klingeman et al., 2000; Pollard, 1959
	Aphelinidae	Neutral arthropod	Viggiani, 1984
	Apidae	Neutral arthropod	Machener, 2000
	Bethylidae	Parasitoid	Murgas and Gonzalez, 2004; Amante et al., 2018
	Braconidae	Parasitoid	Barrientos, 2004; Morente et al., 2018
	Ceraphronidae	Neutral arthropod	Krzyżyński and Ulrich, 2015
Chrysididae	Parasitoid	Kurczewski, 1967	

	Cynipidae	Neutral arthropod	Cooper and Rieske, 2010
	Diapriidae	Parasitoid	Cancino et al., 2009; Muesebeck 1980; Morente et al., 2018
	Elasmidae	Parasitoid	Barrientos, 2004; Villa et al., 2016; Morente et al., 2018
	Encyrtidae	Parasitoid	Barrientos, 2004; Villa et al., 2016; Morente et al., 2018
	Eulophidae	Parasitoid	Barrientos, 2004; Morente et al., 2018
	Eupelmidae	Parasitoid	Giron et al., 2002
	Eurytomidae	Parasitoid	Dawah, 1995
	Formicidae	Omnivore	Moreno-Ripoll et al., 2012; Bristow, 1984; Tinaut et al. 2009; Morente et al., 2018
	Ichneumonidae	Parasitoid	Yu, 2005; Morente et al., 2018
	Mymaridae	Parasitoid	Barrientos, 2004; Morente et al., 2018
	Platygastridae	Parasitoid	Hernández-Suárez et al., 2015; Morente et al., 2018
	Pompilidae	Neutral arthropod	Punzo, 1994
	Pteromalidae	Parasitoid	Barrientos, 2004; Morente et al., 2018
	Scelionidae	Parasitoid	Alrouechdi and Panis, 1981
Lepidoptera	Plutellidae	Neutral arthropod	Alvarado, 2004; Morente et al., 2018
	<i>Prays oleae</i>	Pest	Alvarado, 2004; Morente et al., 2018
Mantodea	Mantidae	Predator	Gullan and Cranston, 2010
Neuroptera	Chrysopidae	Predator	Limburg and Rosenheim, 2001; Solomon et al. 2000; Morente et al., 2018
	Coniopterygidae	Predator	Solomon et al. 2000; Morente et al., 2018
Phasmatodea	Phasmatidae	Neutral arthropod	Sandlin and Willig, 1993
Raphidioptera	Raphidiidae	Predator	Aspöck, 2002

Thysanoptera	Aeolothripidae	Predator	Torres, 2007; Morente et al., 2018
	Phlaeolothripidae	Neutral arthropod	Mound, 1974; Cambero-Campos et al., 2015; Varela and Plasencia, 1986; Morente et al., 2018
	Thripidae	Neutral arthropod	Chaisuekul and Riley 2001; Morente et al., 2018

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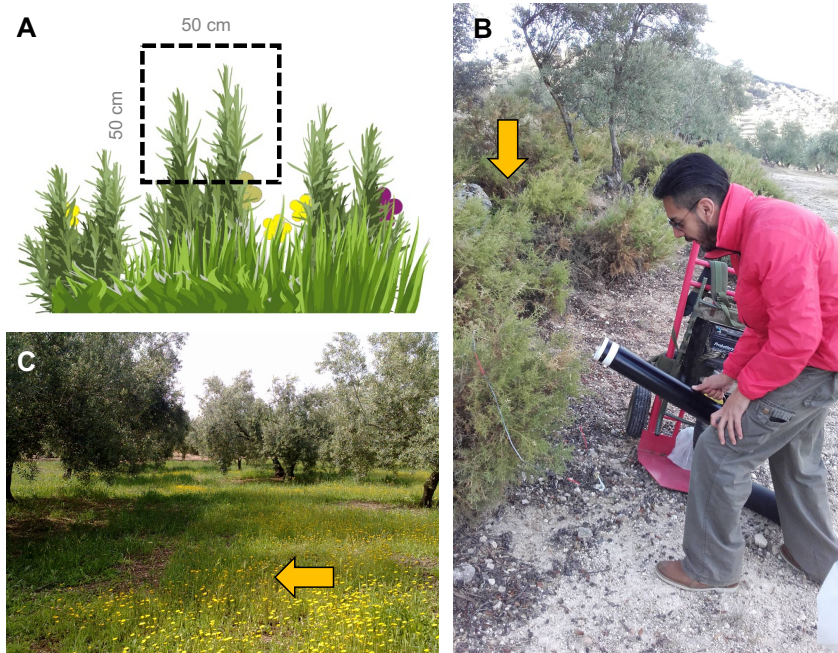


Fig. A1.2. Arthropod sampling within semi-natural habitats in organic olive orchards using the entomological aspirator. Suction sample (A), adjacent natural vegetation (B), and ground cover (C).

Chapter 3 Supplementary data

Ground cover presence in organic olive orchards affects the interaction of natural enemies against *Prays oleae*, promoting an effective egg predation

Table A3.1. Information about sampling and management types of the organic olive orchards.

Orchard ID	Type	Year	Month	Sampling	Locality
DG1	Tilled	2011	6	1	Granada
ON	Tilled	2011	6	1	Deifontes
DG2	Mowed	2011	6	1	Granada
ODM	Mowed	2011	6	1	Deifontes
DG1	Tilled	2011	7	2	Granada
ON	Tilled	2011	7	2	Deifontes
DG2	Mowed	2011	7	2	Granada
ODM	Mowed	2011	7	2	Deifontes
DGA1	Tilled	2012	6	1	Granada
DGB1	Tilled	2012	6	1	Granada
ONA	Tilled	2012	6	1	Deifontes
ONB	Mowed	2012	6	1	Deifontes
ODM	Mowed	2012	6	1	Deifontes
DGA1	Tilled	2012	7	2	Granada
DGB1	Tilled	2012	7	2	Granada
ONA	Tilled	2012	7	2	Deifontes
ODM	Mowed	2012	7	2	Deifontes
ONB	Mowed	2012	7	2	Deifontes
DG1A	Tilled	2013	6	1	Granada
DG1B	Tilled	2013	6	1	Granada
DG3A	Mowed	2013	6	1	Granada
DG3B	Mowed	2013	6	1	Granada
ODM	Mowed	2013	6	1	Deifontes
ONB	Mowed	2013	6	1	Deifontes
ONA	Mowed	2013	6	1	Deifontes
DG1A	Tilled	2013	7	2	Granada

DG1B	Tilled	2013	7	2	Granada
DG3B	Mowed	2013	7	2	Granada
DG3A	Mowed	2013	7	2	Granada
ODM	Mowed	2013	7	2	Deifontes
ONA	Mowed	2013	7	2	Deifontes
ONB	Mowed	2013	7	2	Deifontes

Table A3.2. Summary and formula* of the fitted generalized linear mixed-effects model (GLMM) with nested random effects fit by maximum likelihood with Laplace Approximation, including egg predation, type of management, and abundance of natural enemies (package “lme4”).

Variable	Variance	SD	Estimated coefficient	SE	<i>z</i>	<i>p</i>
Fixed effects:						
Intercept			4.723	0.3980	11.86	0.001
Management (tilled and mowed)			1.127	0.5299	2.12	0.033
Natural enemy			0.0002	0.00009	2.41	0.015
Random effects:						
Year : Site	1.100	1.049				

* glmer (predated.eggs ~ management + natural.enemies + (1 | annual / ID), family = poisson)

Table A3.3. R scrip for the NMDS with smooth surfaces (package “vegan”).

```

——— # weighted scores (NMDS)
>vare.dist <- vegdist(wisconsin(sqrt(data1[, 2:37])))
>vare.mds <- monoMDS(vare.dist)
>vare.points <- postMDS(vare.mds$points, vare.dist)
>vare.wa <- wascores(vare.points, data1[, 2:37])
>plot (scores(vare.points), pch="+", col=0, ylab="NMDS Axis 2", xlab="NMDS Axis 1", ylim=c(-0.6,0.6), xlim=c(-0.6,0.6))
>text (vare.wa, rownames(vare.wa), cex=0.8)

——— #NMDS
> ord<-metaMDS(data1[,2:37])

——— #smooth surface
> ordisurf(ord, predated.eggs, add=TRUE)
> ordisurf(ord, Prays, add=TRUE, data=d2, col=1)

```

Chapter 4 Supplementary data

The biological control of *Prays oleae* in organic olive orchards is enhanced in diversified landscapes with high amounts of scrublands at lower spatial scales

Table A4.1. Information about sampling and management types of the organic olive orchards: Dehesa of Generalife (DG), Deifontes (DEI), and Pñiar (PI), in north (n) and south (s).

Sample ID	Orchard	Type	Year	Month	Sampling	Locality
DG1	DG-n	Tilled	2011	6	1	Granada
ON	DEI-s	Tilled	2011	6	1	Deifontes
ODM	DEI-n	Mowed	2011	6	1	Deifontes
DG1	DG-n	Tilled	2011	7	2	Granada
ON	DEI-s	Tilled	2011	7	2	Deifontes
ODM	DEI-n	Mowed	2011	7	2	Deifontes
DG1	DG-n	Tilled	2012	6	1	Granada
DG1	DG-n	Tilled	2012	6	1	Granada
ON	DEI-s	Tilled	2012	6	1	Deifontes
ON	DEI-s	Mowed	2012	6	1	Deifontes
ODM	DEI-n	Mowed	2012	6	1	Deifontes
DG1	DG-n	Tilled	2012	7	2	Granada
DG1	DG-n	Tilled	2012	7	2	Granada
ON	DEI-s	Tilled	2012	7	2	Deifontes
ODM	DEI-n	Mowed	2012	7	2	Deifontes
ON	DEI-s	Mowed	2012	7	2	Deifontes
DG1	DG-n	Tilled	2013	6	1	Granada
DG1	DG-n	Tilled	2013	6	1	Granada
DG3	DG-s	Mowed	2013	6	1	Granada
DG3	DG-s	Mowed	2013	6	1	Granada
OD	DEI-n	Mowed	2013	6	1	Deifontes
ON	DEI-s	Mowed	2013	6	1	Deifontes
ON	DEI-s	Mowed	2013	6	1	Deifontes
DG1	DG-n	Tilled	2013	7	2	Granada

DG1	DG-n	Tilled	2013	7	2	Granada
DG3	DG-s	Mowed	2013	7	2	Granada
DG3	DG-s	Mowed	2013	7	2	Granada
ODM	DEI-n	Mowed	2013	7	2	Deifontes
ON	DEI-s	Mowed	2013	7	2	Deifontes
ON	DEI-s	Mowed	2013	7	2	Deifontes
ONA	DEI-s	Mowed	2015	6	1	Deifontes
ONB	DEI-s	Mowed	2015	6	1	Deifontes
ONA	DEI-s	Mowed	2015	7	2	Deifontes
ON	DEI-s	Mowed	2015	7	2	Deifontes
IZ-1/2	PI-1	Mowed	2015	7	2	Piñar
IZ-3/4	PI-3	Mowed	2015	7	2	Piñar

Table A4.2. Results of the linear mixed models and generalized linear mixed models subjected to a multi-model inference for the five variables of landscape composition (cover categories), fitted at three spatial scales (100, 300, and 500m). Only significant variables in the best models ($\Delta AIC < 2$) are presented.

Scale	Variables	Landscape composition																
		Dense forest			Dense scrubland			Sparse scrubland			Grassland			Olive orchard				
		Est	z	P	Est	z	P	Est	z	P	Est	z	P	Est	z	P		
500	Pest damage	-0.31	4.13	0.001														
	Egg hatching	0.23	3.39	0.001														
	Egg predation	-0.21	1.96	0.050														
	<i>Prays oleae</i>	-0.54	4.18	0.001														
	NE arachnids NE insects							-0.33	1.90	0.057	-0.29	2.06	0.039					
300	Pest damage	-0.32	2.84	0.004														
	Egg hatching	0.25	2.02	0.043														
	Egg predation	-0.24	1.99	0.046	-0.10	2.17	0.030											
	<i>Prays oleae</i>	-0.45	5.49	0.001	-0.28	2.47	0.013							-0.46	5.55	0.001		
	NE arachnids NE insects				0.29	2.61	0.009							-0.27	1.90	0.058		
100	Pest damage	-0.27	3.47	0.001	-0.18	2.30	0.022	0.12	2.38	0.017	-0.31	3.73	0.001	-0.15	1.99	0.047		
	Egg hatching				0.13	2.21	0.027	-0.15	2.83	0.005				-0.19	3.38	0.001		
	Egg predation				-0.10	3.67	0.001	0.11	4.24	0.001				0.11	4.01	0.001		
	<i>Prays oleae</i>				-0.32	2.92	0.004	0.29	3.38	0.001				0.50	5.55	0.001		
	NE arachnids NE insects				0.34	3.41	0.001	-0.23	2.91	0.004	-0.26	2.04	0.042	0.25	2.17	0.030		
													-0.36	3.26	0.001	0.37	3.16	0.002

Table A4.3. Results of the linear mixed models and generalized linear mixed models subjected to a multi-model inference for the five variables of landscape configuration (patch features), fitted at three spatial scales (100, 300, and 500m). Only significant variables in the best models ($\Delta AIC < 2$) are presented.

Scale	Variables	Landscape configuration															
		ED			PARA_MN			SHDI			AI			CONTAG			
		Est	z	p	Est	z	p	Est	z	p	Est	z	p	Est	z	p	
500	Pest damage																
	Egg hatching	0.21	4.03	0.001	-0.27	2.19	0.029										
	Egg predation				-0.22	2.20	0.028	-1.25	2.30	0.022							
	<i>Prays oleae</i>	-0.49	5.63	0.001							0.49	5.57	0.001				0.017
	NE arachnids																
	NE insects	16.65	3.95	0.001	0.58	3.00	0.003				15.54	3.94	0.001				
300	Pest damage																
	Egg hatching	0.20	3.90	0.001	0.16	2.39	0.017	1.18	3.29	0.001							
	Egg predation				0.09	2.22	0.027	0.71	2.67	0.008							
	<i>Prays oleae</i>	-0.52	4.85	0.001							0.53	4.66	0.001				
	NE arachnids																
	NE insects	12.83	4.21	0.001				-2.18	4.04	0.001	11.42	4.27	0.001				
100	Pest damage																
	Egg hatching	-5.03	2.69	0.007				1.49	2.07	0.038							
	Egg predation	0.19	3.54	0.001				0.19	3.45	0.001							
	<i>Prays oleae</i>	-3.01	2.54	0.011							-4.27	3.32	0.001				
	NE arachnids																
	NE insects	7.14	3.66	0.001				-1.84	3.47	0.001	13.18	3.83	0.001				

Chapter 5 Supplementary data

Maturity of ground covers increases the resilience and presence of natural enemies in the trophic network of olive canopy

La madurez de las cubiertas vegetales aumenta la presencia de enemigos naturales y la resiliencia de la red trófica de la copa del olivo

Tabla A5.1. Taxones y preferencias alimenticias de los artrópodos de copa en el olivar.

Nodo taxón	Gremio	Alimentación	Referencias
Araneae			
Araneidae	Depredador	Araña constructora de tela orbicular. Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Oxyopidae	Depredador	Araña cazadora activa (perseguidora). Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Philodromidae	Depredador	Araña cazadoras activa (emboscadora). Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Salticidae	Depredador	Araña cazadora activa (perseguidora). Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Scariidae	<i>Loxocles</i> sp. Depredador	Araña cazadoras activa (emboscadora). Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Thomisidae	Depredador	Araña cazadoras activa (emboscadora). Generalista	(Uetz et al., 1999; Cardoso et al, 2011)
Coleoptera			
Cerambycidae	Fitófago		(Zaharadník 1990)
Chrysomelidae	Fitófago	Hojas	(Mirzoeva 2000)
Curculionidae	Fitófago		(Chinery 1988)
Dasytidae	Fitófago	Polen	(Liberti 2009)
Dermestidae	Carroñero		(Schroeder et al 2002)
Malachiidae	Fitófago	Flores	(Plata-Negrache 2012)
Staphylinidae	Depredador, omnívoro	Scolitynae, Diptera larvae, polen, flores, madera.	(Chinery 1988)
Diptera			
Bibionidae	Fitófago, carroñero	Madera y raíces en descomposición	(Amorim 1997)
Bombyliidae	Fitófago	Polen y néctar	(Kastinger & Webber 2001)
Cecidomyiidae	Fitófagos y fungívoros	Algunos Cecidomyiinae son plagas de cultivos	(Gagné & Jaschhof 2004)
Sciaridae	Fungívoro	Hongos, algas y materia orgánica en descomposición	(Mansilla et al. 2001)
Tephritidae	Fitófago	Plaga de numerosos cultivos	(Aluja & Mangan 2008)

Hemiptera			
Anthocoridae	<i>A. nemoralis</i>	Depredador	(Morris et al. 1999)
Aphididae		Fitófago	(Vickerman & Wratten 1979)
Berytidae		Fitófago	(Wheeler & Schaefer 1982)
Cicadomorpha		Fitófago	(Dietrich 2005)
Coccidae	<i>Saissetia oleae</i>	Fitófago	(Alvarado 2004)
Fulgoromorpha		Fitófago	(Wilson 2005)
Lygaeidae		Fitófago, algunos depredadores	(Crocker & Whitcomb 1980)
Miridae	<i>B. ferreri</i>	Depredador	(Sweet 1960)
Miridae	<i>B. ferreri</i>	Depredador	(Paredes, Cayuela & Campos 2013)
Miridae	<i>B. ferreri</i>	Depredador	(Sharma et al. 1989)
Miridae	<i>Calocoris</i> sp.	Fitófago	(Eyles & Carvalho 1988)
Miridae	<i>D. punctum</i>	Depredador	(Paredes, Cayuela & Campos 2013)
Miridae	<i>D. punctum</i>	Depredador	(Saini & Polack 2002; Ingegno et al. 2008; Agustí & Gabarra 2009)
Miridae	<i>Dicyphus</i> sp.	Zoofitófago	(Paredes et al. 2013)
Miridae	<i>Dicyphus</i> sp.	Zoofitófago	(Paredes et al. 2013)
Psyllidae	<i>E. olivina</i>	Fitófago	(Alvarado 2004)
Rophalidae			
Hymenoptera			
Aphelinidae		Parasitoide	Huevos de Aphidoidea, Aleyrodoidea y Coccoidea principalmente y otros como Orthoptera y lepidóptera y pupas de Diptera (Viggiani 1984)
Braconidae		Parasitoide	Adultos y larvas de insectos hemimetábolos y ninfas de insectos hemimetábolos Lepidoptera, Diptera (Barrientos 2004)
Chalcididae		Parasitoide	Hymenoptera, Coleoptera, hiperparasitoides ocasionalmente. (Yu 2005)
Cynipidae		Fitófago	Forma agallas en la familia Fagaceae (Stone et al 2002)
Diapriidae		Parasitoide	Diptera (Cancino et al. 2009)
Elasmidae		Parasitoide	Diptera, Lepidoptera, Formicidae. (Muesebeck 1980)
Encyrtidae		Parasitoide	Otros parasitoides, Diptera, Coccinellidae, Hemiptera, Lepidoptera, Araneae, Neuroptera, Coniopterygidae, Formicidae. (Barrientos 2004)
Eulophidae		Parasitoide	Lepidoptera, Coleoptera, Diptera, Hymenoptera, Homoptera. (Barrientos 2004)
Formicidae	<i>C. auberti</i>	Omnívora	Huevos de Trichogrammatidae, Semillas de <i>Lobularia</i> (Herrera et al 1984; Ruano et al 1995; Pereira et al

			<i>maritima</i> , néctar	2004)
Formicidae	<i>P. pygmaea</i>	Parasitoide		
Formicidae	<i>T. ibericum</i>	Parasitoide	Melaza de pulgón y otros insectos	(Tinaut et al. 2009)
Ichneumonidae		Parasitoide	Muchos órdenes, principalmente Lepidoptera y Coleoptera.	(Yu 2005)
			Hiperparasitoides ocasionalmente.	
			Generalistas. Huevos de Auchenorrhyncha,	
Mymaridae		Parasitoide	Coccoidea, Coleoptera, Diptera, Odonata, Thysanoptera and Psocoptera.	(Barrientos 2004)
Platygastridae		Parasitoide	Aleyrodidae, Diptera	(Hernández-Suárez et al. 2015)
Pteromalidae		Parasitoide	Larvas de un gran número de insectos	(Barrientos 2004)
Scelionidae		Parasitoide	Huevos de insectos y arañas	(Barrientos 2004)
Lepidoptera		Fitófago	Lepidoptera	
Lepidoptera	<i>Prays oleae</i>	Fitófago	Plaga del olivo	(Alvarado 2004)
			Neuroptera	
Chrysopidae	Chrysopidae adult	Fitófago	Polen	(Szentkirályi 2001)
				(Limburg & Rosenheim 2001)
Chrysopidae	Chrysopidae larva	Depredador	Insectos de cuerpo blando.	(Solomon et al. 2000)
				(Solomon et al. 2000)
Chrysopidae	<i>Chrysopidia</i> sp. larva	Depredador	Insectos de cuerpo blando.	(Solomon et al. 2000)
Chrysopidae	<i>Chrysoperla</i> sp. adult	Fitófago	Melaza	(Zheng et al. 1993)
Chrysopidae	<i>Chrysoperla</i> sp. larva	Depredador	Psyllidae	(Santas 1987)
				(Atlihan et al 2004)
Chrysopidae	<i>Notochrysa</i> sp. larva	Depredador	Aphididae	(Goßner, Gruppe & Simon 2005)
			Psocoptera	
Psocoptera		Fungívoro	Hongos y bacterias	(Kalinović et al. 2006)
			Thysanoptera	
Aeolothripidae		Fitófago y depredador	<i>A. fasciatus</i> y <i>A. intermedius</i> se alimentan de ácaros del género Cheyletus	(Torres 2007)
				(Mound 1974)
Phlaeothripidae		Fitófago	Esporas	(Cambero-Campos et al. 2015)
				(Varela & Plasencia 1986)
Thripidae		Fitófago	Plagas en diferentes cultivos.	(Chaisuekul & Riley 2001)

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Tabla A5.2. Relaciones tróficas de los taxones de artrópodos de copa en el olivo. 1 representa depredación o parasitismo y el 0 ausencia de relación. La primera columna muestra los depredadores y parasitoides.

2003	Aph	Ceram	Chrysom	Cic	Der	Eoli	Lep	Lyg	Pole	Psoc	Sole	Scia	Thrip	Bferr + Dpunc	Cauber	Neur	Steph	Tibe	Brac	Chalc	Diapr + Plat	Elas	Enc	Eul	Ichm	Pte
Bferr + Dpunc	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Cauber	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Neur	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1
Steph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tibe	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
Brac	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Chalc	0	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	1	1	1	1
Elas	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Enc	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1
Eul	0	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Ichm	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Pte	0	1	1	0	1	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0
Diapr+Plat	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Chapter 6 Supplementary data

Elucidating the trophic role of *Tapinoma ibericum* (Hymenoptera: Formicidae) as potential predator of olive pests

Table A6.1. Date, location, sampled nests (N) and habitat of field pling. Nest signalled with * were transported to the laboratory for the experimental study. # Sampling 15 days after presence of the pest (*P. oleae*) in the olive farms. Total nests sampled, $n = 103$.

Sampling date	Location	N	Type of habitat/management
T0 23 April 2010	Arenales *	12	Olive agroecosystem/ Integrated
30 April 2010	Sierra Nevada	6	Shrubby natural hábitat
	Dehesa Generalife	5	Olive agroecosystem/Organic
	Deifontes	11	Olive agroecosystem/Organic
T1 17 June 2010	Dehesa Generalife	13	Olive agroecosystem/Organic
T2 5 July 2010 #	Arenales	4	Olive agroecosystem/ Integrated
	Pinos Puente	1	Olive agroecosystem/ Integrated
	Deifontes	11	Olive agroecosystem/ Organic
	Dehesa Generalife	10	Olive agroecosystem/ Organic
	Colomera (2)	4	Olive agroecosystem/ Conventional
T3 15 July 2010	Deifontes	3	Olive agroecosystem/ Organic
	Dehesa Generalife	10	Olive agroecosystem/ Organic
T4 26 July 2010	Arenales (1)	2	Olive agroecosystem/ Integrated
	Pinos Puente (1)	2	Olive agroecosystem/ Integrated
	Deifontes (2)	5	Olive agroecosystem/ Organic
	Colomera (2)	4	Olive agroecosystem/ Conventional

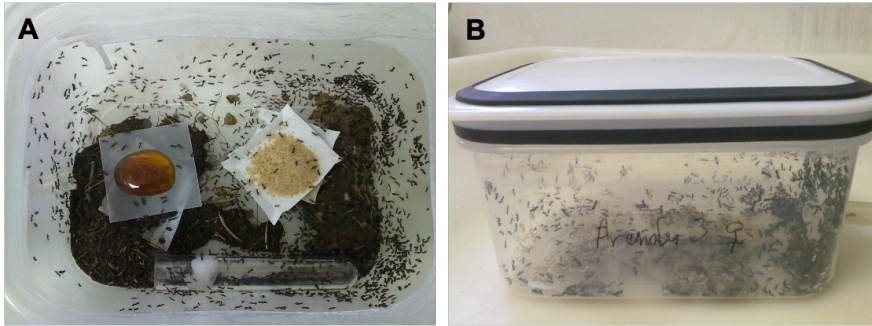


Fig. A6.1. Rearing and maintenance of *Tapinoma ibericum* ants in the laboratory. Food supply and water supply (A) into plastic containers (B). Photographs courtesy of P. Sandoval and F. Ruano.

Table A6.2. Mean, maximum and minimum values of the SIA sampled in the experiment, natural ants and diets.

Isotope	Time	Type of diet	sampled nests	signature	SD	max	min	range
$\delta^{13}C$	T0		12	-25.185	0.67681742	-23.86	-26.15	2.29
	T1		12	-24.290833	0.53552792	-23.43	-25.06	1.63
	T2	honey/yeast	2	-24.16	0.48083261	-23.82	-24.5	0.68
		<i>A. craccivora</i>	3	-24.463333	0.55752429	-23.83	-24.88	1.05
		<i>P. oleae</i>	3	-24.246667	0.39803685	-23.88	-24.67	0.79
		<i>C. carnea s.l.</i>	3	-24.073333	0.65064071	-23.44	-24.74	1.3
		Natural	4	-26.1475	0.24662725	-23.43	-26.46	3.03
	T3	honey/yeast	2	-24.81	0.09899495	-24.74	-24.88	0.14
		<i>A. craccivora</i>	3	-24.463333	0.53724606	-23.86	-24.89	1.03
		<i>P. oleae</i>	3	-25.073333	1.68737469	-23.92	-27.01	3.09
		<i>C. carnea s.l.</i>	3	-24.416667	0.93735443	-23.71	-25.48	1.77
		Natural						
	T4	honey/yeast	2	-24.665	0.57275649	-24.26	-25.07	0.81

	<i>A. craccivora</i>	3	-24.816667	0.39715656	-24.37	-25.13	0.76
	<i>P. oleae</i>	2	-24.45	0.62225397	-24.01	-24.89	0.88
	<i>C. carnea s.l.</i>	3	-24.46	0.66189123	-23.86	-25.17	1.31
	natural	2	-24.94	0.1979899	-24.8	-25.08	0.28
815N							
	T0	12	5.68	0.93678367	6.97	4.03	2.94
	T1	12	6.00166667	1.06138703	7.34	3.13	4.21
	T2						
	honey/yeast	2	5.08	0.4384062	5.39	4.77	0.62
	<i>A. craccivora</i>	3	5.75	0.68022055	6.53	5.28	1.25
	<i>P. oleae</i>	3	5.86333333	1.15992816	7.08	4.77	2.31
	<i>C. carnea s.l.</i>	3	7.02666667	0.54601587	7.52	6.44	1.08
	natural	4	4.7525	0.50009166	5.41	4.2	1.21
	T3						
	honey/yeast	2	6.005	0.23334524	6.17	5.84	0.33
	<i>A. craccivora</i>	3	4.19666667	2.4136556	5.63	1.41	4.22
	<i>P. oleae</i>	3	5.4	0.61147363	5.83	4.7	1.13
	<i>C. carnea s.l.</i>	3	7.21333333	0.52500794	7.74	6.69	1.05
	natural						
	T4						
	honey/yeast	2	4.315	2.66579257	6.2	2.43	3.77
	<i>A. craccivora</i>	3	4.26666667	1.55159058	5.45	2.51	2.94
	<i>P. oleae</i>	2	5.405	1.39300036	6.39	4.42	1.97
	<i>C. carnea s.l.</i>	3	7.36666667	0.43015501	7.86	7.07	0.79
	natural	2	4.775	1.81726443	4.64	3.94	0.7

Chapter 7 Supplementary data

Metabolism and endogamy: effects of a global warming scenario produce trade-offs and constrains on survival and functional traits in a Mediterranean predator

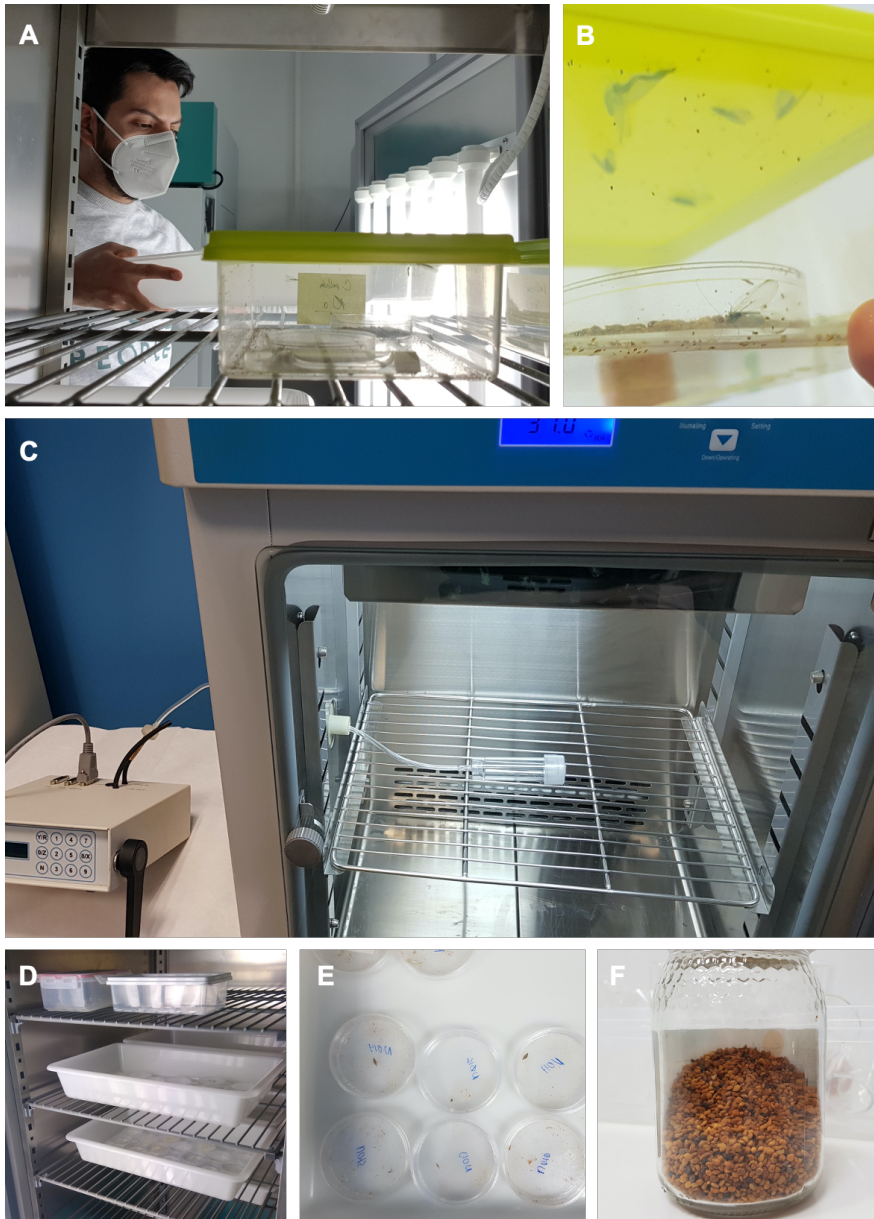


Fig. A7.1. Rearing and maintenance of *Chrysoperla pallida* in the laboratory, and respirometry materials. Food supply and water supply into plastic containers (A); population inside plastic containers (B); respirometer, incubator, and respirometry chamber (C); maintenance on the stock colony in the growth chamber (D); individualization of lacewing larvae (E); bee-pollen pellets (F).

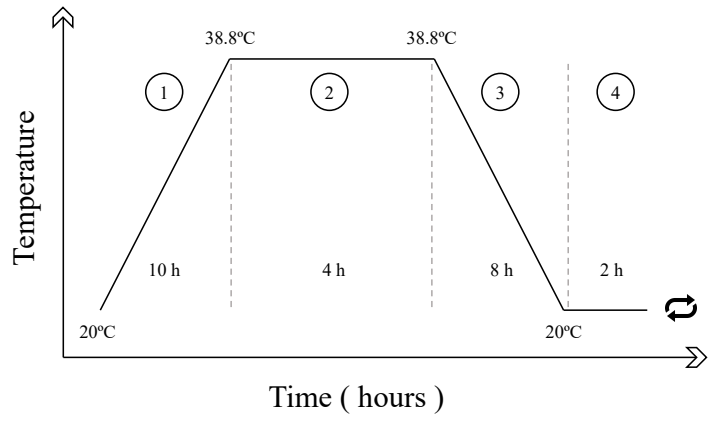


Fig. A7.2. Scheme of the rearing programming in the cooled incubator with refrigeration for the three global climate change experiments (26, 37, and 38.8°C). Example from the experiment at 38.8°C.

Extra production

Papers and collaborations produced during the doctorate by the author which are related to the present thesis (arranged by relevance):

1. Clemente-Orta, G., & Álvarez, H. A. (2019). La influencia del paisaje agrícola en el control biológico desde una perspectiva espacial. *Ecosistemas* 28(3): 13-25 (review paper belonging to the doctoral thesis of Gemma Clemente-Ortal).
2. Álvarez, H. A., & Ruano, F. (2021 in press) ¿Dónde se encuentran los enemigos naturales de *Prays oleae*? atracción de insectos sobre plantas dentro de los hábitats semi-naturales del olivar. Comunicaciones Científicas Simposium Expoliva (Conference paper).
3. Álvarez, H. A., Oi, F., Morente, M., Campos, M., & Ruano, F. (2018). Las barreras vivas y la vegetación adyacente nativa como recurso para aumentar los enemigos naturales y la resiliencia en el agroecosistema de olivo. Libro de Actas. VII Congreso Internacional de Agroecología, 296-300 (Conference paper).

