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Integrated Pest Management in Maize at the Landscape Scale

Gemma María Clemente Orta

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Universitat de Lleida

Doctoral thesis

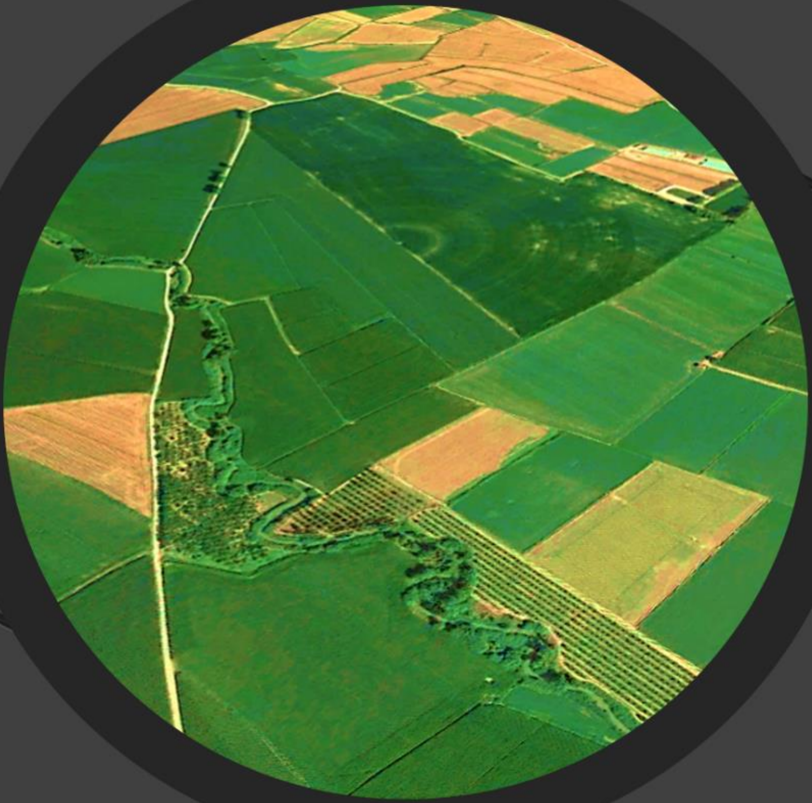
Integrated Pest Management in Maize at the Landscape Scale

Gemma María Clemente Orta

Doctoral dissertation submitted to apply for the degree of Doctor by the University of Lleida

Doctoral Program Food and Agricultural Science and Technology

Directors: Dr. Ramon Albajes and Dr. Maria Ángeles Achón



Universitat de Lleida

Departament de Producció Vegetal i Ciència Forestal

TESI DOCTORAL

INTEGRATED PEST MANAGEMENT IN MAIZE AT THE LANDSCAPE SCALE

Dissertation to obtain the degree of Doctor by the University of Lleida

Memòria presentada per optar al grau de Doctor per la Universitat de Lleida

Gemma María Clemente Orta

Programa de Doctorat Ciència i Tecnologia Agrària i Alimentària

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A mis padres.

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El Alquimista, Paulo Coelho

Contents

Summary

The global demand for food has led to the development of intense agricultural activity resulting in fragmentation, modification and simplification of natural habitats already documented as one of the main causes of extinction and loss of species diversity. The quantity, structure and surface shape of these fragmented natural habitats generate positive or negative effects on the abundance and diversity of species. The biodiversity that ecosystems have provides a series of ecosystem services to humans, and natural biological control is one of the services that has been altered, especially in agroecosystems. Although there is growing scientific literature that suggests that the presence of natural habitats benefits natural enemies in agroecosystems, the efficiency of biological control remains one of the main challenges in these studies, as the effects vary greatly between species and between studies. Understanding the patterns of abundance and movement of natural enemies and herbivores, as well as understanding the interactions between them, is spatially and temporarily complex in agricultural landscapes. While agricultural habitat management offers solutions to reduce yield loss due to pests, in the case of viruses, the excessive simplification of crop diversity, intensive cropping systems and the use of phytosanitary products interfere with the ecological functions of agroecosystems, altering the epidemiology of diseases in plants.

With the aim of offering a general perspective on the influence that the agricultural landscape can have on biological control and viral epidemiology, this thesis has focused on analysing the effects of the agricultural landscape from a spatial composition and field management perspective on species of herbivorous and predatory insects, as well as in the main viruses that affect the cultivation of maize in the area of the Ebro Valley. The first part of the thesis is aimed at (1) broadening the knowledge of identifying the types of studies that are being conducted to analyse the effects of agroecosystem on biological control, the different methodologies and the most recent results (Chapter 1), and (2) the effects of the structure (composition and configuration) of the landscape and the local variables in the predators and herbivores present in the cultivation of maize (Chapter 2). The second part of the thesis is aimed at studying the effects of the landscape on three of the main viruses that affect the cultivation of maize (1) two generalist vector viruses: the sugarcane mosaic virus (SCMV) and the maize dwarf mosaic virus (MDMV) (Chapter 3), and a vector specialist virus: the maize rough dwarf virus (MRDV) (Chapter 4).

The main conclusions of this thesis are as follows: (1) functional studies where landscape composition is studied have shown that natural enemy species need specific habitats, while other variables such as the local effects of the crop can also affect the dynamics of natural enemies and herbivores with greater weight; (2) the surface of orchards negatively affects potential predators in maize, but the plant cover of these positively affects certain species of herbivores; (3) alfalfa acts as a crop that contributes predators and herbivores to the cultivation of maize acting as a resource for species with higher effects than semi-natural habitats; and (4) the viral incidence in maize is mainly influenced by the planting date and the cover and presence of grass species at the edges. These results offer additional knowledge about the effects produced by both the composition of the agricultural landscape and the management of the field itself in the abundance and distribution of herbivores, predators and viruses in the cultivation of maize. In addition, they provide a basis for predicting the consequences of the modification of agricultural practices in the biological control of pests and viruses in the cultivation of maize. These results also suggest that local management measures that guarantee minimum levels of biodiversity and sustainability should be considered as the initial basis for the development of more efficient biological control programmes for pests and viruses.

Resumen

La demanda mundial de alimentos ha llevado al desarrollo de una intensa actividad agrícola produciendo una fragmentación, modificación y simplificación de los hábitats naturales ya documentada como una de las principales causas de la extinción y pérdida de la diversidad de especies. La cantidad, estructura y forma de la superficie de estos hábitats naturales fragmentados genera efectos positivos o negativos sobre la abundancia y diversidad de las especies. La biodiversidad que tienen los ecosistemas provee de una serie de servicios ecosistémicos al ser humano, y el control biológico natural de plagas es uno de los servicios que se ha visto alterado especialmente en los agroecosistemas. Aunque existe una creciente literatura científica que sugiere que la presencia de hábitats naturales beneficia a los enemigos naturales en los agroecosistemas, la eficiencia del control biológico sigue siendo uno de los principales retos en estos estudios, pues los efectos varían mucho entre especies y entre estudios. Entender los patrones de abundancia y movimiento de las especies de enemigos naturales y de herbívoros en los paisajes agrícolas, así como las interacciones entre estos, es espacial y temporalmente complejo. Si bien la gestión de los hábitats agrícolas ofrece soluciones para reducir la pérdida de rendimiento debido a las plagas, en el caso de los virus la simplificación excesiva de la diversidad de los cultivos, los sistemas intensivos de cultivo y el uso de productos fitosanitarios interfieren con las funciones ecológicas de los agroecosistemas alterando la epidemiología de enfermedades en las plantas.

Con el objetivo de ofrecer una perspectiva general sobre la influencia que el paisaje agrícola puede tener sobre el control biológico y la epidemiología viral, esta tesis se ha centrado en analizar los efectos del paisaje agrícola desde una perspectiva de composición espacial y del manejo del campo sobre especies de insectos herbívoros y depredadores, así como en los principales virus que afectan al cultivo de maíz en la zona del Valle del Ebro. La primera parte de la tesis está orientada a (1) la ampliación en el conocimiento de cuáles son los tipos de estudios que se están realizando para analizar los efectos del agroecosistema en control biológico, las diferentes metodologías y los resultados más recientes (Capítulo 1), y (2) los efectos que tiene la estructura (composición y configuración) del paisaje y las variables locales en las especies de depredadores y herbívoros presentes en el cultivo del maíz (Capítulo 2). La segunda parte de la tesis está orientada a estudiar los efectos del paisaje sobre tres de los principales virus que afectan al cultivo del maíz (1) dos virus generalistas de vector: el virus del mosaico de la caña de azúcar (SCMV) y el virus del mosaico enanizante del maíz (MDMV) (Capítulo 3), y un virus especialista de vector: el virus del enanismo rugoso del maíz (MRDV) (Capítulo 4).

Las principales conclusiones de esta tesis son: (1) los estudios de carácter funcional donde se analiza la composición del paisaje han demostrado que las especies de enemigos naturales necesitan de hábitats específicos, pero que otras variables como son los efectos locales del cultivo también pueden afectar a las dinámicas de los enemigos naturales y los herbívoros con más fuerza; (2) la superficie de frutales afecta negativamente a los depredadores potenciales en el maíz, pero que las cubiertas vegetales de estos afectan positivamente a ciertas especies de herbívoros; (3) la alfalfa actúa como un cultivo que aporta depredadores y herbívoros al cultivo del maíz actuando como un recurso para las especies con mayores efectos que los hábitats semi-naturales; (4) la incidencia viral en el maíz está influenciada principalmente por la fecha de siembra y por la cobertura y presencia de especies de gramíneas en los márgenes. Estos resultados abren una vía en el conocimiento de los efectos que produce tanto la composición del paisaje agrícola como el manejo del propio campo en la abundancia y distribución de herbívoros, depredadores y de virus en el cultivo del maíz. Además, son una base para predecir las consecuencias de la modificación de las prácticas agrícolas en el control biológico de plagas y de virus en el cultivo del maíz. Estos resultados además sugieren que deben de contemplarse medidas de gestión a escala local que garanticen niveles mínimos de biodiversidad y sostenibilidad como base inicial para el desarrollo de programas más eficientes de control biológico de plagas y virus.

Resum

La demanda mundial d’aliments ha dut al desenvolupament d’una intensa activitat agrícola produint la fragmentació, modificació i simplificació dels hàbitats naturals ja documentats com una de les principals causes de l’extinció i pèrdua de la diversitat d’espècies. La biodiversitat que tenen els ecosistemes proveeix d’una sèrie de serveis ecosistèmics a l’ésser humà i el control biològic natural de plagues es un dels serveis que s’ha vist alterat especialment als agroecosistemes. Tot i que existeix una creixent literatura científica que suggereix que la presència d’hàbitats naturals beneficia als enemics naturals als groecosistemes, l’eficiència del control biològic segueix sent un dels principals reptes en aquests estudis, oncs els efectes varien molt entre espècies i entre estudis. Entendre els patrons d’abundància i moviment de les espècies d’enemics naturals i d’herbívors, així com les interaccions entre aquests en els paisatges agrícoles, es espacialment i temporal complex. Si bé la gestió dels hàbitats agrícoles ofereix solucions per a reduir la pèrdua del rendiment degut a les plagues, en el cas dels virus, la simplificació excessiva de la diversitat dels cultius, els sistemes intensius de cultiu i l’ús de productes fitosanitaris interfereixen amb les funcions ecològiques dels agroecosistemes alterant la epidemiologia de malalties a les plantes.

Amb l’objectiu d’oferir una perspectiva general sobre la’influència que el paisatge agrícola pot tenir sobre el control biològic i la epidemiologia viral, aquesta tesis s’ha enfocat en analitzar els efectes del paisatge agrícola des d’una perspectiva de composició espacial i del maneig del camp sobre espècies d’insectes herbívors i depredadors, així com en els principals virus que afecten al cultiu del panís a la zona de la Vall de l’Ebre. La primera part de la tesis està orientada a (1) l’ampliació en el coneixement de quins són els tipus d’estudis que s’estan duent a terme per analitzar els efectes de l’agroecosistema en el control biològic, les diferents metodologies i els resultats més recents (Capítol 1), i (2) els diferents efectes que té l’estructura (composició i configuració) del paisatge i les variables locals en les espècies de depredadors i herbívors presents en el cultiu de panís (Capítol 2). La segona part de la Tesi està orientada a estudiar els efectes del paisatge sobre tres dels principals virus que afecten al cultiu de panís (1) dos virus generalistes de vector: el virus del mosaic de la canya de sucre (SCMV) i el virus del mosaic nanitzant del panís (MDMV) (Capítol 3), i un virus especialista de vector: el virus del nanisme rugós del panís (MRDV) (Capítol 4).

Les principals conclusions d’aquesta tesis doctoral són: (1) els estudis de caràcter funcional on s’estudia composició del paisatge han demostrat que les espècies d’enemics naturals necessiten hàbitats specífics, però que altres variables com són els efectes locals del cultiu també poden afectar a les seves dinàmiques i les de les plagues amb més força; (2) la superfície de fruiters afecta negativament als depredadors potencials del panís, però que les cobertes vegetals d’aquests afecten positivament a certes espècies d’herbívors en absència del panís; (3) l’alfals actua com un cultiu que aporta depredadors i herbívors al cultiu de panís actuant com un recurs per a les espècies més importants dels hàbitats seminaturals; (4) la incidència viral al panís està influïda principalment per la data de sembra i per la cobertura i presència d’espècies de gramínies als marges. Aquests resultats obren una via en el coneixement dels efectes que produeixen tant la composició del paisatge agrícola com el maneig del propi camp en l’abundància i distribució d’herbívors, depredadors i de virus en el cultiu de panís. Aquests resultats a més suggereixen que s’han de contemplar mesures de gestió a escala local que garanteixin nivells mínims de biodiversitat i sostenibilitat com a base inicial per al desenvolupament de programes més eficients de control biològic de plagues i virus.

General introduction

Maize farming system

The maize crop is an important element in the composition of the agricultural landscape in the Ebro Valley. Maize crop covers an area of 31,000 ha in Lleida and 64,000 ha in Huesca, which represents 28.61% of the total maize surface in Spain (MAPA 2018). This area has an annual grain production of 10,000-14,000 kg grain/ha and provides 20,000-23,000 kg/ha of dry biomass for forage (Cantero-Martínez 2013). It is important as a crop mainly intended for animal feed (grain, flour and grain for green food), for human food (oils, starch, flours and derived products), for organic agricultural amendments, and for industrial uses such as paper, the textile industry and alcoholic beverages.

The geo-topographic characteristics of irrigated crop areas in Lleida do not allow large fields, so that maize is grown in fields of between 1 and 10 ha and flood irrigation or sprinkler irrigation by pivots are used. In addition, although planting after ploughing is the most common practice in the area, direct sowing is still used in a small proportion of cases. Due to the climate characteristics of this area, growers use long-cycle or short-cycle hybrid cultivars depending on the rotation characteristics of the field. March and April planting use long-cycle cultivars after winter fallow. Planting from May and June, or late plantings, are made with short-cycle maize after winter cereal or alfalfa. Depending on the planting date, different varieties are grown, and the commercial destination of the grain will vary. Finally, the harvest is carried out from the month of October, but it depends on the rainfall that occurred during the year and can be extended until December (Cantero-Martínez C 2013).

Pests, diseases and weeds in maize crops

One of the characteristics of field crops is that they form an agricultural landscape whose matrix is spatially and temporally ephemeral. Maize is an annual crop whose temporality means that the organisms that reside in it have to adapt their biological cycles to such circumstances. Numerous herbivores colonize the crop at the beginning and leave it when harvested. Predators and parasitoids, which feed on herbivores, adapt their cycle to that of herbivores, a process that creates low temporal stability in the relationships (Albajes et al. 2013; di Lascio et al. 2016; Madeira and Pons 2016).

Despite being ephemeral crops, the adaptability of natural herbivore-natural enemy relationships to the temporality of maize is high (Pons and Eizaguirre 2008). This process is similar to the way diseases and weeds adapt their cycles and requirements to the maize reproductive cycle.

Following to the MAPA Integrated Pest Management (IPM) Guide (2015) of maize crop:

Pest according to the part attacked of the plant by herbivorous insects:

Soil	Coleoptera: *Agriotes lineatus* L., *A. obscurus* L. or *Anoxia villosa* (Fabricius, 1781).
	Lepidoptera: *Agrotis segetum* (Ochsenheimer, 1816) and *A. psilon* (Hufnagel, 1766).
Foliage	Lepidoptera: *Mythimna unipuncta* (Haworth, 1809) and *Spodoptera exigua* (Hübner, 1808).
	Trombidiformes (*Tetranychus* sp.).
	Hemiptera: aphids as *Rhopalosiphum padi* L., *Sitobion avenae* Fabricius and *Metopolophium dirhodum* (Walker, 1849) and homopterans as *Zyginidia scutellaris* (Herrich-Schaffer, 1838).
Stalk and the inflorescence	Lepidoptera: *Helicoverpa armigera* (Hübner, 1805) and *Ostrinia nubilalis* (Hübner, 1796), *Sesamia nonagrioides* (Lefèbvre, 1827).

Diseases according to the type of causative agent:

Nematodes	*Meloidogyne* sp. and *Pratylenchus* sp.
Bacteria	Stem rot *Dickeya dadantii* Samson et al. 2005 syns. *Erwinia chrysanthemy* pv. Zeae.
Fungi	Root rot *Pythium* sp., *Fusarium* sp. and *Rhizoctonia solani* Kühn.
	Fungal rot the stem *Stenocarpella maydis* (Berk.) Sutton syns. *Diplodia maydis* (Berk.) Sacc., *Gibberella zeae* (Schwein.) Petch, (1936) and *Fusarium* sp..
	Cob rot *Gibberella zeae* (Schwein.) Petch, (1936), *G. fujikuroi* (Sawada) Wollenw., *Fusarium* sp., *Nigrospora oryzae* (Berk. & Broome) Petch, 1924, and *Aspergillus flavus* Link.
	Corn leaf blight *Setosphaeria turcica* (Luttr.) K.J. Leonard & Suggs, (1974).
	Late wilt of corn *Cephalosporium maydis* Samra, Sabet & Hing.
	Maize common rust *Puccinia sorghi* Schwein, corn smut *Ustilago maydis* (Persoon) Roussel.
	Maize head smut *Sphacelotheca reiliana* (J.G.Kühn) G.P.Clinton (1902).
Virus	Reoviridae maize rough dwarf virus (MRDV), and Potyviridae maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV).

Weed species most problematic:

Difficult species to control	Johnsongrass (*Sorghum halepense* L.).
Common species present	*Echinocloa* spp., *Setaria* spp., *Digitaria* spp., *Amaranthus* sp., *Chenopodium* sp., *Datura* sp., *Poligonum* sp., *Salsola* sp., *Solanum* sp., *Xanthium* sp., *Cyperus* sp. and *Abutilon theophrasi* Med.
	The recent appearance of teosinte (subspecies of *Zea mays*).

Pest control practices in maize crops

Given the temporal characteristics of maize in the productive period, most phytophagous arthropods show explosive population growth and a subsequent rapid decline typical of an “r” strategy, and crop recolonization occurs in greater or lesser intensity, year after year (Albajes et al. 2013; Comas et al. 2014). Despite the presence of phytophagous that can cause economic losses on a regular or occasional basis, extensive crops are not subject to major intervention in relation to pest control if we compare them with other crops such as fruit (horticultural or ornamental) (Pons and Eizaguirre 2008).

Maize is susceptible to being attacked by a large number of insects, which can be cited as "traditional pests" of Lleida as follows: stem borers, soil worms, aphids, leafhoppers, mites, and armyworm. Of all these pests, borers, aphids, and leafhoppers are present in maize fields either at a time or throughout the entire cycle. Moreover, in the last years, mites have been increasing the presence and the populations in some maize fields. Although the use of varieties of Bt-maize has largely reduced the presence of stem and cob borers and the presence of scarring does not affect the production of the cob, chemical treatments that can affect the species are still used (Pons and Eizaguirre 2008). The use of chemical control has been possible due to its ease of use, its short-term effectiveness and the existence of relatively cheap insecticides. But the growing lack of plant protection products authorized in maize and the relatively low economic yield of extensive crops, are important stimuli to develop IMP systems of pest prevention and control techniques and in this context, conservation biological control is fundamental.

For weed control, chemical herbicidal treatments are carried out systematically in pre-emergence and in post-emergence with specific herbicides. Sometimes a second post-emergence treatment is performed if specific problems occur, especially with broadleaf weeds (Cantero-Martínez 2013).

For disease control, cultural measures such as crop rotation, adaptation of planting dates and weed control are commonly used (García-Arenal and McDonald 2003). Especially in the case of viruses, more effective control measures against these viruses are the cultivation of tolerant varieties and the maintenance of clean grass weed fields, at least in the initial stages of cultivation. However, currently, the increase in maize as a second crop, the direct sowing, and the use of several-cycle varieties together with climatic oscillations make it difficult to optimize the planting dates or for them to be effective (Achon and Clemente-Orta 2017).

To know more to enhance IPM programs in maize crops

Some of the pests and diseases (especially vector-borne viruses) that affect the cultivation of maize can be perfectly controlled by natural enemies if they are not interfered in their action by the use of chemicals (Rusch et al. 2010). Biological control is based on the periodic colonization of crops by natural enemies of surrounding habitats (Wissinger 1997). This movement of natural enemies between crops or semi-natural habitats is not exclusive to predators; some parasitoids also have insect-pest hosts in different crops and take advantage of the spatial and temporal alternation of field crops (Albajes et al. 2011; Chaplin-Kramer et al. 2011). It has been found that these species are able to install naturally in crops and exert their action on pests, reducing their densities (Tscharntke et al. 2005; di Lascio et al. 2016; Madeira and Pons 2016; Ardanuy et al. 2018). Therefore, it seems logical to think that the conservation of these natural enemies is the biological control technique to consider first in field crops. Not only is the conservation of this fauna necessary, it is also necessary to favour it through habitat management and the appropriate application of other control techniques (Landis et al. 2000).

In the case of viruses, the effect of biodiversity on the ability of viruses to infect their host plant and to cause disease is a major question in plant pathology that is central to understanding the emergence of infectious diseases and developing strategies for their management (Pagan et al. 2012). Furthermore, this reduction of biodiversity could increase disease incidence as a result of the increased abundance of susceptible major hosts, thus facilitating disease spread (Keesing et al. 2006, “Dilution Effect” hypothesis). Although the spread of infectious diseases is inherently a spatial process often embedded in physically complex landscapes (Biek and Real 2010) little is known about the linkage between spatial processes at the landscape scale, the ecology of vector colonisation and the virus transmission rate in the epidemiological disease process (Meentemeyer et al. 2012).

Despite this applicability, biological control by conservation requires for its practice and the reduction of the use of insecticides as well as the existence of a deep knowledge about the dispersion of predators and herbivores among crops to improve habitat management at the local level, although this effect is noticeable at larger scales.

Thesis outline

The Thesis aims to know which maize field and landscape characteristics influence (1) the composition and abundance of phytophagous and predatory arthropods living on maize and (2) the epidemiology of maize viral diseases. To achieve the general objective of the Thesis, research is divided in two main parts.

The first part focuses on (i) identifying the types of studies that are being carried out to analyse the trophic relationships at the landscape scale, the different methodologies used and the most recent results that have been achieved (Chapter 1), and (ii) the effects that the structure (both the composition and the configuration) of the landscape and the local variables have on the abundance of predators and herbivores in the maize crop (Chapter 2). The second part of the thesis is aimed at studying the effects of the landscape and field local variables on three of the main viruses affecting the maize yield, (i) the sugarcane mosaic virus (SCMV) and the maize dwarf mosaic virus (MDMV), two generalist viruses (Chapter 3), and (ii) the maize rough dwarf virus (MRDV), a specialist virus (Chapter 4).

In Chapter 1, we review literature that analyses the landscape from the perspective of spatial composition and spatial complexity. Our aim was to present an overall view of the influence that an agricultural landscape may have on insect biological control. Patterns of movement and abundance of insect herbivores and their natural enemies in agricultural landscapes are highly complex (temporally and spatially), and this complexity hinders the interpretation and comparison amongst studies.

(1) Introduction to landscape terminology: concepts and definitions.

(2) Functionality of landscape elements (composition and configuration).

(3) An emerging trend: trophic networks.

Chapter 2 was based on the preliminary results obtained by authors in the area who had reported, first, the role alfalfa as a source of predators for maize and, second, the potential negative consequences of the increasing proportion of highly sprayed orchards in the landscape on the abundance and diversity of natural enemies. Specifically, we tried to disentangle the influence of the actual agricultural landscape on the composition and abundance of 17 insect groups, 11 predators and 6 herbivores, in maize fields.

(1) The intensive chemical spraying that is usually practised in orchards in this area has negative consequences for the biological control functions in surrounding maize crops.

(2) Alfalfa can act as a reservoir of natural enemies in intensive agricultural landscapes.

Chapter 3 was devoted to the epidemiology of diseases caused by potyviruses, which are transmitted by aphids. Based on the knowledge achieved by previous studies, we knew that in our area, the number of aphids colonizing maize was closely linked to migrations from winter cereals. We therefore hypothesized that the increase in winter cereal surface area might directly lead to an increase in aphid abundance as a resource concentration effect. The amount of virus host habitats and their connectivity may influence the global infection pressure on maize in a certain area. However, the knowledge of larger-scale interactions between host spatiotemporal heterogeneity, environmental conditions, and the rates at which pathogens disperse through and among fragmented host populations is limited. We quantified the landscape composition at three spatial scales (i.e., 200 m, 500 m and 1000 m) within concentric circular buffers around maize fields sampled for virus incidence.

(1) Which are the mains drivers of maize infection risk by MDMV and SCMV among landscape and field variables?

(2) Does the mains driver of infection risk vary with different landscape scales?

(3) What is the best explanatory spatial scale to elucidate the infection risk of two closely related potyviruses?

Chapter 4 is based on the generally accepted feature that the epidemiology of the MRD disease, similar to that in other *Fijivirus*, is strictly linked to the abundance and distribution of its vector. On the other hand, the planting date has been reported to be an important factor in the epidemiology of MRDV. Planting date varies from area to area according to the climate characteristics and crop rotation, and consequently, the expected length of the maize growing season changes rather frequently. In the study area, maize producers have traditionally sown in March or April; however, in recent years, growers have delayed the planting date, probably due to milder springs and earlier winter cereal harvesting. We quantified the landscape composition at 500 m using concentric circular buffers from maize fields.

(1) Can elucidate from a landscape perspective the epidemiology of an endemic virus?

(2) What are the landscapes and field variables involved in maize infection risk by MRDV?

(3) Are the same the main factors involved in early and late maize planted fields?

Some general conclusions issued from the different parts of the work close the Thesis.

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Chapter 1

La influencia del paisaje agrícola en el control biológico desde una perspectiva espacial

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La influencia del paisaje agrícola en el control biológico desde una perspectiva espacial

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Resumen

La intensificación agrícola modifica y simplifica el paisaje agrícola alterando los servicios ecosistémicos que la biodiversidad proporciona a los agroecosistemas, especialmente el control biológico de plagas. Con el objetivo de ofrecer una perspectiva general sobre la influencia que el paisaje agrícola puede tener sobre el control biológico, en la presente revisión se recopilan diversos artículos que analizan los efectos del paisaje desde una perspectiva de complejidad y composición espacial. Encontramos que existe una creciente literatura científica, que sugiere que la presencia de hábitats naturales beneficia a los enemigos naturales en los agroecosistemas. Sin embargo, la baja eficacia del control biológico sigue siendo uno de los principales retos en estos estudios. Entender los patrones de abundancia y movimiento de las especies de enemigos naturales y de herbívoros en los paisajes agrícolas es altamente complejo (espacial y temporalmente), lo que dificulta su interpretación y comparación entre estudios. Aunque el uso de redes tróficas todavía es muy escaso en la literatura, su aplicación en este tipo de estudios supone un desarrollo prometedor.

Palabras clave: enemigos naturales; paisaje; escalas del paisaje; ecología del paisaje; agroecosistema, complejidad del paisaje; composición del paisaje; hábitat natural; redes tróficas.

Abstract

Agricultural intensification simplifies and modifies the agricultural landscape, disturbing the ecosystem services that biodiversity provides to agroecosystems, particularly the biological control. In this review we gathered several articles that analyse landscape from the perspective of spatial composition and spatial complexity. Our aim was to present an overall view of the influence that an agricultural landscape may have on biological control. We found that there is an increasing scientific literature that suggests that the presence of natural habitats beneficiates natural enemies within agroecosystems. However, inefficient biological control supposes a great challenge in this type of studies. Understanding the patterns of movement and abundance of the species of herbivores and natural enemies in agricultural landscapes is highly complex (temporal and spatial) and this hinder its interpretation and comparison amongst studies. Although the use of a trophic network approach is still scarce in the literature, however, its application at different scales may entail a promising development in such research.

Keywords: natural enemies; landscape; landscape scales; landscape ecology; agroecosystem; landscape complexity; landscape composition; natural habitat; food webs.

Introducción

La pérdida de la biodiversidad y los cambios correspondientes en la composición de las especies alteran los servicios que los ecosistemas proporcionan a la humanidad (Cardinale et al. 2012). Concretamente en los agroecosistemas, la intensificación agrícola, los monocultivos, el uso continuo de productos fitosanitarios y la fragmentación de los hábitats naturales, ha resultado en la pérdida de uno de los servicios ecosistémicos más importantes para la producción agrícola: el control biológico (Eilenberg, 2006). El control biológico se distingue de otras formas de control de plagas por actuar de una manera denso-dependiente, es decir, la población de enemigos naturales se incrementa y depredan o parasitan una gran proporción de presas cuando éstas incrementan su población en un cultivo (Debach 1964; DeBach y Rosen 1991). En cualquier programa de control biológico, la conservación de los enemigos naturales es un elemento crítico. Esto implica que es necesario identificar el o los factores que limitan la cantidad y/o efectividad de los enemigos naturales en el agroecosistema. De manera que es preciso entender que los paisajes agrícolas son ecosistemas simplificados (agroecosistemas) donde se producen diversos recursos pero también donde se establecen complejas interacciones ecológicas entre todos sus componentes.

El Paisaje

El paisaje como una unidad de organización

Existen varias definiciones aplicadas al paisaje, consecuencia de su evolución multidisciplinar y de la diversidad de perspectivas con las que se puede identificar este concepto (McGarigal y Cushman 2005). El Convenio Europeo del Paisaje (ELC) lo define como “un área, como la perciben las personas, cuyo carácter es el resultado de la acción e interacción de factores naturales y/o humanos”. Desde una perspectiva más ecológica, el paisaje está definido como “una unidad de organización mayor que el ecosistema” (Burel y Baudry 1999). Según la Teoría General de Sistemas, un paisaje, (1) no está necesariamente definido por su tamaño, sino por un mosaico de parches que interactúan entre sí, los cuales son relevantes para el fenómeno de estudio (McGarigal y Cushman 2005); (2) es un sistema abierto donde los flujos de energía se mueven hacia dentro o hacia fuera del mismo; y (3) está caracterizado por su heterogeneidad tanto espacial como temporal (von Bertalanffy 1993; Wagner y Fortin 2005; Martin et al. 2016).

Desde el laboratorio hasta el paisaje

Los estudios tradicionales de control biológico en ensayos de laboratorio desarrollaron medidas de control eficientes desde un enfoque del comportamiento del insecto (la herbivoría, el parasitismo, la colonización y la competencia). La extrapolación de estos resultados entre el laboratorio y el campo estaba bajo el supuesto de que las parcelas donde se obtenían las muestras de un experimento debían ser esencialmente iguales, asumiendo una homogeneidad en el espacio y el tiempo. Este hecho permitía controlar estadísticamente la variación ambiental y las relaciones entre diferentes variables (Wagner y Fortin 2005). Pero, los procesos ecológicos son inherentemente espaciales y las parcelas o zonas de estudio, son afectadas por la interacción local y el entorno circundante ("neighbouring units", Levin 1992; y posteriomente "landscape context", Pearson 2002) lo que da lugar a patrones entrelazados en múltiples escalas.

El desarrollo de herramientas en sistemas de información geográfica (SIG) y de paquetes estadísticos libres, propició una cascada de metodologías para abordar desde diferentes enfoques el control biológico. Pero no siempre se puede comparar y mantener la resolución de un estudio de laboratorio en uno de campo (Scherber et al. 2012). Este reto científico se puede abordar desde diferentes escalas: regional, paisaje o local (Figura 1).

Figura 1. Diferentes escalas de estudio en el agroecosistema. Escala regional (a), escala de paisaje basada en un área de influencia alrededor del campo de muestreo (b) y escala local a

nivel de campo (c). Las escalas espaciales cambian dependiendo del tipo de organismos: pequeñas en plantas (primer nivel trófico) e intermedias en herbívoros (segundo nivel trófico). En cambio, la escala espacial en poblaciones de depredadores (tercer nivel trófico) es amplia y puede experimentar muchos cambios y depende del tamaño corporal y de la especialización de la especie (e. g. parasitoides especializados).

Figure 1. Different scales of study in the agroecosystem. Regional scale (a), landscape scale based on an area of influence around the sampling field (b), and local scale at field level (c). The spatial scales change depending on the type of organisms: small in plants (first trophic level) and intermediate in herbivores (second trophic level). In contrast, the spatial scale in populations of predators (third trophic level) is wide and can undergo many changes, which depends on the body size and specialization of the species (e.g., specialized parasitoids).

Por otro lado, la estructura (configuración y composición) de la matriz agrícola ejerce una influencia tanto en insectos herbívoros y sus enemigos naturales, como en las interacciones entre estos (Tscharntke et al. 2005). Así, en un estudio ideal del agroecosistema, la parte experimental debería contemplar: (1) el establecimiento de un borde o limite, (2) fragmentos de distintos tipos de hábitats, (3) una caracterización de la composición y configuración de la matriz agrícola, (4) un registro de tratamientos fitosanitarios (en el cultivo y en los hábitat circundantes), (5) abundancias de herbívoros y enemigos naturales, (6) tasas de depredación y/o parasitismo y finalmente (7) una cuantificación de la producción final. Sin embargo, llegar a conseguir todas estas variables en muchos casos es complicado por razones de logística y de limitaciones económicas y humanas debido a que los estudios a escalas de paisaje cubren grandes áreas agrícolas, cuyos campos son manejados por diferentes agricultores. En estas circunstancias, donde existe una variabilidad tan alta, la cual es difícil de controlar, los estudios son establecidos en gradientes de complejidad y/o composición y configuración.

Ecología del paisaje

Históricamente, la definición de ecología del paisaje y el paisaje han evolucionado de manera conjunta y continua. El término ecología del paisaje mantiene una clara vinculación con la geografía (Vila Subirós et al. 2006). Troll (1939) fue el primero en utilizar la expresión "landscape ecology", y la definió como "el estudio de toda la complejidad de relaciones causa-efecto que existen entre las comunidades de seres vivos y sus condiciones ambientales, en una sección específica de paisaje". En general, la principal contribución que hace la ecología del paisaje es aceptar que: (1) la mayoría de los procesos ecológicos son inherentemente espaciales (Levin 1992), y (2) están limitados por las condiciones ambientales que varían en el espacio y el tiempo, así como por la interacción local con otros procesos a múltiples escalas (Wagner y Fortin 2005). La ecología del paisaje particularmente se ha desarrollado en los últimos años para establecer cuál es el efecto de la antropización sobre los ecosistemas y la repercusión sobre los servicios ecosistémicos, los cuales dependen del mantenimiento de una alta diversidad biológica y de sus interacciones (Altieri 1994; 1999) (Figura 2).

Figura 2. Manejo del paisaje agrícola: vistas aéreas y panorámicas de dos agroecosistemas de cereales en el norte de España. Paisaje moderadamente simplificado (izquierda). Paisaje altamente simplificado (derecha). La actividad humana destaca como una de las principales actividades que modifican la estructura espacial del paisaje. Una actividad moderada favorece la diversificación de formas en el paisaje mientras que, una actividad intensa aumenta la simplificación de este. Fuente: G. Clemente-Orta.

Figure 2. Agricultural landscape management: aerial and panoramic views of two cereal agroecosystems in northern Spain. Moderately simplified landscape (left). Highly simplified landscape (right). Human activity stands out as one of the main activities that modify the spatial structure of the landscape. A moderate activity favors the diversification of forms in the landscape while, an intense activity increases the simplification of this. Source: G. Clemente-Orta.

El paisaje como una variable cuantitativa

El concepto base para llevar a cabo la interpretación de un paisaje es el mosaico, que puede ser aplicado desde una escala microscópica hasta una planetaria. El mosaico está compuesto a su vez por un conjunto de elementos (landscape-elements): los fragmentos (patches), los corredores (corridors) y la matriz (matrix). En lo que respecta a la "composición de un paisaje", esta viene definida por los tipos de parches que coexistan en un paisaje y su abundancia relativa (Wagner y Fortin 2005). Estos parches, además, pueden ser de varias formas y tamaños y su disposición puede variar en el espacio (Steffan-Dewenter et al. 2002), por lo que "la configuración de un paisaje" describe la forma de los parches y la disposición de uno respecto al resto (Gustafson 1998). De manera que, para describir la heterogeneidad de un paisaje (también llamada estructura del paisaje), se pueden utilizar ambas aproximaciones: heterogeneidad de la composición y heterogeneidad de la configuración (Fahrig y Nuttle 2005). La existencia de "índices de paisaje" que resultan de la aplicación de métodos cuantitativos en ecología del paisaje, permiten comparar entre distintas composiciones y configuraciones espaciales en distintos momentos, tanto a nivel de fragmentos como de paisaje (FRAGSTATS, McGarigal y Marks 1995) (Botequilha et al. 2006; McGarigal et al. 2012).

Funcionalidad de los elementos del paisaje

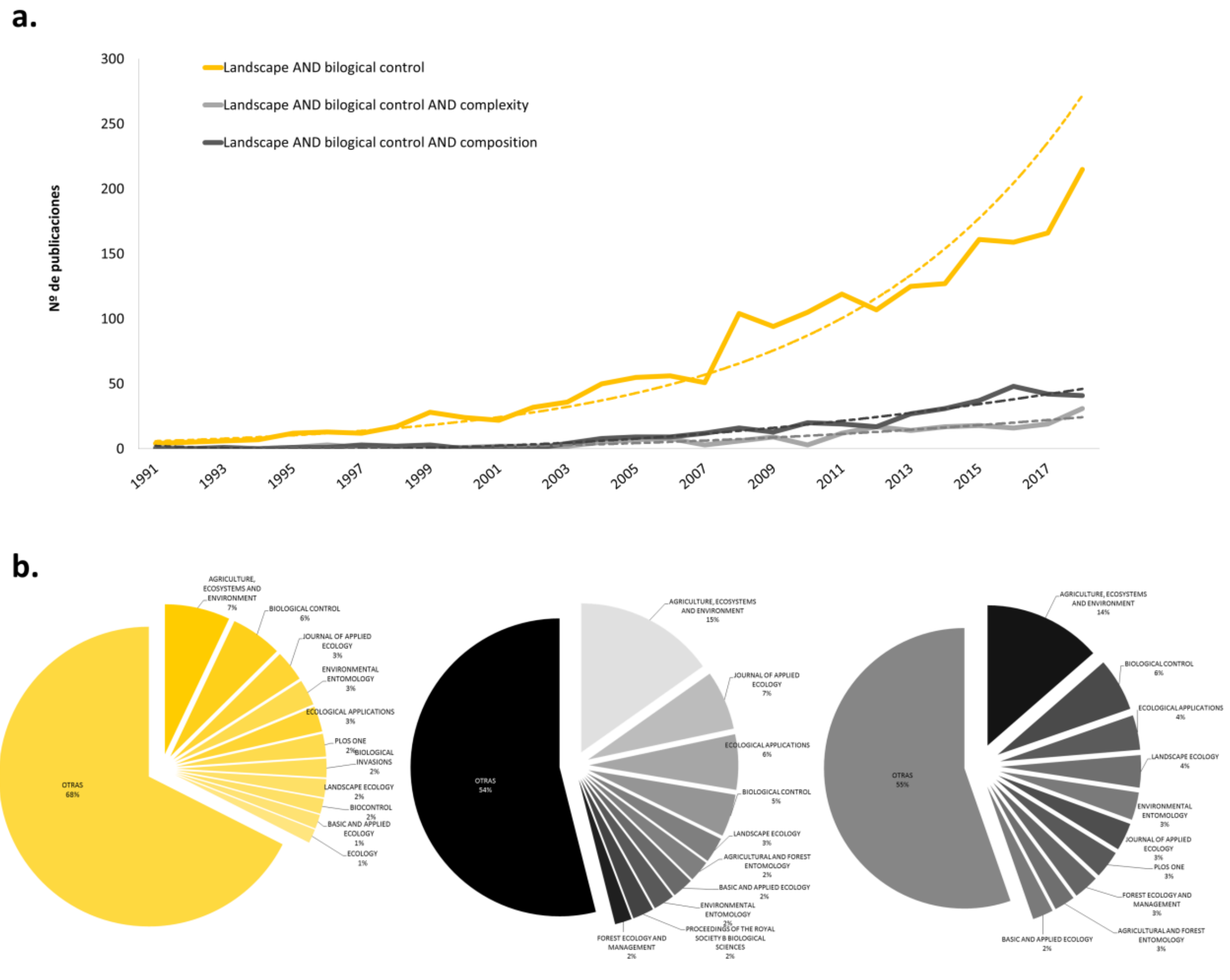
En los agroecosistemas, las prácticas agrícolas tienen efectos sobre la biodiversidad (Rusch et al. 2010). Estos efectos pueden ser observados tanto a escala local (el propio campo) como a escala de paisaje (hábitats circundantes) (Landis et al. 2000; Tscharntke et al. 2007). La fragmentación del hábitat natural ha sido documentada como una de las principales causas de la extinción y pérdida de la biodiversidad de las especies (Tilman et al. 2001; 2002). Por ejemplo, la cantidad, estructura y forma de la superficie de estos fragmentos (parches) genera efectos positivos o negativos sobre la abundancia y diversidad de los insectos (Bianchi et al. 2006; Tscharntke et al. 2012). Diversos autores sugieren que la respuesta de las especies a la forma y calidad del hábitat se puede entender desde un contexto de disponibilidad del recurso (Ries y Sisk 2004; Ries et al. 2004) y que a través de mecanismos como: (1) la distribución complementaria del recurso (Dunning et al. 1992; McCollin 1998; Fagan et al. 1999); (2) el desbordamiento (“spillover”) (Shmida y Wilson 1985); y (3) los hábitats mejorados (Cadenasso et al. 1997) pueden jugar un papel muy importante para predecir cómo los organismos se concentrarán en diferentes tipos de hábitats (Álvarez et al. 2016; 2017; Cotes et al. 2018). Esta disponibilidad de los recursos se traduciría en el desplazamiento de las especies: (1) entre hábitats no-cultivados, (2) desde el hábitat natural (como fuente de especies) al cultivo, y (3) desde el cultivo (como fuente de especies generalistas) al hábitat natural circundante (Tscharntke et al. 2007). Debido a esto, es posible que en muchos agroecosistemas se produzcan efectos de concentración (Root 1973) o de dilución de las poblaciones (Otway et al. 2005) y que las diferencias de abundancia de las especies se asocien a un determinado hábitat y/o recurso (Moreira et al. 2016). Estos patrones de respuesta de la abundancia de las especies a dicho recurso permiten establecer un criterio de calidad en los paisajes agrícolas a través de la identificación y cuantificación de la diversidad de grupos funcionales presentes como un estimador de la resiliencia del sistema (Bengtsson et al. 2003; Loreau et al. 2003).

En consecuencia, a lo largo de los años, los agricultores han aprendido a estimular las poblaciones de EN (depredadores y parasitoides) a través del manejo y la conservación de los agroecosistemas (Symondson et al. 2001; Rusch et al. 2010). Por ejemplo, en Europa el reconocimiento de la pérdida de la biodiversidad se ha traducido en programas agroambientales para mejorar la biodiversidad en diferentes cultivos, como lo es el uso de cubiertas vegetales (García et al. 2018) y de márgenes entre cultivos (IOBC 2018) o entre invernaderos (Rodríguez et al. 2018; Cotes et al. 2018). Estas perspectivas se basan en la hipótesis de que el aumento de la abundancia y diversidad de enemigos naturales impacta directamente en las plagas, disminuyendo su abundancia y con ello las pérdidas en la producción (Rusch et al. 2010; Tscharntke et al. 2012).

Relación entre la complejidad del paisaje y su función

Si bien algunos autores definen el paisaje en términos de complejidad del hábitat, midiendo los tipos de hábitats presentes en un área de influencia, área de estudio o región, este término ha sido más comúnmente utilizado como la cantidad o proporción de hábitat no cultivado, también definido como hábitat natural o hábitat semi-natural (variable de composición) en los agroecosistemas. Ésta es posiblemente la métrica más simple para caracterizar la complejidad de un hábitat y se usa ampliamente porque a menudo se correlaciona con los índices de diversidad de Shannon o de Simpson (Thies y Tscharntke 1999). Así, paisajes muy complejos (altos porcentajes de hábitat natural) normalmente presentan altos índices de diversidad. La Figura 3 muestra la reciente evolución de los estudios que abordan la complejidad y composición del paisaje, así como las principales revistas en las que se han publicado estos resultados (tendencia basada en los resultados de búsquedas en la Web of Science, WoS). Estos gráficos ilustran que desde hace una década el marco de trabajo ha tomado relevancia y que son las revistas de corte ecológico las que un mayor número de publicaciones tienen.

El paradigma establece que los paisajes complejos incrementan la abundancia de enemigos naturales y que a consecuencia de este fenómeno se produce un efecto positivo en el control biológico de plagas (Bianchi et al. 2006) lo que se ha denominado como “la hipótesis del hábitat-complejo” (Álvarez et al. 2019). Así, por ejemplo, Marino y Landis (1996) mostraron que la diversidad de especies de parasitoides en campos de maíz no variaba ni se veía influenciada por la cercanía del hábitat natural en paisajes simples o complejos (campos pequeños con márgenes y hábitat natural), pero que el porcentaje medio de parasitismo era significativamente mayor en paisajes complejos. Otros autores, mostraron que la presencia de márgenes y barbechos incrementaban la biodiversidad de enemigos naturales, las tasas de depredación y el parasitismo (Thies y Tscharntke, 1999). Asociar la abundancia y la diversidad de enemigos naturales con el control biológico de plagas ha mostrado resultados positivos en la mayoría de los casos, pero existen unos pocos estudios que muestran efectos neutros e incluso efectos negativos (Finke y Denno 2002; 2005).



Landscape AND bilogical control

Landscape AND bilogical control AND complexity

Landscape AND bilogical control AND composition

Figura 3. Evolución del número de publicaciones (a.) y porcentaje de revistas (b.) que estudiaron el paisaje junto con el control biológico de plagas, basado en búsqueda avanzada en la Web of Science. Se representan tres parámetros: (1) paisaje + control biológico; (2) paisaje + control biológico + complejidad; y (3) paisaje + control biológico + composición (categorías de refinamiento: Ecología, Entomología, Ciencias ambientales, Conservación de la biodiversidad, Agricultura multidisciplinaria, Ciencias multidisciplinarias, Ciencias de las plantas, Agronomía, Silvicultura, Biología, Estudios ambientales).

Figure 3. Evolution of the number of papers (a.) and percentage of journals (b.) that studied the landscape and biological control of pests, based on advanced search in the Web of Science. It is represented three parameters: (1) landscape and biological control; (2) landscape and biological control and complexity; and (3) landscape and biological control and composition (categories of refinement: Ecology or Entomology or Environmental Sciences or Biodiversity Conservation or Agriculture Multidisciplinary or Multidisciplinary Sciences or Plant Sciences or Agronomy or Forestry or Biology or Environmental Studies).

*Para mayor detalle, ver versión online.

Tylianakis y Romo (2010) apuntaban al hecho de que es necesario conocer mucha más información acerca de las presas para poder establecer un buen control biológico en los sistemas agrícolas. Por su parte Chaplin-Kramer et al. (2011) cuestionaban si una alta diversidad de enemigos naturales mejora la función del control biológico *per se,* por lo que realizaron un metaanálisis con 46 estudios a nivel de paisaje. Estos encontraron que los enemigos naturales tenían una fuerte respuesta positiva a la complejidad del paisaje, siendo más fuerte esta respuesta en los enemigos naturales generalistas en todas las escalas medidas; sin embargo, los enemigos naturales especialistas respondieron con más fuerza a escalas más pequeñas. Como ya habían apuntado Chaplin-Kramer et al. (2011), la respuesta positiva de los enemigos naturales a la complejidad del paisaje no tenía por qué traducirse necesariamente en un control biológico más efectivo (Bianchi et al. 2006; Rusch et al. 2010), ya que puede ocurrir que la abundancia de plagas muestre una respuesta significativa a la complejidad del paisaje (Chaplin-Kramer et al. 2011). Concepción et al. (2012) en un estudio realizado con 232 campos ubicados en seis países, concluyen que el manejo del cultivo tenía efectos sobre la riqueza de las especies pero que era dependiente de la complejidad de cada agroecosistema, siendo los más de efectivos los paisajes de complejidad intermedia (medido como km márgenes semi-naturales y % hábitat no cultivado). Otros estudios centrados en la abundancia y diversidad de polinizadores y enemigos naturales, sugieren que las prácticas de manejo y de la calidad de los hábitats naturales locales, especialmente de setos y márgenes, son las variables más importantes para muchas especies (Garratt et al. 2017).

Por otro lado, variables como la medición de dinámicas poblacionales (en lugar de los recuentos estáticos), no se están considerando en los estudios para poder caracterizar mejor la variabilidad de respuestas en relación con la complejidad del paisaje y el control biológico. Así, Chaplin-Kramer et al. (2013) midieron la abundancia semanal de enemigos naturales (larvas de sírfidos) y de pulgones en cultivos de brócoli durante tres años. Los resultados mostraron que la abundancia de larvas de sírfidos aumentó potencialmente con la proporción de hábitat natural disminuyendo la abundancia de los pulgones. Además, los autores señalan que cuando agregaron los datos en promedios anuales (una métrica común en las investigaciones dirigidas al control biológico) no se observó dicho efecto. Estos resultados sugieren que una resolución temporal más alta de los datos de los enemigos naturales y la dinámica de abundancia de las plagas puede revelar un control “top-down” en los agroecosistemas, que de otra manera puede estar enmascarado por la variación estacional e interanual en los factores ambientales (Plećaš et al. 2014). Raymond et al. (2015) encontraron que, aunque la eficiencia del control biológico parecía ser mayor en paisajes estructuralmente simples, los paisajes complejos mostraron una colonización más temprana de los enemigos naturales que podría facilitar y asegurar un control biológico temprano y eficiente sobre las poblaciones de pulgones. Recientemente Karp et al. (2018) en un análisis donde comparan 132 estudios realizados en 6759 parcelas concluyen que, en la mayoría de los casos, los hábitats no cultivables circundantes a los cultivos no mejoraron el control biológico, y que este control sólo se observa en pocos cultivos con características muy específicas. Por lo que plantea si el hecho de no encontrar una relación positiva entre la diversidad de enemigos naturales y la regulación del control biológico podría deberse a que la mayoría de estudios espaciales no incluyen realmente la dinámica temporal como variable explicativa, además de que existen diversas metodologías para cuantificar el control biológico. De manera que investigar tanto la diversidad como la dinámica temporal de los diferentes gremios de enemigos naturales, podría ayudar a entender mejor la relación entre diversidad funcional y control biológico en los agroecosistemas (Ortiz-Martínez y Lavandero, 2018; Álvarez et al. 2019). Otra posible explicación aportada por Tscharntke et al. (2016) es que el hecho de que los hábitats naturales incrementen la abundancia de enemigos naturales, pero no produzcan un control biológico dentro del agroecosistema puede ser explicado en un contexto de interacciones ecológicas y manejo humano (Figura 4).

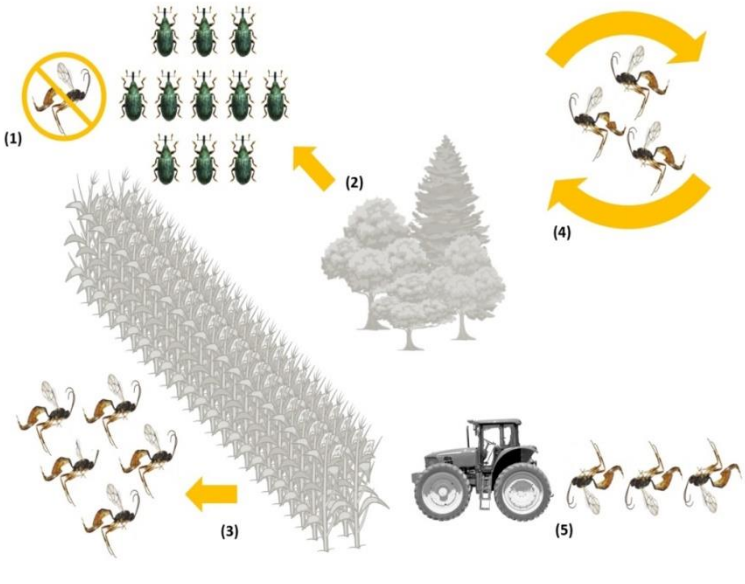


Figura 4. Procesos por los cuales el hábitat natural no provee un control biológico de plagas efectivo. (1) Las plagas no tienen enemigos naturales efectivos en la región. (2) El hábitat

natural es un “recurso-fuente” mayor para las plagas. (3) Los cultivos proveen recursos más importantes para los enemigos naturales. (4) El hábitat natural es insuficiente para generar poblaciones de enemigos naturales. (5) Las prácticas agrícolas contrarrestan el establecimiento de los enemigos naturales (adaptado de Tscharntke et al. 2016).

Figure 4. Processes by which natural habitat fail to provide an effective biological pest control: (1) Pest populations have no effective natural enemies in the region. (2) Natural habitat is a greater source of pests. (3) Crops provide more important resources for natural enemies. (4) Natural habitat is insufficient to provide natural enemy populations. (5) Agricultural practices counteract natural enemy establishment (adapted from Tscharntke et al. 2016).

Aún con una larga lista de literatura científica al respecto, continua la variabilidad de los resultados obtenidos y el desconocimiento de un control biológico más efectivo, ver tabla 1.

Tabla 1. Resumen de los efectos de la complejidad del paisaje en distintos estudios medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos, así como el efecto sobre el control biológico (CB) en los agroecosistemas.

Table 1. Summary of the effects of the complexity of the landscape in different studies measured on abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in agroecosystems.

Autores	**Escala espacial (m)**	**Taxón**	**Categoría**	**Variable**	**Efectos en:**			
					A	**D**	**P**	**CB**
Marino y Landis, 1996	3200	Lepidoptera	Herbívoro	% HN	-			
		Hymenoptera	Parasitoide	% HN	+	+	+	+
Thies y Tscharntke, 1999	1500	Coleoptera	Herbívoro	% semi-HN	-			
		Hymenoptera	Parasitoide	% semi-HN	+		+	+
Finke y Denno, 2002	Jaula	Hemiptera	Depredador	% HN	+			+
		Araneae	Depredador	% HN	+			0
Finke y Denno, 2005	Invernadero	Araneae	Depredador	% HN	+	+		+
		Coleoptera	Depredador	% HN	+	+		+
		Hemiptera	Depredador	% HN	+	+		+
		Araneae	Depredador	% HN	+	+		+
Chaplin-Kramer et al. 2013	500, 100 y 1500	Diptera	Depredador	% HN	+			+
Plećaš et al. 2014	1000 a 6000	Hemiptera	Herbívoro	% HN	+			
	500 a 2000	Hymenoptera	Parasitoide	% HN	+		+	0
Raymond et al. 2015	500	Coleoptera	Depredador	% HN	+	+		+
		Coleoptera	Depredador	% HN	+	+		+
Garratt et al. 2017	500	Hymenoptera	Polinizador	% semi-HN	+			
		Araneae	Depredador	% semi-HN	+			+
Ortiz-Martínez y Lavandero, 2018	500	Hemiptera	Herbívoro	% HN	-			
		Hymenoptera	Parasitoide	% HN	-		-	0
		Hymenoptera	Parasitoide	Int. agrícola	+		+	+
		Coleoptera	Depredador	% HN	+	+		+
Paredes et al. 2019	1000	Lepidoptera	Herbívoro	% HN	-			
		Hemiptera	Depredador	% HN	+			+

Además, son escasos los estudios que puedan cuantificar en rendimientos económicos los beneficios aportados por la estructura del paisaje y el control biológico en los cultivos. Uno de los pocos estudios que cuantifica dicho efecto es el de Paredes et al. (2019) que muestran como la presencia de parches de hábitat natural en el agroecosistema del olivo aumenta el control biológico sobre *Prays oleae*, produciendo rendimientos por valor de 186,36 € / ha.

Relación entre la composición del paisaje y su función

A pesar del aumento reciente de las investigaciones científicas sobre la complejidad del hábitat y los enemigos naturales (Figura 3), así como el poder predictivo que reflejan, se ha argumentado que la funcionalidad del hábitat (fuente/recurso) podría ser más acertada para una especie o grupo en concreto (Fahrig et al. 2011). Los hábitats pueden clasificarse en categorías de acuerdo con su potencial para proporcionar refugio, alimento, sitios de oviposición o algún otro beneficio a las especies de enemigos naturales (Östman et al. 2001). Por ejemplo, una aproximación a esta medida sería tener en cuenta todo el perímetro de los parches (Martin et al. 2016), el tamaño del campo muestreado (Bosem et al. 2017), o la métrica de coste-distancia (Perović et al. 2010).

La composición y organización espacial del agroecosistema son dos aproximaciones importantes para determinar la dinámica poblacional de los enemigos naturales (Rusch et al. 2010). Además, en este tipo de estudios es más común encontrar variables locales ya que, factores como la elección del cultivo, la fecha de siembra y prácticas de fertilización o los tratamientos fitosanitarios pueden modificar las interacciones entre las plagas y los cultivos (en el tiempo o en el espacio) (Médiène et al. 2011). Así, en estos análisis, la cantidad de variables que se generan con datos espaciales y locales es alta y necesitan ser optimizadas y simplificadas (Zuur et al. 2010; Dormann et al. 2013; Pasher et al. 2013), ver tabla 2.

Maisonhaute et al. (2010) estudiaron si la estructura del paisaje era la variable que explicaba la mayor parte de la variación en especies de escarabajos depredadores en comparación con las prácticas agrícolas y el ambiente local. Ellos encontraron que el hábitat natural y la heterogeneidad del paisaje tuvieron una influencia positiva tanto en la abundancia como en la diversidad de escarabajos depredadores, aunque la estructura del paisaje fue el factor principal. Holzschuh et al. (2010) encontraron diversas respuestas en función de las especies, de manera que las abejas fueron más sensibles a altos porcentajes de hábitat natural en el paisaje; las avispas dependieron de altas densidades de márgenes; y que los parasitoides estuvieron fuertemente ligados a sus huéspedes. Ellos concluyeron que la conversión de hábitat cultivable en no cultivable no era una estrategia lo suficientemente exitosa para mejorar las poblaciones de estos himenópteros porque son más afectados por el aislamiento que por la pérdida del hábitat. Otras especies como los carábidos (depredadores generalistas) en cambio pueden verse beneficiadas en paisajes agrícolas simplificados. En ese sentido, los autores resaltan que este hecho no implica necesariamente un mejor control biológico de plagas en estos ambientes, puesto otros factores como que algunas especies de enemigos naturales pueden competir entre ellos (depredación intragremial), podría limitar su capacidad para controlar las plagas (Caballero-López et al. 2012). Ardanuy et al. (2018) encontró que la abundancia de *Orius* spp., uno de los depredadores generalistas más importantes en el maíz, no respondía a la composición del hábitat, sino que presentaba una fuerte relación positiva con la abundancia de su principal presa y con la densidad de márgenes en el paisaje.

La diversidad de enemigos naturales junto con los rendimientos en los cultivos, podrían mejorar si se optimizan los efectos de distintos parámetros del paisaje, especialmente la configuración y diversidad del paisaje a diversas escalas de estudio (Martin et al. 2016). En línea con esto, Maisonhaute et al. (2017) señalan que el control biológico de los pulgones de la soja podría mejorar si se reduce la proporción de soja en el agroecosistema, se aumenta la riqueza de cultivos y se conservan los bosques naturales. También, Bosem et al. (2017) muestran (por primera vez) que la abundancia de pulgones de cereal podría ser reducida en el agroecosistema si se optimizará la composición (diversificación de cultivos), la configuración (mantener pequeños campos con márgenes); y añaden que la heterogeneidad temporal (rotación) se muestra como un factor clave dentro del mosaico de cultivos del agroecosistema.

En estos estudios de estructura del paisaje la elección, simplificación y agrupación de las variables no es sencilla. Por ejemplo, Janković et al. (2017) muestran que la superficie de cultivo no tiene ningún efecto en los enemigos naturales pero que al separar en pequeñas categorías los distintos tipos de hábitat natural, la variable correspondiente a los setos tuvo un papel importante tanto para los enemigos naturales como para las plagas. Este patrón no se podría haber revelado si se hubiesen sumado todos los tipos de hábitats naturales del paisaje. Lo anterior sugiere que considerar un enfoque funcional del agroecosistema está intrínsecamente ligado con las características propias de las especies que se vayan a contemplar en los estudios de paisaje. Kebede et al. (2018) encontraron que, aunque la abundancia de especies de parasitoides y moscas parásitas no estaba influenciada por el tipo de margen, los campos más pequeños y con más bordes podían soportan densidades de enemigos naturales relativamente más altas. Además, señalan que la proporción de un monocultivo puede anular todos los factores de manejo y gestión a nivel del campo, por lo que para el manejo de ciertas plagas es necesario considerar un enfoque a escalas de paisaje amplias, por ejemplo, en el caso los barrenadores del maíz. Por su parte, Martin et al. (2019) en un análisis con datos de 49 estudios en 1515 paisajes, muestran que la interacción entre la composición (% de hábitats) y la configuración (densidad de márgenes en el paisaje) aumentan la polinización y la abundancia de enemigos naturales, mejorando finalmente el control biológico concretamente en los agroecosistemas europeos. No obstante, la reciente literatura científica parece estar enfocada en estudiar los efectos de las superficies de cultivos de frutales en las especies. Estos estudios están sugiriendo que el manejo de estos cultivos puede estar afectando negativamente a la colonización (Aviron et al. 2016) y a la abundancia de los enemigos naturales (Samnegård et al. 2018; Yang et al. 2018; 2019), y cuyo efecto no se ha observado en frutales ecológicos (Happe et al. 2019). Markó et al. (2017) muestran que los efectos obtenidos podrían estar enmascarados por la continua inmigración de enemigos naturales desde cultivos herbáceos hasta los frutales, determinado fuertemente por un patrón estacional. Asimismo, proponen que otros cultivos podrían estar actuando como un recurso más importante para los enemigos naturales que ciertos hábitats semi-naturales. Además, sugieren que el uso intensivo de pesticidas en los agroecosistemas podría estar enmascarando los efectos positivos esperados de los hábitats semi-naturales (Ricci et al. 2019). Sin embargo, para que haya una reducción del uso de estos productos debe de producirse una mejora de estos hábitats naturales que garantice un control biológico natural efectivo.

Tabla 2. Resumen de los efectos de la composición del paisaje en distintos estudios medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos así como el efecto sobre el control biológico (CB) en los agroecosistemas. La integración de las variables locales (VL) son más comunes en este tipo de análisis.

Table 2. Summary of the effects of the composition of the landscape in different studies measured on the abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in agroecosystems. The integration of local variables (VL) are more common in this type of analysis.

Autores	**Escala espacial (m)**	**Taxón**	**Categoría**	**Variable**	**Efectos en:**				**VL**
					A	**D**	**P**	**CB**	
Perović et al. 2010	3000	Hemiptera	Herbívoro	% Pastos	+				
	1500	Coleoptera	Depredador	% HN	+			+	
	120	Araneae	Depredador	% HN	+			+	
	750	Hymenoptera	Parasitoide	% Algodón	+			+	
Maisonhaute et al. 2010	200 y 500	Coleoptera	Depredador	% No cultivo	+	+		+	x
Holzschuh et al. 2010	500	Hymenoptera	Polinizador	% No cultivo	+				x
		Hymenoptera	Polinizador	% semi-HN	+				x
		Hymenoptera	Parasitoide	% semi-HN	+		+	+	x
Caballero-López et al. 2012	2000	Hemiptera	Herbívoro	% Pastos	+				
		Coleoptera	Depredador	% Pastos	+			+	
		Araneae	Depredador	% Pastos	+			0	
		Coleoptera	Depredador	% Pastos	+			0	
		Hymenóptera	Parasitoide	% semi-HN	+			+	
Aviron et al. 2016	100, 200 y 300	Hemiptera	Depredador	% semi-HN	+			+	x
		Hemiptera	Depredador	% Frutales	-			-	x
Martin et al. 2016	100 a 1000	Hemiptera	Herbívoro	Manejo IMP y config.	+				x
		Hymenoptera	Parasitoide	Manejo OR / Config.	+ / +	+ / +		+ / +	x
		Diptera	Depredador	Manejo OR / Config.	+ / +	+ / +		+ / +	x
		Araneae	Depredador	Tipo de cultivo	+				x
		Coleoptera	Depredador	% semi-HN	+			+	x
		Coleoptera	Depredador	Configuración	+	+		+	x
		Hymenoptera	Depredador	Manejo OR / Config.	+ / +	+ / +		+ / +	x
Bosem et al. 2017	1000	Hemiptera	Herbívoro	% semi-HN y diversidad cultivos	-				
		Hymenoptera	Parasitoide	% semi-HN	+		+	+	
		Diptera	Depredador	% semi-HN	+			+	
		Araneae	Depredador	% semi-HN	+			+	
		Neuroptera	Depredador	% semi-HN	+			+	
		Coleoptera	Depredador	% semi-HN	+			+	
Janković et al. 2017	1000	Hemiptera	Herbívoro	semi-HN / Manejo IN	+ / +				
		Hymenoptera	Parasitoide	semi-HN / Manejo IN	- / -			- / -	
		Hymenoptera	H-parasitoide	semi-HN / Manejo IN	+ / +			+ / +	
		Coleoptera	Depredador	% Cultivos	+	-		+	
		Hemiptera	Depredador	% Cultivos / semi-HN	- / -			- / -	
Maisonhaute et al. 2017	1500	Hemiptera	Herbívoro	Diversidad cultivos	-				x
		Coleoptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Neuroptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Neuroptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hemiptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hemiptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Araneae	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hymenoptera	Parasitoide	% Soja / % HN	- / +	- / +		- / +	x
		Fungi	Depredador	% Soja / % HN	- / +	- / +		- / +	x

Markó et al. 2017	1000	Hemiptera	Herbívoro	Insecticidas	-				
		Coleoptera	Depredador	% Urbano / % HN / Arables	+			+	
		Coleoptera	Depredador	% Urbano / % HN / Arables	+			+	
		Coleoptera	Depredador	% HN / Arables	- / +			- / +	
Ardanuy et al. 2018	500	Hemiptera	Herbívoro	% semi-HN	+			+	
	1000	Hemiptera	Herbívoro	% semi-HN / % Cereals	- / +			+	
		Hemiptera	Depredador	% semi-HN y presa	+			+	
Kebede et al. 2018	Parcela	Lepidoptera	Herbívoro	% Maíz	+				x
		Dermaptera	Depredador	Diversidad cultivos	+			+	x
		Coleoptera	Depredador	Diversidad cultivos	+			+	x
		Hymenoptera	Depredador	Diversidad cultivos	+			+	x
		Coleoptera	Depredador	Diversidad cultivos	+			+	x
Samnegård et al. 2018	1000	Hemiptera	Herbívoro	Manejo IMP	-				x
		Lepidoptera	Herbívoro	Manejo IMP	-				x
		Hymenoptera	Polinizador	Manejo OR / Vegetación adyacente	+	+			x
		Diptera	Polinizador	Manejo OR / Vegetación adyacente	+	+			x
		Dipteros	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Dermaptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Coleoptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Coleoptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Hemiptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Neuroptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Opiliones	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
Yang et al. 2018	500 y 2000	Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
		Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
		Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
Happe et al. 2019	1000	Araneae	Depredador	Manejo OR	+			+	x
		Coleoptera	Depredador	Manejo OR	+			+	x
		Dermaptera	Depredador	% HN / Manejo OR	- / +			+	x
		Diptera	Depredador	Manejo OR	+			+	x
		Hemiptera	Depredador	Cubierta / Manejo OR	- / +			+	x
		Opiliones	Depredador	Manejo OR / % HN	- / +			+	x
Ricci et al. 2019	1000	Depredación pulgones en suelo	Depredador	Insecticidas / % No cultivo / Diversidad cultivos	- / + / +			- / + / +	x
		Depredación pulgones en el cultivo	Depredador	% Prados / % HN	+ / +			+ / +	x
		Depredación presa centinela	Depredador	Insecticida / Cultivo / semi-HN	- / - / +			- / - / +	x
		Depredación semillas en suelo	Depredador	Cultivo / Manejo	- / -				x
Yang et al. 2019	500,1000, 1500 y 2000	Lepidoptera	Herbívoro	% Non-crop / % Maiz y algodón	- / +				
		Hymenoptera	Parasitoide	Campos pequeños / % Maíz	+ / +		+ / +	+ / +	

Una tendencia emergente: las redes tróficas

En los últimos años, los estudios ecológicos se mueven cada vez más hacia enfoques basados en rasgos funcionales para entender con más detalle los servicios ecosistémicos que presta la biodiversidad e impulsar sus efectos positivos en los agroecosistemas.

Como ya hemos visto, aunque los patrones de los enemigos naturales y su papel en el control biológico están fuertemente ligados a factores intrínsecos del paisaje (Tscharntke et al. 2012; 2016; Veres et al. 2013; Karp et al. 2018), dichos patrones son también afectados por las interacciones tróficas entre los organismos en diferentes nichos y hábitats (Bohan et al. 2013; Massol y Petit 2013).

El enfoque de redes tróficas tiene un alto potencial para añadir valor a las investigaciones en materia de control biológico (Tylianakis y Binzer 2014). Una red describe la interacción entre los componentes de un sistema dado, en forma de enlaces (Bohan et al. 2013). La teoría de redes ecológicas (Strogatz 2001) tiene como objetivo entender cómo las propiedades de una red y sus enlaces se relacionan con los sistemas ecológicos. Así, las redes tróficas describen una serie de interacciones tróficas en una comunidad biológica. Dentro de las redes tróficas, y dependiendo de la naturaleza del objeto de interés (individuos, poblaciones, especies o hábitats), las más utilizadas son las redes de interacciones antagonistas e interacciones mutualistas (Bohan et al. 2013).

Recientemente, los patrones de respuesta de los enemigos naturales y sus efectos sobre las plagas en los agroecosistemas han sido revisados y detallados bajo un contexto de redes ecológicas y redes tróficas (Woodward y Bohan 2013; Tilyanakis y Binzer 2014). Por ejemplo, en su revisión de los efectos de los cambios ambientales sobre el control biológico y las redes tróficas parasitoide – hospedador, Tilyanakis y Binzer (2014) investigan como las redes parasitoide – hospedador afectan directamente al control biológico en los agroecosistemas. Ellos sugieren que la intensificación agrícola tiende a producir redes parasitoide – hospedador de una baja complejidad y donde la fuerza de las interacciones es desigual, lo que en teoría podría diezmar la efectividad del control biológico. Sin embargo, estos autores, encuentran pocos estudios que liguen el control biológico con la estructura de las redes parasitoide – hospedador. También, sugieren que no hay patrones claros que muestren que a mayor complejidad del paisaje se genere una mejor estructura en las redes parasitoide – hospedador. De acuerdo con lo anterior, Derocles et al. (2014) utilizan datos moleculares y evalúan el nivel de compartimentación entre las redes tróficas de pulgones y parasitoides en márgenes y áreas de cultivos. Ellos encuentran que la contribución de los márgenes como fuente de enemigos naturales para el control biológico es muy limitada y proponen que se necesita ampliar este tipo de estudios a escalas temporales y espaciales más grandes.

Si bien, se ha comenzado a integrar el estudio del control biológico con redes tróficas, estudios que utilicen metodologías espaciales y análisis de redes tróficas son muy escasos. Para ejemplificar esto nosotros realizamos una búsqueda dentro de la base de datos en la WoS. Específicamente, nuestro objetivo era encontrar artículos científicos que estudiaran a los enemigos naturales en agroecosistemas y que integraran a la par metodologías de análisis de redes tróficas y análisis espaciales por medio de áreas de influencia (buffers). Para ello, en el buscador avanzado de la WoS se introdujeron como criterios de búsqueda: paisaje (Landscape), trófico (trophic), redes (networks), y redes (webs), dando énfasis a las palabras paisaje y trófico (*). Se pidió específicamente buscar artículos científicos en idioma inglés que hayan sido publicados entre los años 1990 y 2019, dentro de los índices: SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC.

Se obtuvieron 46 artículos que integraban alguno o varios de los criterios de búsqueda. Se separaron los artículos que se enfocaban en enemigos naturales o comunidades de insectos, dentro de agroecosistemas, y que en sus metodologías se especificara la integración de las metodologías de nuestro interés. Como resultado sólo 3 artículos mostraron las características deseadas, (ver tabla 3):

(1) McFayden et al. (2009) investigaron en 20 áreas de estudio (farms) bajo manejo ecológico (orgánico) y convencional, si las diferencias en la estructura de las redes tróficas, afectaban al control biológico. Ellos caracterizaron la composición del paisaje basada en cada uno de los componentes del paisaje y colectaron plantas, pulgones y parasitoides para crear una red trófica de tres niveles. La interacción planta- hospedador -parasitoide les permitió calcular índices cualitativos y cuantitativos de dichas redes tróficas. Sus análisis sugieren que la estructura de las redes tróficas es diferente según el manejo y que la riqueza de especies en los tres niveles tróficos es mayor en las áreas con manejo ecológico. Más aún, ellos muestran que los pulgones en las áreas de estudio con manejo ecológico son atacados por más especies de parasitoides. Sin embargo, no encontraron diferencias significativas en la proporción de parasitismo de las redes tróficas entre ambos manejos.

(2) Gacic et al. (2012) investigaron los efectos de la complejidad del paisaje sobre las redes tróficas de pulgón - parasitoide - híperparasitoide en campos de trigo. Ellos encontraron que la intensificación agrícola es importante para la estructura

de dichas redes tróficas y para el control biológico. Además, la abundancia de pulgones y el híperparasitismo, fue mayor en campos con menor intensificación agrícola. Sorprendentemente, sus datos muestran que la complejidad de las redes tróficas tiende a ser mayor con la intensificación agrícola y con una variabilidad temporal alta.

(3) Ye et al. (2017) por su parte, muestran resultados similares a Gacic et al. (2012) pero ellos integran a la red pulgón - parasitoide - híperparasitoide el efecto de bacterias endosimbiontes en pulgones. Ellos investigan si la endosimbiosis facultativa confiere protección contra los parasitoides y si ésta es afectada por la complejidad del paisaje. Sus resultados sugieren que la complejidad del paisaje no tiene ningún efecto significativo positivo sobre la endosimbiosis facultativa, pero la tendencia del patrón muestra que las tasas de endosimbiosis facultativa (infección) en las momias de pulgones son menores en campos fertilizados que en campos no fertilizados.

Tabla 3. Resumen de los efectos de la estructura del paisaje en estudios de redes tróficas medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos, así como el efecto sobre el control biológico (CB) en los agroecosistemas. Integración de las variables locales (VL).

Table 3. Summary of the effects of landscape structure in trophic network studies measured on abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in the agroecosystems Integration of local variables (VL).

Autores	**Escala espacial (m)**	**Taxón**	**Categoría**	**Variable**	**Efectos en:**					**Estructura del paisaje**	**VL**
					A	**D**	**P**	**CB**	**RT**		
Macfadyen et al. 2009	Farm	Diptera	Herbívoro	Manejo (orgánico)		+	+		+	Composición (Orgánico vs Convencional)	x
		Hymenoptera	Parasitoide			+		≈	+		
		Lepidoptera	Herbívoro			+	+		+		
Gagic et al. 2012	500	Hemíptera	Aphididae	Intensificación agrícola	-				+	Complejidad (Orgánico vs Convencional)	
		Hymenoptera	Parasitoide		+ / -		-	≈	+		
		Hymenoptera	Híper-parasitoide		-		-		-		
Derocles et al. 2014	Parcela	Hemíptera	Aphididae	Márgenes	+	+				Complejidad (cultivo vs márgenes)	
		Hymenoptera	Parasitoide				+	+ / -	-		
Ye et al. 2017	500	Hemíptera	Aphididae + endosimbionte	% Habitats semi-naturales + fertilización	+ / -					Complejidad (HN)	x
		Hymenoptera	Parasitoide				+ / -	-			
		Hymenoptera	Híper-parasitoide				+		+		

Conclusiones

El estudio del paisaje, así como su efecto sobre la abundancia y diversidad de enemigos naturales, y su relación con el control biológico, ha tenido un gran crecimiento en los últimos años. Sin embargo, es posible que en muchas investigaciones cierta información se esté perdiendo debido a que los enemigos naturales responden a diversos y complejos tipos de variables como: dinámicas temporales; la composición y configuración del paisaje; interacciones tróficas; o el manejo del cultivo. Los estudios de carácter funcional donde se estudia la composición del paisaje han demostrado que las especies de enemigos naturales necesitan de hábitats específicos, pero que otras variables como son los efectos locales del cultivo también pueden afectar a las dinámicas de los enemigos naturales y las plagas con más fuerza. Consideramos que los futuros esfuerzos realizados en las investigaciones de paisaje necesitan abordar el establecimiento de metodologías o protocolos en común, para simplificar y facilitar la comparación entre estudios. Así también, es necesario desarrollar modelos dinámicos que puedan abordar la interacción entre heterogeneidad espacial y los procesos ecológicos que causan los efectos en las especies. Finalmente, y en base a los resultados recabados en esta revisión cabe destacar que urge la necesidad de promover y fomentar paisajes agrícolas que garanticen niveles mínimos de biodiversidad y sostenibilidad como base inicial en el desarrollo de programas de control biológico a múltiples escalas espaciales.

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Chapter 2

Changes in landscape composition influence the abundance of insects on maize: the role of fruit orchards and alfalfa crops

Gemma Clemente-Orta, Filipe Madeira, Iván Batuecas, Samuel Sossai, Alejandro Juárez-Escario and Ramon Albajes

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Changes in landscape composition influence the abundance of insects on maize: the role of fruit orchards and alfalfa crops

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Abstract

The traditional agricultural landscape of Ebro Basin (NE Spain), which is mainly composed of alfalfa and cereal crops, has undergone changes in recent years, mainly consisting of an increase in the area occupied by intensively managed irrigated orchards. Recently, it has been reported that the presence of a higher proportion of orchards in the landscape and their management negatively affect the abundance and diversity of natural enemies. Two hypotheses are tested in this study: (1) the increased orchard surface has led to a reduction in natural enemies in neighbouring maize crops, and (2) the higher alfalfa proportion of agricultural land enhances the predatory fauna on maize. Maize fields were selected across a landscape gradient created by orchards and field crops (alfalfa and maize) in a buffer of 500 m. The abundance of 17 insect taxa in each maize field was estimated by means of 3 yellow sticky traps per season over three years. The insect abundance was related to the landscape structure (proportions of landscape elements and landscape diversity) and local variables (maize phenology, perimeter/area, weed diversity of the maize edges and abundance of the potential predators or potential prey). Our results show that the proportion of orchards in the landscape had negative effects on the main predators, and alfalfa had positive effects on herbivores and their predators. Semi-natural habitats (non-crop habitats and forest) and landscape diversity had low effects on insect abundance. However, variables at the local level included more significant effects than landscape structure; maize growth stages and abundance of potential prey or predators on the crop were the most influential variables at a local level. Here we show the interplay between different land uses types and local management and their impact on natural enemies and herbivores in maize crops in the Mediterranean area.

Keywords: Agricultural landscape; Crop rotation system; Landscape structure; Local variables; Natural enemy abundance; Maize pest abundance.

1. Introduction

Agroecosystems are not static systems over time but are linked to market demand for different food commodities, among other factors. Insects exploiting such agroecosystems and their associated natural or semi-natural habitats need to be able to find the resources provided by the different cover types in ephemeral and disturbed environments (Rusch et al., 2010; Schellhorn et al., 2014). Thus, herbivores and their natural enemies must move among habitats, resulting in spatial or temporal emigrations (Landis et al., 2000; Rand et al., 2006; Tscharntke et al., 2012; Bianchi et al., 2013). The combination of many trophic level interactions, the landscape structure (i.e., its composition and configuration), the management of the crop fields (i.e., tillage, irrigation, pesticide inputs, harvesting/cutting or rotation) and the constant changes in agricultural policy make it difficult to understand and predict the changing patterns of insect abundance in particular agricultural habitats. Recently, studies have been performed to understand the negative and positive effects of agricultural land use on the conservation of biodiversity and its relation to ecosystem services, with a landscape perspective (Tscharntke et al., 2005). The spatial scale that best predicts the natural enemy density and population dynamics may depend on the specialisation, dispersal capability, and trophic level of a particular natural enemy (Perović et al., 2010; Chaplin-Kramer et al., 2011).

Most of the literature on landscape structure and insect abundance relationships has been devoted to the natural enemies of insect pests with the objective of managing habitats for cost-effective pest control (Symondson et al., 2001; Bianchi et al., 2006; Rusch et al., 2010; Tscharntke et al., 2012). By contrast, herbivore responses to landscape variables are much less conclusive in the literature than the data on natural enemies (Bianchi et al., 2006); this is a knowledge gap that should be filled to allow the design of better forms of biological control of crop pests.

In the Ebro Basin (NE Iberian Peninsula), in the last 25 years, the authors have studied the composition and abundance of arthropods in winter cereals, maize, and alfalfa in irrigated arable crop rotations. In this area, agricultural landscapes are traditionally dominated by arable crops that are managed by the rotation of winter and summer cereals and alfalfa. In these landscapes, small separate areas of fruit orchards are cultivated. In addition, natural or semi-natural habitats are scattered within the agricultural matrix, shaping the agricultural landscape. More recently, changes in market demand have led to modifications to the composition of agricultural landscapes in the region, with the most significant being an increase in the area of stone fruit orchards (National Bureau of Statistics of Spain, 2017), which have led to the transformation of a landscape dominated by arable fields to an orchard-field crop mix landscape. These changes can modify the abundance of pests and their natural enemies that occur on the crops that make up the landscape.

The low economic threshold of stone fruit pests has led to intensive crop management and repeated pesticide treatments, which are considered a main cause of natural enemy reduction in the landscape because pesticides affect their behaviour and habitat recolonisation (Rusch et al., 2010). Consequently, landscapes dominated by stone fruit orchards have been reported to negatively affect the richness of beneficial arthropod species (Samnegård et al., 2018). In contrast, alfalfa fields in this area have been reported to be important reservoirs of natural enemies (Núñez, 2002; Pons et al., 2005; Ardanuy et al., 2018), from which predators show bidirectional movement between neighbouring alfalfa and maize fields (di Lascio et al., 2016; Madeira et al., 2014, 2018; Madeira and Pons, 2016). Additionally, the cover and the composition of herbaceous plants in hedgerows surrounding maize fields may provide resources and shelter for natural enemies of maize pests (Ardanuy et al., 2018).

The aim of the present work is to disentangle the influence of the actual agricultural landscape on the composition and abundance of insect fauna in maize fields. Based on the preliminary results obtained by authors in this area, we present two hypotheses: (1) the intensive chemical spraying that is usually practised in orchards in this area has negative consequences for the biological control functions in surrounding maize crops, and (2) alfalfa can act as a reservoir of natural enemies in intensive agricultural landscapes. To test these two hypotheses, we analysed the influence of the landscape structure and local variables on herbivore and predatory insect abundance on maize. A total of 52 maize fields over three years were sampled to determine the abundance of 17 insect groups, 11 predators and 6 herbivores. The abundance of these insect groups was related in spring and summer in an agricultural landscape in a circle of 500 m around the sampled maize fields.

2. Methods

2.1. Study area

This study was carried out in 2015, 2016 and 2017 in the Ebro Basin in north-eastern Spain (41°48'12.20"N, 0°32'45.77"E; 120–346 m altitude; 200–400 mm rainfall, Tmin: 8º-24º C and Tmax: 18º-38º C) (Fig. 1a). Most of the crops in this region are irrigated, and crop fields are interspersed with patches of non-crop habitats (non-productive areas, longer fallows, natural habitats and wetland) and forest repopulated by *Pinus halepensis* (Mill). Crop rotation mostly includes winter (mainly wheat and barley) and summer (mainly maize) cereals and alfalfa. Traditionally, pome fruit orchards and field crops are grown in separate areas. Recently, the surface area of the stone fruit orchards (mainly peaches) has grown exponentially, leading to a mixed landscape characterised by orchards and field crop plots with different shapes and sizes. Pest management in the cereals includes pre- and post-emergence herbicide applications, treatment of seeds of winter cereals with fungicides, and treatment of maize with both insecticides and fungicides. Management of alfalfa consists of 5/6 cuttings during the productive period (March–October), and the crop is in the field for 4-5 years (Madeira et al., 2014). In orchards, management includes from 7 to 14 chemical sprays (insecticides, fungicides and bioregulators), herbaceous cover mowing (approximately once per month), and herbicide and tree fertilisation (Cantero, 2013).

2.2. Landscape structure variables

During the 3-year study, 52 maize fields were selected according to the initial gradient of the orchard and field crop proportion in the landscape using aerial photography in a circle buffer of 500 m surrounding the maize fields. Due to crop rotation, some of the sampled maize fields changed in this period; thus, we selected 6 maize fields in 2015 and 23 in 2016 and 2017. The size of the maize fields varied between 0.9 and 13.68 ha, and these fields were located at least 2 km apart from each other. The agricultural landscape covered was 700 km^2 (Fig. 1b) (Appendix A.1).

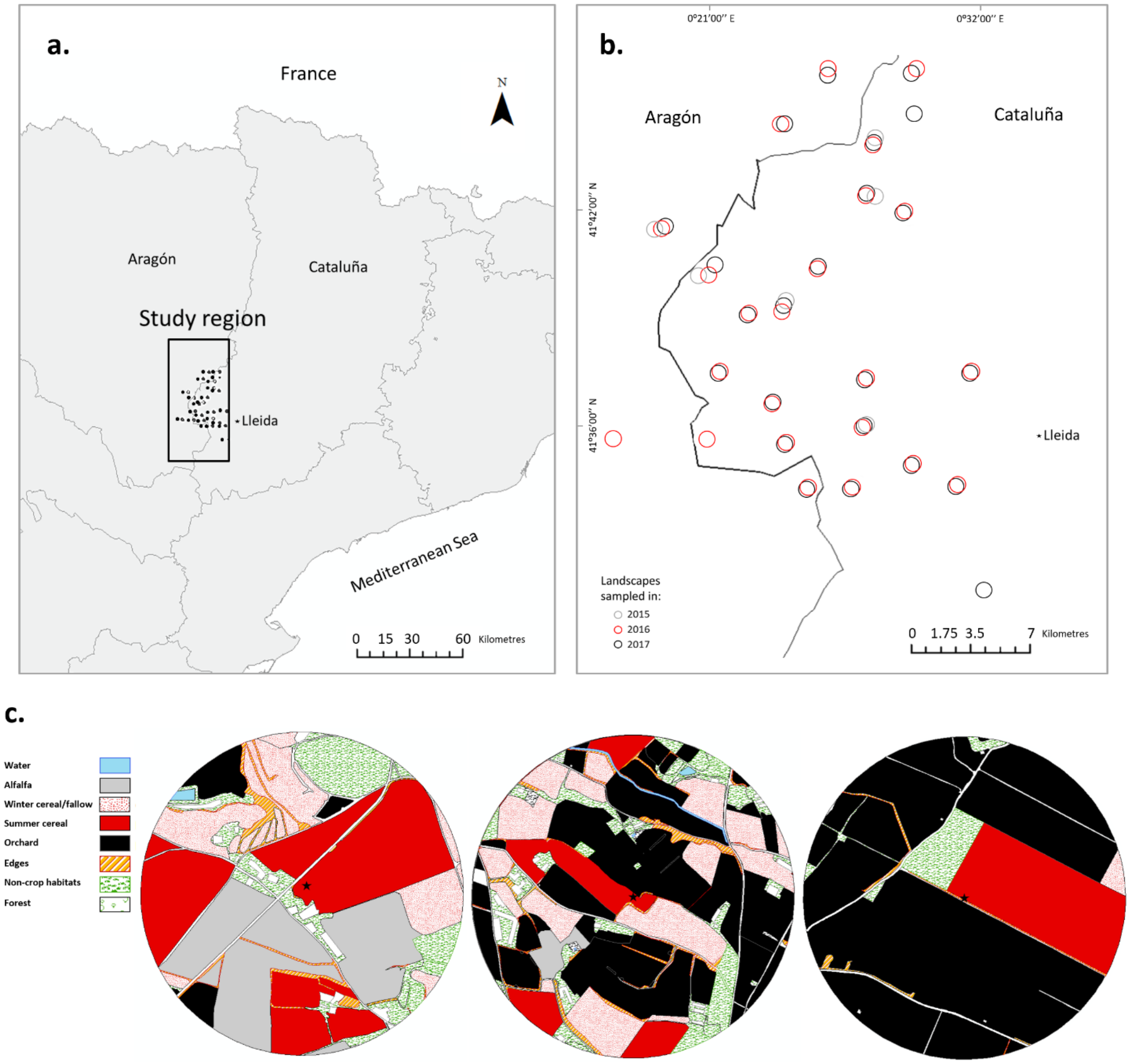

Fig. 1. A. Study region in the Ebro Basin in north-eastern Spain. B. Landscape sampled (2015, 2016 and 2017). C. The star point indicates the middle sticky trap in the maize field. Additionally, the different orchard proportions are shown in the landscapes.

The landscape composition was characterised by the proportion of the different landscape elements embedded in a circle buffer with a 500 m radius surrounding the maize fields. In addition, spring and summer characterisations of the landscape composition were conducted to incorporate the seasonal variations of the proportions of cereals in spring and winter cereal-fallows in summer. The landscape composition was described each year by direct field observations, an orthophoto from the Plan Nacional de Ortografía Aérea (PNOA), and geographical information maps of the Instituto Geográfico Nacional of Spain. Then, we quantified the proportions of the landscape elements using ArcGIS software 10.3.1 (ESRI, 2015). Next, the 34 landscape elements initially identified in the study were grouped into eight categories: orchards, summer and winter cereals, winter cereal-fallow, alfalfa, non-crop habitats, forest and edges (Table 1 and Fig. 1b) (Appendix A.2).

Table 1. Landscape structure and local variables used in this study.

Variables	**Categories**	**Description**
Landscape structure	Winter cereals	Proportion of winter cereal (mainly wheat and barley)
	Winter cereal-fallow	Proportion of fallow when winter crop is end (fields under no crop rotation)
	Summer cereals	Proportion of summer cereal (mainly maize)
	Orchard	Proportion of fruits orchards, figs, citrus, dried fruit, vineyard and olive
	Alfalfa	Proportion of alfalfa
	Edges	Proportion of the margin strip (see (Marshall and Moonen, 2002)
	Non-crop habitats	Proportion of no productive areas, longer fallows, natural habitat and waterland
	Forest	Proportion of forest repopulate of *Pinus halepensis*
	SHDI-L	Shannon diversity index calculated as landscape diversity in the buffers
Local environment	SHDI-E	Shannon diversity index calculated in edges between maize and neighbouring crops*(Marshall and Moonen, 2002)
	Maize phenology	Stage of maize development (Ritchie *et al*, 1986)
	Perimeter/area	Perimeter to area ratio of the sampled maize field (m^{-1})
	Prey/Predator	Abundance of mainly prey and predator by each group of insects

The landscape configuration was characterised by landscape diversity (hereinafter SHDI-L). SHDI-L was calculated as a function of the proportional abundance of each landscape element type, Li, using FRAGSTAT (McGarigal et al., 2012) as follows:

$$\text{SHDI-L} = -\sum_{i=1}^{34} L_i \times lnL_i$$

2.3. Local variables

Local variables included the maize phenology, perimeter to area of the maize fields, Shannon index in maize field edges (hereinafter SHDI-E), and abundance of potential predators (for the study of herbivore species) and potential prey (for the study of predators) (Appendix A.3). In recent years, maize is variably sown in the early (March-April) or late season (at the end of June); consequently, we sampled both early (17 fields in 2016 and 18 fields in 2017) and late sown maize fields (6 fields in 2015 and 2016 and 5 fields in 2017). Maize phenology was recorded at each sampling date according to Ritchie et al. (1992). The perimeter to area of the maize fields was calculated using ArcGIS software. The SHDI-E index was calculated from flora surveys carried out in the edges between the maize and neighbouring fields (orchards, alfalfa or maize) during May and June in 2016 and 2017. In addition, for each sampling point, the cover-abundance of weed species was recorded using the Braun-Blanquet scale (1979) in three rectangular plots (2×5 m^2) along the edges. Then, the cover-abundance values were transformed into the mean value of the percent cover according to each field, and we calculated the Shannon index as a function of the proportional weed species abundances, E_i:

SHDI-E $= -\sum_{i=1}^{52} \mathrm{E}i \times \ lnE_i$

In addition, we used floristic surveys of the edge cover compositions to transform the cover abundance of species into the mean value of the percent cover according to three types of edges (maize-orchard, maize-alfalfa and maize-maize), calculated the Shannon index (hereinafter H'), and grouped the recorded plant species as dicotyledons or monocotyledons.

Autocorrelation can be a problem for classical statistical tests, such as regression, which rely on independently distributed errors (Legendre, 1993), as it may lead to erroneous conclusions regarding the significance of covariates in studies of species-environment relationships (Wagner and Fortin, 2005). Therefore, the degree of correlation between variables was assessed through a Spearman rank correlation between landscape composition, landscape configuration and local variables (Appendix A.4). According to Campbell and Swinscow (2009), some variables were weakly to moderately correlated (Spearman's rho<0.59), but they were not excluded to build the models as done by Schmidt et al. (2019).

2.4. Yellow trap catches of herbivores and predators

The abundance of insects in maize fields was estimated using yellow sticky traps (30 ×25 cm, Serbios, Badia Polesine, Italy). Samplings were conducted once a month, and the traps were left active for 1 week. In each field, we placed 3 traps on stakes at the crop canopy height, depending on the growth stage, along a transect perpendicular to the nearest edge (approx. 30 m), with the traps 15 m away from each other (Albajes et al., 2013). The traps were then collected and conserved at 6-8°C until insect identification. Individuals were identified at the family, genus or species level depending on their state of conservation. Vouchers of individuals identified at species level were deposited in the laboratory of Entomology of the University of Lleida.

2.5. Statistical analyses

The effects of the landscape structure and local variables on the insect abundance on maize were analysed separately for each of the two seasons—spring and summer. We used a linear mixed-effects model with the ‘year’ as the random structure for each mode using the ‘nlme’ package (Pinheiro et al., 2018) for R software (R Development Core Team, 2018). For each field and sampling date, the mean number of each insect taxa selected for identification per trap was log transformed [log10(x+1)] to achieve, as much as possible, a normal distribution of the model residual. In addition, we tested the spatial autocorrelation in the abundance of insects among all fields using Moran’s I statistic (Paradis, 2019) (Appendix A.5). We standardised (mean centred and scaled) landscape metrics for each model using the ‘caret’ package (Max et al., 2018). We applied a multi-model inference approach to obtain a robust parameter estimate using the ‘MuMIn’ package (Bartoń, 2018). The dredge function of the models was used to describe the effects of independent variables on each dependent variable. Models were selected by comparing the Akaike information criterion (AICc) with the values of the full model. Model averaging was performed on the model while set to ΔAICc < 2 (Burnham and Anderson, 2004). The model residuals were graphically inspected with qqplot and histogram graphics to ensure no violation of normality and homoscedasticity assumptions (Zuur et al., 2010). Finally, we used the ‘effects’ package (Fox et al., 2016) to represent the effects in partial residual plots.

3. Results

A total of 316,564 insects were trapped on 585 yellow sticky traps in 52 maize fields during the three years of the study: 39,539 in 2015 (*n* = 6 fields), 201,775 in 2016 (*n* = 23) and 75,250 in 2017 (*n* = 23). The identified taxa were: *Coccinella septempunctata* (L.), *Empoasca vitis* (Göethe), *Hippodamia variegata* (Goeze), *Frankliniella occidentalis* (Pergande), *Laodelphax striatellus* (Fallén), *Propylea quatuordecimpunctata* (L.) and *Zyginidia scutellaris* (Herrich-Schäffer), *Aeolothrips* *spp.*, *Nabis spp.*, *Orius spp.*, and *Stethorus spp.* At the family level, Aphididae, Chrysopidae, Miridae, Staphylinidae, Syrphidae and other Thripidae species (other than *F. occidentalis*) were identified. The insect abundances varied between seasons and especially were higher for herbivores in spring (Fig. 2). The most abundant herbivore was *F. occidentalis*, followed by *Z. scutellaris*, other Thripidae and Aphididae (Fig. 2). In the case of predators, *Aeolothrips spp.* was the most abundant, followed by Syrphidae, *Stethorus* spp. and *Orius* spp. (Fig. 2). Models of Nabidae and *H. variegata* were not considered because of their low abundance. Miridae were also not considered because of their extremely diverse feeding regimes. Models of Nabidae, *H. variegata* and Miridae can be observed in Appendix B.

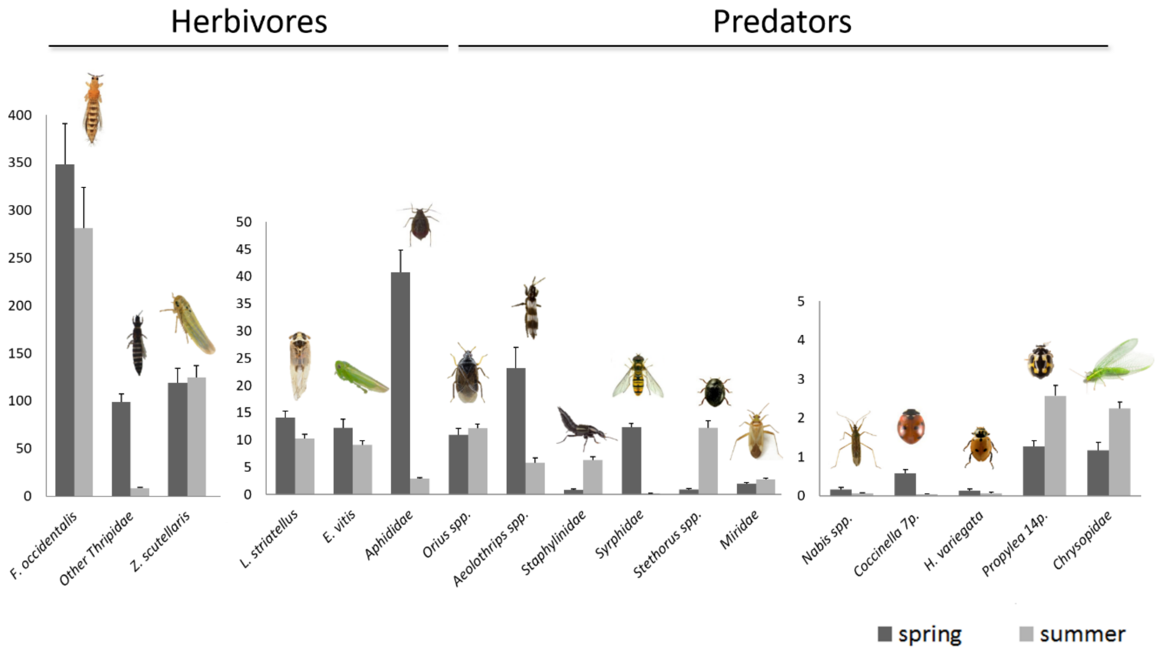

Fig. 2. Abundances of herbivores and predators trapped during the study in spring and summer.

3.1. Flora abundance and composition survey in maize field edges

A total of 190 weed species were identified in the maize field edges. The most abundant monocotyledon species were: *Hordeum murinum* (L.), *Sorghum halepense* (L.), *Poa annua* (L.), *Cynodon dactylon* (L.), *Avena sterilis* (L.) and *Lolium rigidum* (Gaudin). In the case of dicotyledons, the most abundant species were: *Malva sylvestris* (L.), *Taraxacum officinale* (L.), *Capsella bursa-pastoris* (L.), *Sonchus oleraceus* (L.), *Chenopodium album* (L.) and *Veronica arvensis* (L.). The edges between the maize and orchards showed the highest plant cover (80%) (Fig. 3a) and a dominance of dicotyledons (80%) (Fig. 3b). On the other hand, the edges between maize and alfalfa had low plant cover (48.97%) but the highest H’ (1.7) (Fig. 3a). Finally, the edges between maize fields had the lowest H’ (1.66) (Fig. 3a) and the highest proportion of monocotyledons (30%) (Fig. 3b).

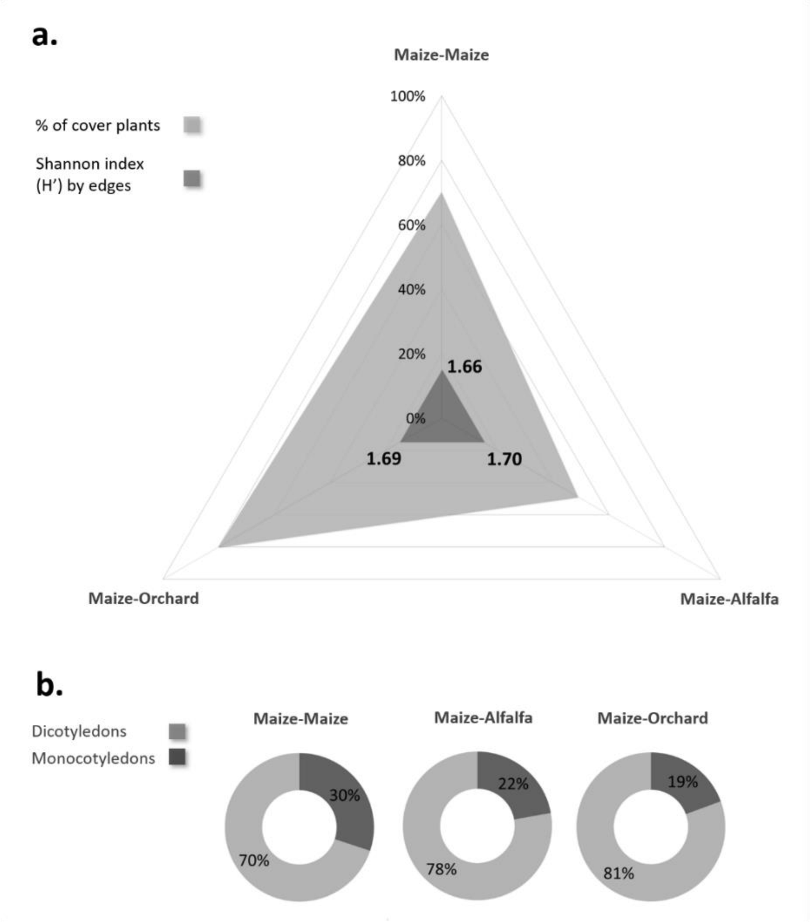

Fig. 3. Flora abundance and composition survey in maize field edges. A. Mean percentage of edge cover by flora in sampled maize fields and H’ according to field neighbouring crop. B. Flora were grouped into dicotyledons and monocotyledons.

3.2. Responses of insects to landscape structure variables

Most of the parsimonious models for predators and herbivores are shown in Appendix B (1 and 2, respectively). The results with only significant variables for predators are shown in Table 2 and for herbivores in Table 3. Overall, the abundance of insects was influenced by the landscape structure, with a characteristic seasonal pattern. The landscape variables with higher effects on the insect abundance were the proportion of alfalfa, orchard and edges. Alfalfa was the variable that was most positively related to insect abundances. Especially, in summer, the alfalfa had positive effects on the abundance of aphids and their predators and also on the herbivore thrips (*Frankliniella occidentalis* and other Thripidae) (Fig. 4). In addition, the proportion of orchards was the variable with more negative effects on insect abundances. In Fig.5 it can be seen that orchards were negatively related to two predators in spring, but in summer, they were positively related to two herbivores. In spring, the edges were positively related to *Orius spp*., the main generalist predator in this area, and to *Z. scutellaris,* this predator's main (Fig. 6). Overall, the proportion of cereals in the landscape was poorly related to insects. The winter cereal was positively related to two specialist predators in spring, and the maize was negatively related to *L. striatellus* in summer. In addition, some semi-natural habitats (forest and non-crop habitat) had a minor impact on the abundance of predators and herbivores.

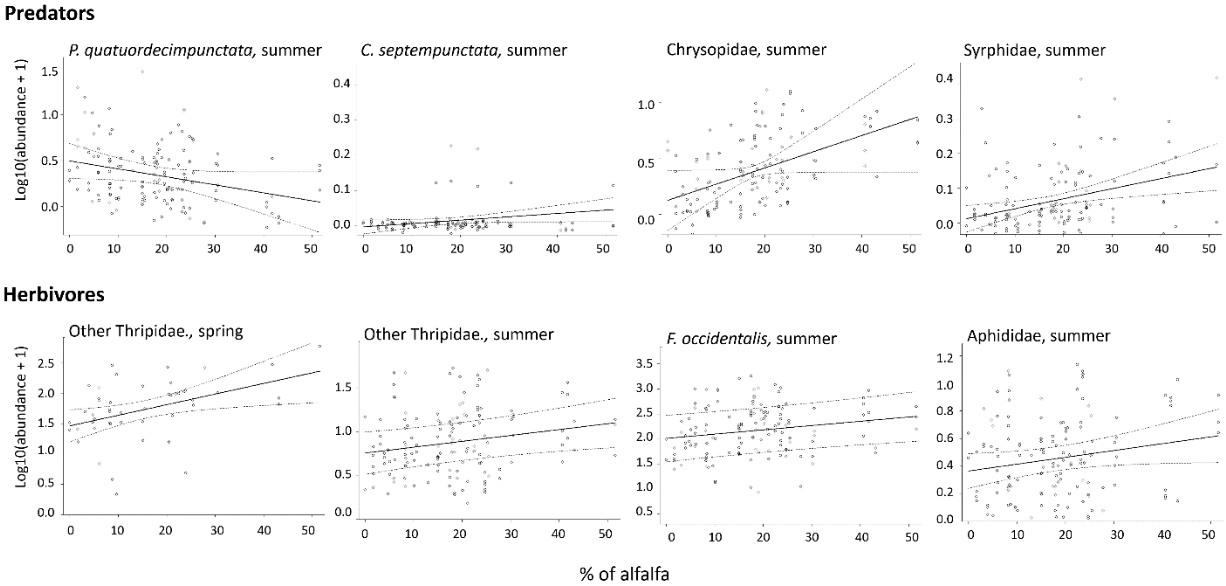

Fig. 4. Effects of the proportion of alfalfa (spring and summer) on the abundance of predators (*P. quatuordecimpunctata*, *C. septempunctata*, Chrysopidae, Syrphidae) and herbivores (other Thripidae, *F. occidentalis* and Aphididae).

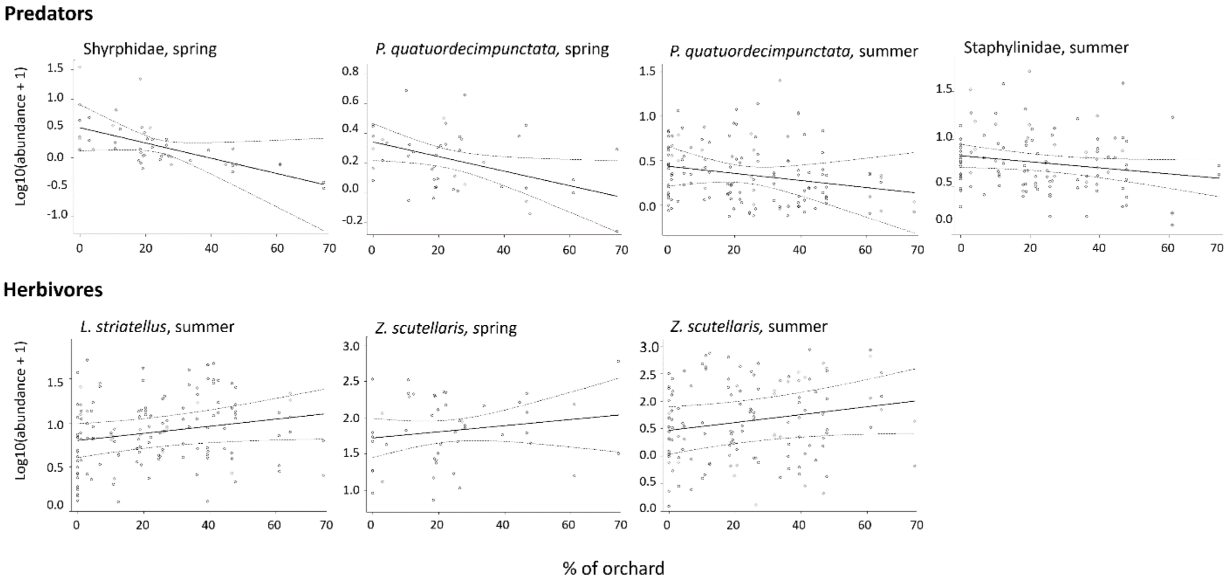

Fig. 5. Effects of the percentage of orchard (spring and summer) in the landscape on the abundance of predators (*P. quatuordecimpunctata*, Staphylinidae, Syrphidae) and herbivores (*Z. scutellaris* and *L. striatellus).*

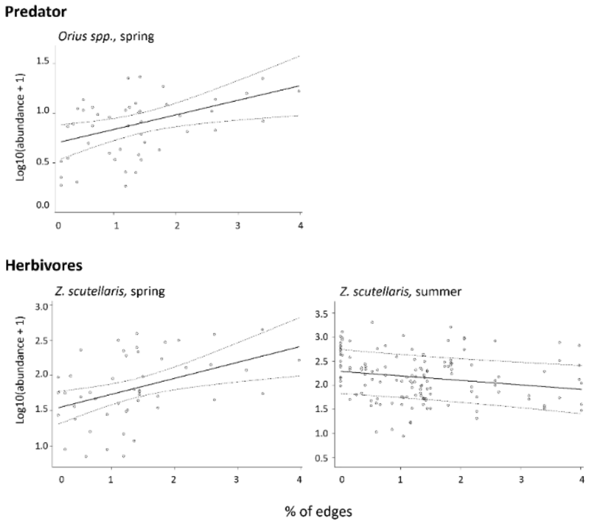

Fig. 6. Effects of the proportion of edges in the landscape on the abundance of the predator *Orius spp.* and its main prey, *Z. scutellaris.*

Table 2. Model results of the best models relating predator abundance with landscape and local variables. Significant variables in the best models (ΔAIC < 2) are presented. Variables are standardised (mean-centred and scaled). Relative importance is the sum of Akaike's weight associated with the variables in the best models.

	Spring season					**Summer season**				
Specie/Group	**Variables**	**Est.**	**z value**	**Pr(>|z|)**	**Relative importance**	**Variables**	**Est.**	**z value**	**Pr(>|z|)**	**Relative importance**
Orius spp.	(Intercept)	-2,78	3,34	<0.001		(Intercept)	0,26	0,50	0,61	
	Edges	0,29	2,33	0,019	1	Prey	0,32	7,01	<0.001	1
	Prey	0,77	5,56	<0.001	1	SHDI-E	-0,30	4,62	<0.001	1
	Maize phenology	0,88	7,30	<0.001	1					
Nabidae	(Intercept)	1,93	3,85	0,0001		(Intercept)	-0,06	0,79	0,429	
	Prey	-0,29	3,84	0,0001	1	Prey	0,03	2,14	0,0325	1
Miridae	n.a.					(Intercept)	0,90	3,58	0,0003	
						SHDI-E	-0,23	3,84	<0.001	1
						SHDI-L	0,18	2,49	0,013	1
						Maize phenology	-0,11	2,00	0,046	0,96
Stethorus spp.	(Intercept)	0,31	3,85	<0.001		(Intercept)	1,60	5,95	<0.001	
	Maize phenology	-0,12	2,10	0,036	1	Forest	-0,22	2,00	0,045	1
	Winter cereal	0,15	2,45	0,014	1	Non-crop habitat	0,31	2,19	0,028	1
						Maize phenology	0,33	3,31	<0.001	1
						SHDI-L	-0,29	2,07	0,038	0,89
P. quatuordecimpu	(Intercept)	0,52	6,48	<0.001		(Intercept)	0,86	5,72	<0.001	
	Maize phenology	0,31	3,70	<0.001	1	Alfalfa	-0,20	2,27	0,023	1
	Orchard	-0,19	1,93	0,05	0,66	Edges	-0,33	4,35	<0.001	1
						Maize phenology	-0,24	3,59	<0.001	1
						Orchard	-0,18	2,23	0,025	0,59
						Summer cereal	0,18	0,07	0,01	0,41
C. septempunctata	n.a.					(Intercept)	0,01	0,21	0,83	
						Alfalfa	0,02	2,30	0,021	1
H. variegata	(Intercept)	0,58	2,61	0,009		(Intercept)	0,02	0,75	0,454	
	Prey	-0,14	2,02	0,044	1	Maize phenology	-0,05	3,69	0,000	1
Staphylinidae	(Intercept)	-0,54	0,90	0,36		(Intercept)	-0,37	0,96	0,33	
	Prey	0,70	5,03	<0.001	1	Forest	0,18	2,16	0,031	1
	p/a	-0,26	2,71	0,006	1	Prey	0,35	4,58	<0.001	1
	Maize phenology	-0,29	3,74	<0.001	1	p/a	-0,22	2,56	0,011	1
						SHDI-E	-0,21	2,43	0,015	1
						Edges	0,19	2,01	0,044	0,85
						Orchard	-0,17	1,98	0,048	0,64
Aeolothrips spp.	(Intercept)	0,85	1,15	0,25		(Intercept)	-0,71	3,00	0,002	
	Forest	-0,34	2,42	0,015	1	Prey	0,37	7,96	<0.001	1
	Prey	0,33	2,44	0,014	1	Maize phenology	-0,25	3,46	<0.001	1
	p/a	0,39	2,59	0,009	1	Summer cereal	0,24	3,45	<0.001	1
						Fallow-winter cereal	0,15	2,27	0,023	1
Chrysopidae	(Intercept)	0,40	1,99	0,046		(Intercept)	0,82	8,79	<0.001	
	SHDI-L	-0,23	3,12	0,001	1	Edges	-0,16	2,34	0,019	1
	Winter cereal	0,18	2,58	0,009	1	Non-crop habitat	0,30	3,02	0,002	1
	Maize phenology	0,13	1,99	0,046	0,19	p/a	0,14	2,07	0,038	1
						Alfalfa	0,35	2,04	0,041	0,11
Syrphidae	(Intercept)	0,56	3,72	<0.001		(Intercept)	0,03	1,00	0,31	
	Orchard	-0,33	2,08	0,038	0,76	Alfalfa	0,04	2,23	0,025	1
						Prey	0,09	3,62	<0.001	1
						SHDI-L	-0,04	1,96	0,049	0,74

Table 3. Model results of the best models relating herbivore abundance with landscape and local variables. Significant variables in the best models (ΔAIC < 2) are presented. Variables are standardised (mean-centred and scaled). Relative importance is the sum of Akaike's weight associated with the variables in the best models.

	Spring season					**Summer cereal season**				
Specie/Group	**Variables**	**Est.**	**z value**	**Pr(>|z|)**	**Relative importance**	**Variables**	**Est.**	**z value**	**Pr(>|z|)**	**Relative importance**
Frankliniella spp.	(Intercept)	2,59	2,05	0,04		(Intercept)	2,14	3,04	0,002	
	Predator	0,64	2,55	0,011	1	Alfalfa	0,24	2,66	0,007	1
						Edges	-0,24	2,19	0,028	1
						Predator	0,91	8,68	<0.001	1
						Maize phenology	-0,51	4,92	<0.001	1
						SHDI-E	0,41	4,11	<0.001	1
						SHDI-L	-0,25	2,00	0,045	1
						Fallow-winter cereal	-0,18	2,01	0,044	1
Other Thripidae	(Intercept)	3,39	3,44	<0.001		(Intercept)	0,12	0,32	0,74	
	Maize phenology	-0,67	3,95	<0.001	1	Alfalfa	0,17	2,35	0,018	1
	Alfalfa	0,46	2,56	0,011	0,96	Predator	0,61	6,89	<0.001	1
						Maize phenology	-0,36	4,24	<0.001	1
						SHDI-E	0,17	2,10	0,035	0,84
						SHDI-L	-0,18	1,95	0,051	1
						Fallow-winter cereal	-0,21	2,73	0,006	1
Z. scutellaris	(Intercept)	2,27	2,63	0,008		(Intercept)	2,24	3,95	<0.001	
	Edges	0,47	2,75	0,005	1	Edges	-0,32	2,21	0,02	1
	Predator	0,60	2,22	0,026	1	Predator	0,49	3,27	0,001	1
	Winter cereal	-0,41	2,30	0,021	0,64	Orchard	0,29	2,30	0,021	1
	Orchard	0,42	1,91	0,05	0,51	p/a	0,29	2,32	0,021	1
						Maize phenology	-0,57	4,11	<0.001	1
						SHDI-E	0,26	2,00	0,045	0,77
E. vitis	(Intercept)	1,86	4,28	<0.001		(Intercept)	0,86	2,51	0,012	
	Non-crop habitat	0,57	2,59	0,009	1	Predator	0,40	4,18	<0.001	1
	Maize phenology	-0,35	2,16	0,031	1	p/a	0,20	2,31	0,021	1
	SHDI-L	-0,44	2,03	0,042	1					
L. striatellus	(Intercept)	0,62	0,72	0,47		(Intercept)	1,41	4,12	<0.001	
	Predator	0,56	2,32	0,02	1	p/a	0,20	2,54	0,011	1
	Maize phenology	0,39	2,44	0,014	1	Maize phenology	-0,37	4,26	<0.001	1
						Predator	0,25	2,73	0,006	0,92
						Non-crop habitat	-0,25	2,22	0,026	0,81
						Summer cereal	-0,30	2,51	0,012	0,67
						Orchard	0,28	2,06	0,039	0,61
Aphididae	(Intercept)	2,96	6,72	<0.001		(Intercept)	1,02	7,63	<0.001	
	Maize phenology	-0,97	5,70	<0.001	1	Maize phenology	-0,14	2,33	0,02	1
						Alfalfa	0,13	1,96	0,05	0,83

3.3. Responses of insects to local variables

The local variables had important effects in both insect groups. Especially, the variables related to the maize phenology and the predator-prey relationship on maize had high effects on insect abundances (see more parsimonious models for predators and herbivores in Appendix 1 and 2 and the significant variables in Tables 1 and 2, respectively). The results show that predators depended more on phenology in spring and herbivores in summer. In addition, the perimeter/area of maize fields was positively related to herbivores and especially SHDI-E (a descriptor of flora diversity in the maize edges) was negatively related to *Orius spp.* (Fig. 7) but positively related to its main preys in summer.

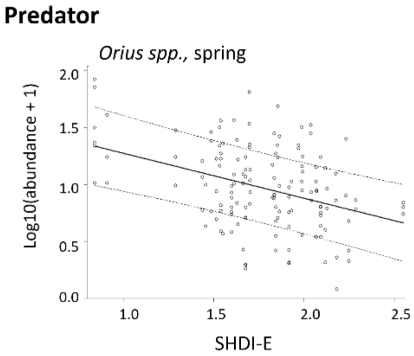

Fig. 7. Effect of SHDI-E on the abundance of the predator *Orius spp*.

4. Discussion

As initially hypothesised, the proportions of orchards and alfalfa fields in the buffer were the most influential landscape variables for maize insect abundance (Fig. 8). We report for the first time results of the effects of orchard cultivation on herbivore and predator species in neighbouring Mediterranean maize crops. Specifically, the proportion of orchards in the landscape had a negative effect on the aphid predators, such as *P. quatuordecimpunctata* and Syrphidae, as well as on Staphylinidae, the second most abundant generalist predator in maize in both seasons. Some authors have seen similar negative relationships between the orchard surfaces and predator abundance (Samnegård et al., 2018; Yang et al., 2018, 2019). Aviron et al. (2016) concluded that intensively managed orchards had negative effects on the amount of natural colonisation of vegetable crops by predatory mirid bugs coming from surrounding plots. In addition, Markó et al. (2017) reported that the toxic effect of chemicals on predators in orchards was masked by the continuous immigration of predators from surrounding crops, mainly arable crops, which explains why the proximity of orchards is associated with a lower amount of aphid predators in arable crops. Indeed, the influence of orchard management practices on natural enemies has been supported by data showing that their abundance and diversity were higher in organic than in non-organic orchards (Happe et al., 2019).

In contrast to the observations for predators, the abundance of some herbivores on maize fields was positively related to the proportion of orchards, a feature especially relevant for two homopteran maize pests, *L. striatellus* (in summer) and *Z. scutellaris* (in both seasons). These two homopterans mainly feed on Poaceae, that is, on orchard ground cover (Wang et al., 2009), which provides greater coverage in comparison with the edges close to the maize fields. Orchard ground cover could act as an abundant source of the two species for surrounding crops, as Frei and Mahnhart (1992) found. The close and positive relationship between the orchard proportion and *L. striatellus* abundance on maize is particularly relevant because that is the main vector of Maize Rough Dwarf Virus (MRDV), a common disease in the area (Achon et al., 2013). In the case of *Z. scutellaris*, its higher abundance on maize relative to the higher orchard proportion in the landscape could have positive consequences for maize, as *Z. scutellaris* has been identified as a key prey to facilitate the early establishment of *Orius spp.* on maize (Albajes et al., 2011).

The alfalfa surface was a source of predators for maize, mainly aphid predators in summer, confirming the results of previous studies conducted at the field level in the area (Madeira et al., 2014; Núñez, 2002; Pons et al., 2005). Continuous predator movement of Coccinellidae between alfalfa and maize has been shown in the area in summer and, facilitated by regular alfalfa cutting in the season, explains the positive relationship between the proportion of alfalfa in the landscape and the abundance of those predators on maize (di Lascio et al., 2016). The same explanation can be extended to the other aphid predators found on that crop (Madeira et al., 2014; Madeira and Pons, 2015). However, the abundance of maize aphids was found to be related to the proportion of alfalfa, although the two crops do not share aphid species (Asín and Pons, 1998; Pons et al., 2005; Madeira et al., 2014). A possible reason could be the common presence of aphids on *S. halepense* (an invasive weed that is increasingly abundant in agricultural habitats (Juárez-Escario et al., 2018), which grows permanently around irrigation sprinklers in alfalfa fields, and it has been observed as a source of aphid migration from alfalfa to maize. In fact, it is a relevant feature for the epidemiology of *Maize Dwarf Mosaic Virus* (MDMV) and *Sugarcane Mosaic Virus* (SCMV), two important maize viruses vectored by Poaceae aphids (Achon et al., 1996; Peerzada et al., 2017) from the common virus reservoir. Additionally, the proportion of alfalfa is also related to the abundance in both seasons of *F. occidentalis* and other herbivores of the Thripidae family on maize. Although thrips rarely are damaging to these crops in this area (Meissle et al., 2010), they serve as prey for some predators such as *Orius spp.* The abundance of *Orius spp.* on maize was significantly related to the amount of potential prey on that crop but not on the alfalfa, according to a previous study in the area (Ardanuy et al., 2018). As reported by these authors, the role of alfalfa in relation to maize is to provide it with an abundant amount of prey to enhance *Orius* spp. establishment (Madeira et al., 2018). We need more studies to test if the positive effect of alfalfa on predator abundances can be hampered by the orchard surface.

Edges constitute a non-permanent habitat in the landscape of the study area, especially in annual crops. We did not find weed diversity differences between sampled edges but we found different weed covers that could be more important than the diversity in these habitats. The positive relationship between the edges and the abundance of *Z. scutellaris* and *Orius* spp. is similar to previous results describing the role of edges as a source for both species in the early season (Ardanuy et al., 2018). Thus, the presences of edges are a feature that allows the early establishment of the predator-prey system on the crop and prevents the later development of pest populations in this area, as Albajes et al. (2011) found. Later, the negative relationship of *Z. scutellaris* and the proportion of edges in summer is probably because edges become dry, and these species prefer the irrigated cover of orchards.

Summer and winter cereals are important components of the landscape in our study region. The proportions of cereals in the buffers studied varied from 0.4% to 50.6% in spring (winter cereal) and 11.2% to 57.1% in summer (mostly maize). However, few relationships were found between insect abundance and the proportion of summer cereals, so that the phenomena of the concentration or dilution of resources do not seem to play an important role in the study area, at least for most of the insects studied, as found by other authors (Otway et al., 2005). Only in the case of *L. striatellus*, for which a negative relationship between its abundance and maize surface in the area was found in summer, can a resource dilution mechanism be postulated, perhaps due to the slow insect population increase during the later development stages of the crop. In contrast, the increased abundance of predators such as *Aeolothrips* spp. And *P. quatuordecimpunctata* may be the consequence of higher prey densities resulting from the concentration of developed maize in the landscape in summer. However, this potential mechanism would require further studies. The influence of the proportion of winter cereals on maize insects may occur in spring due to the role of these winter crops as overwintering sites or as a base for early population increase of some insects. In summer, these insects may come from fallows that remain in fields that are not sown again with a summer crop after winter cereal harvesting. *Zyginidia scutellaris* was the only maize herbivore insect related to the amount of winter cereal, and that relationship was significantly negative in spring. This result contrasts with that reported by Ardanuy et al. (2018), who found a significantly positive relationship between the amount of winter cereals and abundance of *Z. scutellaris* on maize in spring. In this case, the authors included the field edges with the surface of winter cereals, which could be the source of the leafhopper for maize in spring. Instead, the greater presence of aphid predators on maize, such as Chrysopidae, in spring could be attributed to the greater abundance of winter cereals because aphids are abundant on winter cereals in spring in the area (Lumbierres et al., 2007). In addition, the greater amount of *Stethorus* spp. On maize in spring in areas with a higher proportion of winter cereals can be explained by the potential abundance of tetranychid mites (Burgio et al., 2004).

Non-crop habitats have classically been regarded to enhance the abundance and diversity of natural enemies in the landscape and therefore serve as pest population suppressors (Bianchi et al., 2006 and the review by Gurr et al. (2017)). In this study, the non-crop habitat proportion detected was between 0% min and 26%. However, few significant relationships between the abundance of insects on maize and the proportion of non-crop habitats in the landscape were found. In addition, the low diversity flora of herbaceous plants in non-crop habitats and in edges could have an effect on the maize insects that overwinter in trees or bushes, such as *E. vitis*, as shown by Decante and van Helden (2006). The significantly positive relationship found for the proportion of non-crop habitats and some predators could indicate the roles these non-crop habitats play as a source of predators in our latitudes, although only for a few predatory species. However, this limited role of non-crop habitats may complement the role played by the habitats categorised as edges that have been mentioned above. Forest habitats were a poor source of predators because the diversity of tree species (mostly *P. halepensis*) was low. The forest proportion detected in the buffers showed rather low variation, between 0% and 11.2%. In fact, one of the reasons proposed to explain the limited contribution of non-agricultural habitats on pest suppression has been the relative low proportion of these habitats in the landscape as has been hypothesised by Tscharntke et al. (2016). On the other hand, we need more studies to test whether the low effect of semi-natural habitats and edges on predator abundances can be hampered by the orchard surface as found by Ricci et al. (2019).

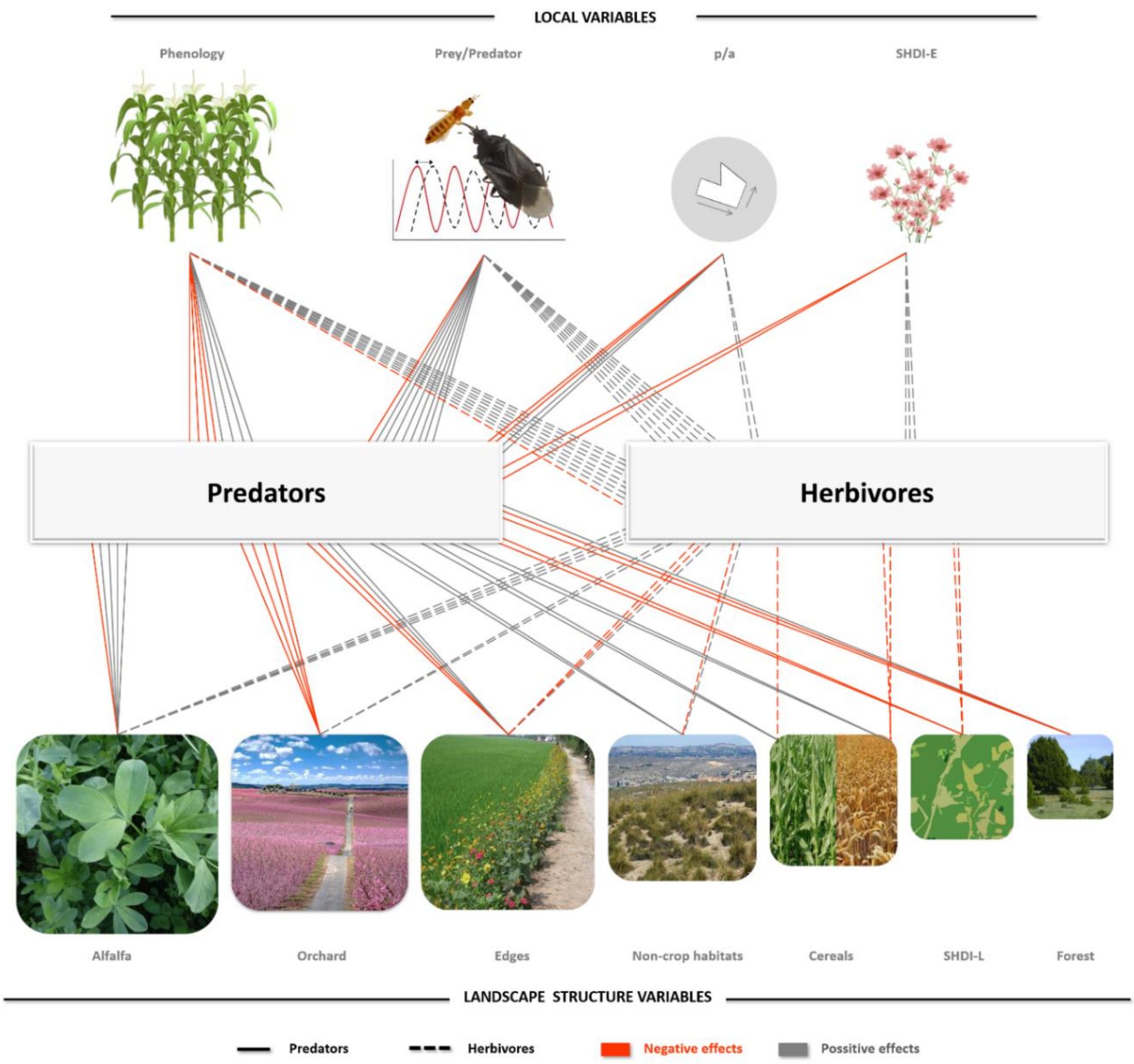

Fig. 8. Significant effects of local and landscape structure variables on each insect group detected. Size of squares indicates the number of relations of the variables with predators or herbivores group.

The landscape diversity, as expressed by the Shannon diversity index in the landscape (SHDI-L), showed six significant relationships with maize insects (3 predators and 3 herbivores), all of which were negative. However, much literature on the relationships between landscape diversity and ecosystem services has reported positive values (see the review by Rusch et al., 2016). Some other authors, however, have indicated that landscape diversity itself is not a meaningful characteristic that affects biological control services and pest suppression (f.i. Martin et al., 2016; Rusch et al., 2016;

Tscharntke et al., 2016; Landis, 2017; Karp et al., 2018). A deeper analysis is probably necessary to understand the relationships between landscape diversity and pest suppression (Médiène et al., 2011; Chisholm et al., 2014).

Local variables of sampled maize fields modulated the influence of the landscape on the abundance of the maize insects (Fig. 8). The maize growth stage was the most influential local variable. Most of the significant relationships for predators were positive in spring and negative in summer (abundance of predators increased or decreased, respectively, as the season progressed), whereas the relationships were mostly negative for herbivores (herbivore abundance mostly decreased along both seasons). These insect abundance-crop phenology relationships should prevent us from making definitive conclusions about how the surrounding landscape affects crop insect abundance because this landscape and insect abundance relationship may have temporal patterns rather than being permanent (Raymond et al., 2015) for aphids and their predators. Additionally, coupled predator-prey relationships on the crop were also the most significant variable. Predator-prey relationships may alter the influence of the landscape on crop insect abundance, as seen in this study and in which several of the predators and herbivores recorded were positively related with the abundance of their potential prey and predators, respectively, a feature reported by others (Ardanuy et al., 2018). Other local variables, such as the relation of the perimeter to the area and the diversity in maize field edges, play lesser roles than landscape variables on predators but are noticeable in herbivore insects in summer.

5. Conclusions

1. Landscapes dominated by orchards could highly negatively impact the abundance of predators on maize, likely as a result of the intensive management of orchards. In contrast, orchards are a relevant source of homopterans due to the presence of Poaceae in orchard ground cover, especially for vectors of maize virus species.

2. The presence of alfalfa in the agricultural landscape enhances the abundance of aphids and their predators in maize crops. Alfalfa also enhances herbivore thrips but not their common predators, such as *Orius* spp. and *Aeolothrips* spp.

3. The presence of edges is a relevant feature, especially in the early establishment of prey-predator system of *Z. scutellaris* and *Orius* spp. in spring.

4. Semi-natural habitats (non-crop habitats and forest) and landscape diversity play minor role in determining the abundance of insects in Mediterranean maize crops.

5. Local variables contribute greatly to explaining insect abundance, especially maize growth stages and the abundance of prey or predators.

The results of the present study allow the improvement of maize management practices and the arrangement of landscape composition to enhance biological pest control by the conservation of naturally occurring predators. However, further tests of whether the low effects of semi-natural habitats on naturally occurring predators are due to the intensive orchard management are necessary.

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Author contribution
G.C.O. collected the data, contributed data and analysis tools, performed the analysis and wrote the paper. F.M. contributed to study design, collected the data and revised the final version. I.B. and S.S collected the data. A.J.E collected the data and revised the final version. R.A. contributed to study design, collected the data, wrote the paper and revised the final version. All authors read and approved the final version of the manuscript.

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Appendix A

1. Specific information on coordinates, area size and sampling date for selected maize fields.

Site	Year	Latitude	Longitude	Field area (ha)	1 sampling	2 sampling	3 sampling	4 sampling	5 sampling
1	2015	41.5964056	0.49829722	4.78	16-June	14-jul	10-August	31-August	
2	2015	41.7637278	0.48048889	8.26	16-June	15-jul	10-August	31-August	
3	2015	41.6813139	0.4143	6.39	16-June	16-jul	10-August	31-August	
4	2015	41.7374056	0.47555556	2.10	16-June	17-jul	10-August	31-August	
5	2015	41.7005917	0.36340278	5.43	16-June	18-jul	10-August	31-August	
6	2015	41.7247139	0.33173889	8.99	16-June	19-jul	10-August	31-August	
7	2016	41.7255639	0.50210556	10.02		6-July	10-August	5-September	
8	2016	41.5841333	0.52859722	3.54		6-July	10-August	5-September	
9	2016	41.5964056	0.49829722	1.19		6-July	10-August	5-September	
10	2016	41.6157278	0.46467778	4.78		6-July	10-August	5-September	
11	2016	41.7758694	0.41687222	2.26		6-July	10-August	5-September	
12	2016	41.8012833	0.45139444	2.13	8-June	6-July	10-August	5-September	
13	2016	41.6158667	0.29285	0.90	8-June	6-July	10-August	5-September	
14	2016	41.7637278	0.48048889	8.26	8-June	6-July	10-August	5-September	
15	2016	41.6413028	0.46846389	2.56	8-June	6-July	10-August	5-September	
16	2016	41.6298361	0.40223333	7.00	8-June	6-July	10-August	5-September	
17	2016	41.6813139	0.4143	6.39	8-June	6-July	10-August	5-September	
18	2016	41.6476667	0.36586944	3.12	8-June	6-July	10-August	5-September	
19	2016	41.6424778	0.54061667	2.03	8-June	6-July	10-August	5-September	
20	2016	41.7374056	0.47555556	2.10		6-July	10-August	5-September	
21	2016	41.5857222	0.45993056	6.13	8-June	6-July	10-August	5-September	
22	2016	41.6091889	0.41255	6.89	8-June	6-July	10-August	5-September	
23	2016	41.6128111	0.35600278	4.84	8-June	6-July	10-August	5-September	
24	2016	41.6758	0.38911667	4.57	8-June	6-July	10-August	5-September	
25	2016	41.7005917	0.36340278	5.43	8-June	6-July	10-August	5-September	
26	2016	41.5852111	0.42567222	10.71	8-June	6-July	10-August	5-September	
27	2016	41.8014694	0.50940278	2.30	8-June	6-July	10-August	5-September	
28	2016	41.7001278	0.43849444	5.00	8-June	6-July	10-August	5-September	
29	2016	41.7247139	0.33173889	8.99	8-June	6-July	10-August	5-September	
30	2017	41.7255639	0.50210556	10.00			10-August	6-September	4-October
31	2017	41.5841333	0.52859722	3.54			10-August	6-September	4-October
32	2017	41.5964056	0.49829722	1.19			10-August	6-September	4-October
33	2017	41.6157278	0.46467778	4.78			10-August	6-September	4-October
34	2017	41.7758694	0.41687222	2.26	08-may	22-June	10-August	6-September	
35	2017	41.8034167	0.45074167	2.68			10-August	6-September	4-October
36	2017	41.7779667	0.50997222	13.68	08-may	22-June	10-August	6-September	
37	2017	41.7637278	0.48048889	8.42	09-may	22-June	10-August	6-September	
38	2017	41.6413028	0.46846389	2.56	10-may	22-June	10-August	6-September	
39	2017	41.5284861	0.54404167	12.96	11-may	22-June	10-August	6-September	
40	2017	41.6298361	0.40223333	3.82	12-may	22-June	10-August	6-September	
41	2017	41.6813139	0.4143	5.67	13-may	22-June	10-August	6-September	
42	2017	41.6476667	0.36586944	3.12	14-may	22-June	10-August	6-September	
43	2017	41.6424778	0.54061667	2.03			10-August	6-September	4-October
44	2017	41.7374056	0.47555556	2.10	14-may	22-June	10-August	6-September	
45	2017	41.5851583	0.45881667	1.38	15-may	22-June	10-August	6-September	
46	2017	41.6091889	0.41255	6.80	16-may	22-June	10-August	6-September	
47	2017	41.6752111	0.38916944	4.64	17-may	22-June	10-August	6-September	
48	2017	41.7016917	0.36513611	3.68	18-may	22-June	10-August	6-September	
49	2017	41.5855361	0.42595556	7.54	19-may	22-June	10-August	6-September	
50	2017	41.7996694	0.50986389	4.26	20-may	22-June	10-August	6-September	
51	2017	41.7001278	0.43849444	9.05	21-may	22-June	10-August	6-September	
52	2017	41.7247139	0.33173889	8.99	22-may	22-June	10-August	6-September	

Appendix A

2. Summary statistics (mean, SE, minimum and maximum) of landscape proportion variables in spring and summer (alfalfa, winter cereal, fallow-winter cereal, summer cereal, orchard, edges, non-crop habitat and forest), perimeter to area in maize fields (m^{-1}), Shannon index (SHDI-L and SHDI-E) and maize phenology (stage of development followed Ritchie *et al.* 1992). Variables were measured around each selected maize field in 500m of radii circle in northern Spain in 2015, 2016 and 2017.

	Variable	Mean	Max.	Min.	SE
Spring	Alfalfa	16.56	51.58	0.00	2.18
	Winter cereal	22.86	50.65	0.37	2.38
	Summer cereal	19.26	49.93	0.00	2.24
	Orchard	22.95	74.41	0.00	3.07
	Edges	1.46	3.98	0.15	0.17
	Non-crop habitat	8.45	25.96	0.90	0.90
	Forest	2.10	11.24	0.00	0.59
	p/a	0.02	0.08	0.01	0.00
	SHDI-L	1.71	2.15	0.87	0.05
	SHDI-E	1.91	2.55	1.44	0.05
	Maize phenology		VT-R1	V3-V5	
Summer	Alfalfa	17.34	51.58	0.00	1.56
	Fallow-winter cereal	9.57	40.39	0.00	1.31
	Summer cereal	31.83	57.08	11.23	2.05
	Orchard	23.74	74.41	0.00	2.73
	Edges	1.36	4.02	0.15	0.15
	Non-crop habitat	8.80	33.07	0.32	0.91
	Forest	1.90	11.24	0.00	0.47
	p/a	0.03	0.08	0.01	0.00
	SHDI-L	1.67	2.15	0.87	0.04
	SHDI-E	1.79	2.55	0.84	0.05
	Maize phenology		R5-R6	V6-V13	

Appendix A

3. The abundances of potential predators (for herbivores) and abundances of potential prey (for predators) trapped with sticky yellow traps and it used as local variables in the models.

Potential predator	Potential prey (herbivores)
P. quatuordecimpunctata	Aphididae
C. septempunctata	Aphididae
Chrysopidae	Aphididae
Syrphidae	Aphididae
H. variegata	Aphididae
Stethorus spp.	Specialist of *Tetranychus spp*. No included any prey in the model
Orius spp.	Aphididae, *F. occidentalis*, other Thripidae, *Z. scutellaris, E. vitis* and *L. striatellus*
Staphylinidae	Aphididae, *F. occidentalis*, other Thripidae, *Z. scutellaris, E. vitis* and *L. striatellus*
Aeolothrips spp.	*F. occidentalis* and other Thripidae
Nabidae	Aphididae, *F. occidentalis*, other Thripidae, *Z. scutellaris*, *E. vitis* and *L. striatellus*
Miridae	Phytophagous. No included any prey in the model

Appendix A

4. Correlations between variables

Spearman rank correlation coefficients (Spearman's rho) between landscape composition, landscape structure and local environment within 500m diameter landscape buffer around sampled maize fields. Significant at: * $p < 0.05$; ** $p < 0.01$.

Spring season	Alfalfa	Winter cereal	Summer cereal	Orchard	Edges	Non-crop habitat	Forest	SHDI-L	Maize phenology	SHDI-E	p/a
Alfalfa	1										
Winter cereal	-0.12	1									
Summer cereal	-0.04	-0.14	1								
Orchard	-0.51**	-0.33*	-0.42**	1							
Edges	-0.20	-0.03	-0.05	0.12	1						
Non-crop habitat	-0.25	-0.11	-0.24	0.08*	0.08	1					
Forest	0.17	-0.22	-0.25	0.09	0.19	0.05	1				
SHDI-L	-0.15	0.21	-0.18	-0.17	0.28**	0.63**	0.20	1			
Maize phenology	-0.08	-0.01	-0.09	0.17	-0.15	0.17	-0.01	0.06	1		
SHDI-E	-0.04	0.16	0.22	-0.24*	-0.03	-0.05	0.09	0.13	-0.08	1	
p/a	-0.14	0.06	-0.06	-0.07	0.39**	0.40**	-0.01	0.33**	-0.04	0.04	1

Summer season	Alfalfa	Fallow-winter cereal	Summer cereal	Orchard	Edges	Non-crop habitat	Forest	SHDI-L	Maize phenology	SHDI-E	p/a
Alfalfa	1										
Fallow-winter cereal	-0.01	1									
Summer cereal	-0.13*	0.18	1								
Orchard	-0.37**	-0.46**	-0.64**	1							
Edges	-0.18*	-0.18*	-0.05	0.15	1						
Non-crop habitat	-0.35**	-0.12	-0.18*	0.10*	0.19**	1					
Forest	0.23**	-0.07	-0.28	-0.04	-0.07	0.05	1				
SHDI-L	-0.15	-0.12	-0.34**	0.11**	0.34**	0.63**	0.27	1			
Maize phenology	-0.01	-0.10	0.08	-0.06	-0.22	0.12	0.10	-0.01	1		
SHDI-E	-0.03	-0.29	-0.08	0.03	0.12	0.24**	0.33**	0.41**	0.24	1	
p/a	-0.15	0.04	-0.06	0.04*	0.37**	0.23	-0.19	0.27**	-0.09	-0.01	1

Values of |rho| ≤ 0.39, 0.4 and 0.59, ≥ were considered respectively as weak and moderate (Campbell & Swinscow 2009).

Campbell, M.J. & Swinscow, T.D.V. (2009) *Statistics at Square One*, 11th Edition. Wiley-Blackwell, Chichester, West Sussex.

Appendix A

5. Moran's Index (correlation coefficient) calculated in predator and herbivores groups sampled with sticky yellow traps in 52 points during 3 years in northeastern Spain.

	Specie/Group	**Moran's I (observed)**	***p*-value**
Predators	*Orius spp.*	-0.0257	0.9127
	Stethorus spp.	0.0233	0.4459
	P. quatuordecimpunctata	0.0676	0.1252
	C. septempunctata	-0.0410	0.6843
	Staphylinidae	-0.0612	0.4814
	Aeolothrips spp.	-0.0923	0.1103
	Chrysopidae	-0.0200	0.9948
	Syrphidae	0.0091	0.4516
	Nabidae	-0.0183	0.9612
	H. variegata	-0.0087	0.7838
	Miridae	0.0004	0.7327
Herbivores	*Frankliniella spp.*	-0.0246	0.9256
	Other Thripidae	0.0752	0.1013
	Z. scutellaris	-0.0180	0.9788
	E. vitis	-0.0630	0.4565
	L. striatellus	0.0523	0.2255
	Aphididae	-0.0083	0.8439

Appendix B

1. Most parsimonious model results of the best models explaining predator abundance (log10(x+1) transformed). All variables present in the best models (ΔAIC < 2) are presented; significant *p* values are in bold characters. Abundance was calculated as average of three traps by field, 6 fields in 2015 and 23 fields in 2016 and 2017. All explanatory variables are standardised (mean-centred and scaled).

	Spring season							**Sumer season**						
Specie/Group	**Variables best model**	**Est.**	**SE**	**z**	**Pr(>|z|)**	**Relative importance**	**N containing model**	**Variables best model**	**Est.**	**SE**	**z**	**Pr(>|z|)**	**Relative importance**	**N containing model**
Orius spp.	(Intercept)	-2.78	0.81	3.34	0.000828			(Intercept)	0.26	0.51	0.50	0.6166		
	Edges	**0.29**	**0.12**	**2.33**	**0.019992**	**1**	**2**	**Prey**	**0.32**	**0.05**	**7.01**	**< 2e-16**	**1**	**15**
	Prey	**0.77**	**0.13**	**5.56**	**3.00E-08**	**1**	**2**	**SHDI-E**	**-0.30**	**0.06**	**4.62**	**3.80E-06**	**1**	**15**
	Maize phenology	**0.88**	**0.12**	**7.30**	**< 2e-16**	**1**	**2**	Orchard	-0.11	0.06	1.83	0.0675	0.77	11
	Forest	-0.22	0.12	1.85	0.064499	0.69	1	Edges	0.11	0.07	1.55	0.1208	0.57	8
								Non-crop habitat	0.07	0.06	1.04	0.2979	0.13	2
								Alfalfa	-0.07	0.07	1.02	0.31	0.13	3
								Forest	0.07	0.07	1.03	0.3033	0.12	2
								Fallow-winter cereal	0.09	0.06	1.36	0.1742	0.11	2
								SHDI-L	0.06	0.07	0.84	0.3999	0.11	2
								p/a	-0.05	0.06	0.73	0.4658	0.06	1
Stethorus spp.	(Intercept)	0.31	0.08	3.85	0.000117			(Intercept)	1.60	0.27	5.95	< 2e-16		
	Maize phenology	**-0.12**	**0.06**	**2.10**	**0.036098**	**1**	**5**	**Forest**	**-0.22**	**0.11**	**2.00**	**0.045489**	**1**	**6**
	Winter cereal	**0.15**	**0.06**	**2.45**	**0.014466**	**1**	**5**	**Non-crop habitat**	**0.31**	**0.14**	**2.19**	**0.028752**	**1**	**6**
	SHDI-L	-0.08	0.08	1.02	0.306267	0.3	2	**Maize phenology**	**0.33**	**0.10**	**3.31**	**0.000947**	**1**	**6**
	Edges	-0.05	0.06	0.90	0.366216	0.17	1	**SHDI-L**	**-0.29**	**0.14**	**2.07**	**0.038312**	**0.89**	**5**
	Forest	-0.05	0.06	0.78	0.437193	0.16	1	SHDI-E	0.18	0.11	1.63	0.103758	0.7	4
	Non-crop habitat	0.12	0.08	1.47	0.141906	0.14	1	Orchard	-0.17	0.09	1.83	0.067859	0.6	3
								Summer cereal	0.15	0.11	1.39	0.164354	0.25	2
								Alfalfa	0.15	0.10	1.44	0.150366	0.12	1
P. quatuordecimp	(Intercept)	0.52	0.08	6.48	< 2e-16			(Intercept)	0.86	0.15	5.72	< 2e-16		
	Maize phenology	**0.31**	**0.08**	**3.70**	**0.000218**	**1**	**9**	**Alfalfa**	**-0.20**	**0.09**	**2.27**	**0.023353**	**1**	**9**
	Orchard	**-0.19**	**0.10**	**1.93**	**0.053668**	**0.66**	**5**	**Edges**	**-0.33**	**0.08**	**4.35**	**1.37E-05**	**1**	**9**
	Edges	0.12	0.08	1.50	0.134001	0.45	4	**Maize phenology**	**-0.24**	**0.07**	**3.59**	**0.000328**	**1**	**9**
	Alfalfa	-0.16	0.09	1.69	0.09027	0.4	3	SHDI-L	0.13	0.08	1.72	0.086029	0.61	5
	Summer cereal	0.11	0.08	1.34	0.17946	0.15	2	**Orchard**	**-0.18**	**0.08**	**2.23**	**0.025961**	**0.59**	**6**
	Forest	0.08	0.08	0.96	0.337007	0.08	1	**Summer cereal**	**0.18**	**0.07**	**2.58**	**0.009838**	**0.41**	**3**
								Prey	-0.12	0.09	1.30	0.194234	0.38	4
								Fallow-winter cereal	-0.12	0.08	1.38	0.166718	0.18	2
								p/a	0.04	0.07	0.53	0.599448	0.08	1
C. septempunctat	(Intercept)	0.48	0.24	1.95	0.0507			(Intercept)	0.00	0.02	0.21	0.832		
	Non-crop habitat	-0.16	0.09	1.67	0.0951	0.66	11	**Alfalfa**	**0.02**	**0.01**	**2.30**	**0.0215**	**1**	**7**
	Forest	-0.13	0.09	1.50	0.1343	0.41	7	Prey	0.02	0.01	1.67	0.0954	0.84	6
	Orchard	-0.11	0.08	1.24	0.2152	0.18	3	Summer cereal	0.01	0.01	1.04	0.2971	0.13	1
	Alfalfa	0.11	0.09	1.21	0.2262	0.26	5	Orchard	-0.01	0.01	0.94	0.3479	0.13	1
	SHDI-L	0.12	0.11	1.05	0.293	0.11	2	Non-crop habitat	-0.01	0.01	0.93	0.3506	0.13	1
	Prey	0.05	0.06	0.89	0.3749	0.09	2	Forest	-0.01	0.01	0.60	0.5469	0.1	1
	Winter cereal	0.09	0.09	1.03	0.3038	0.09	2	Edges	-0.01	0.01	0.52	0.6022	0.1	1
Staphylinidae	(Intercep	-0.54	0.58	0.90	0.365992			(Intercep	-0.37	0.38	0.96	0.3373		
	Prey	**0.70**	**0.14**	**5.03**	**5.00E-07**	**1**	**11**	**Forest**	**0.18**	**0.08**	**2.16**	**0.0308**	**1**	**9**
	p/a	**-0.26**	**0.09**	**2.71**	**0.006684**	**1**	**11**	**Prey**	**0.35**	**0.08**	**4.58**	**4.70E-06**	**1**	**9**
	Maize phenology	**-0.29**	**0.07**	**3.74**	**0.000184**	**1**	**11**	**p/a**	**-0.22**	**0.09**	**2.56**	**0.0106**	**1**	**9**
	Edges	-0.15	0.08	1.87	0.062003	0.61	6	**SHDI-E**	**-0.21**	**0.09**	**2.43**	**0.0152**	**1**	**9**
	SHDI-L	0.17	0.09	1.83	0.066619	0.61	6	Maize phenology	-0.20	0.11	1.88	0.0607	0.86	8
	Winter cereal	0.10	0.08	1.31	0.188725	0.22	3	**Edges**	**0.19**	**0.09**	**2.01**	**0.0442**	**0.85**	**7**
	SHDI-E	0.09	0.07	1.26	0.208818	0.17	2	**Orchard**	**-0.17**	**0.08**	**1.98**	**0.0482**	**0.64**	**5**
	Non-crop habitat	-0.13	0.10	1.35	0.176119	0.1	1	Alfalfa	-0.15	0.09	1.70	0.0892	0.41	3
	Orchard	-0.12	0.07	1.57	0.116711	0.08	1	Non-crop habitat	0.11	0.08	1.33	0.1843	0.19	2
								Summer cereal	0.15	0.09	1.65	0.0998	0.19	2

Appendix B

Continue 1.

	Spring season							Sumer season						
Specie/Group	Variables best model	Est.	SD	z	Pr(>|z|)	Relative importance	N containing model	Variables best model	Est.	SD	z	Pr(>|z|)	Relative importance	N containing model
Chrysopidae	(Intercept)	0.40	0.20	1.99	0.04682			(Intercept)	0.82	0.09	8.79	< 2e-16		
	SHDI-L	**-0.23**	**0.07**	**3.12**	**0.00178**	**1**	**8**	**Edges**	**-0.16**	**0.07**	**2.34**	**0.01912**	**1**	**16**
	Winter cereal	**0.18**	**0.07**	**2.58**	**0.00982**	**1**	**8**	**Non-crop habitat**	**0.30**	**0.10**	**3.02**	**0.00254**	**1**	**16**
	Forest	0.10	0.07	1.42	0.15627	0.35	3	**p/a**	**0.14**	**0.07**	**2.07**	**0.03847**	**1**	**16**
	Edges	0.09	0.07	1.27	0.20415	0.31	3	Orchard	0.21	0.24	0.85	0.39557	0.62	10
	Maize phenology	**0.13**	**0.07**	**1.99**	**0.04677**	**0.19**	**6**	SHDI-L	-0.14	0.08	1.70	0.0901	0.57	8
	Alfalfa	0.09	0.07	1.25	0.21021	0.18	2	Prey	0.11	0.08	1.26	0.20954	0.3	5
								Summer cereal	0.27	0.25	1.07	0.28536	0.26	5
								Fallow-winter cereal	0.17	0.17	0.94	0.34592	0.26	3
								Forest	-0.05	0.07	0.79	0.42844	0.14	3
								Alfalfa	**0.35**	**0.17**	**2.04**	**0.04151**	**0.11**	**2**
Syrphidae	(Intercept)	0.56	0.15	3.72	0.0002			(Intercept)	0.03	0.03	1.00	0.315352		
	Orchard	**-0.33**	**0.16**	**2.08**	**0.038**	**0.76**	**16**	**Alfalfa**	**0.04**	**0.02**	**2.23**	**0.025919**	**1**	**10**
	Alfalfa	0.27	0.14	1.83	0.0679	0.56	12	**Prey**	**0.09**	**0.02**	**3.62**	**0.000292**	**1**	**10**
	Non-crop habitat	-0.21	0.12	1.60	0.1091	0.45	10	**SHDI-L**	**-0.04**	**0.02**	**1.96**	**0.049613**	**0.74**	**7**
	Maize phenology	-0.16	0.12	1.26	0.2068	0.31	8	Forest	-0.02	0.02	1.25	0.212244	0.27	3
	SHDI-L	-0.22	0.12	1.69	0.0919	0.27	6	Non-crop habitat	-0.03	0.02	1.21	0.225286	0.26	3
	Summer cereal	-0.17	0.14	1.19	0.2336	0.13	3	p/a	-0.02	0.02	1.12	0.263375	0.18	2
	Winter cereal	-0.21	0.14	1.40	0.1609	0.09	2	Fallow-winter cereal	0.01	0.02	0.64	0.524696	0.08	1
	Prey	-0.11	0.10	1.17	0.2432	0.03	1	Maize phenology	-0.01	0.02	0.62	0.538462	0.08	1
	SHDI-E	0.13	0.11	1.10	0.2711	0.03	1	Orchard	-0.01	0.02	0.53	0.599379	0.08	1
Aeolothrips spp.	(Intercept)	0.85	0.72	1.15	0.25007			(Intercept)	-0.71	0.23	3.00	0.002678		
	Forest	**-0.34**	**0.14**	**2.42**	**0.01573**	**1**	**4**	**Prey**	**0.37**	**0.05**	**7.96**	**< 2e-16**	**1**	**8**
	Prey	**0.33**	**0.13**	**2.44**	**0.01475**	**1**	**4**	**Maize phenology**	**-0.25**	**0.07**	**3.46**	**0.000533**	**1**	**8**
	p/a	**0.39**	**0.15**	**2.59**	**0.00962**	**1**	**4**	**Summer cereal**	**0.24**	**0.07**	**3.45**	**0.000559**	**1**	**8**
	SHDI-E	-0.16	0.14	1.15	0.25049	0.23	1	**Fallow-winter cereal**	**0.15**	**0.06**	**2.27**	**0.023068**	**1**	**8**
	Edges	-0.15	0.15	0.97	0.33125	0.18	1	Forest	-0.12	0.07	1.75	0.079378	0.77	6
	Alfalfa	-0.14	0.15	0.92	0.35763	0.17	1	SHDI-L	0.13	0.07	1.84	0.066066	0.77	6
								p/a	0.11	0.06	1.65	0.098715	0.61	5
								Edges	-0.08	0.07	1.01	0.312484	0.19	2
								Orchard	0.07	0.11	0.69	0.487675	0.09	1
Nabidae	(Intercept)	1.93	0.49	3.85	0.000119			(Intercept)	-0.06	0.07	0.79	0.429		
	Prey	**-0.29**	**0.07**	**3.84**	**0.000124**	**1**	**5**	**Prey**	**0.03**	**0.01**	**2.14**	**0.0325**	**1**	**7**
	Winter cereal	-0.10	0.06	1.68	0.092569	0.71	4	Alfalfa	0.03	0.02	1.86	0.0635	0.88	6
	p/a	0.05	0.06	0.83	0.405554	0.14	1	p/a	-0.01	0.02	0.65	0.518	0.12	2
	Forest	-0.05	0.06	0.87	0.386231	0.13	1	Edges	-0.01	0.02	0.59	0.5569	0.12	1
	SHDI-L	0.04	0.06	0.69	0.491456	0.12	1	Fallow-winter cereal	0.01	0.02	0.60	0.5505	0.12	1
								Non-crop habitat	-0.01	0.02	0.56	0.5767	0.12	1
								Summer cereal	0.01	0.02	0.51	0.6138	0.11	1
Miridae	(Intercept)	0.95	0.29	3.14	0.00169			(Intercept)	0.90	0.25	3.58	0.000349		
	Non-crop habitat	-0.15	0.10	1.48	0.13983	0.32	3	**SHDI-E**	**-0.23**	**0.06**	**3.84**	**0.000125**	**1**	**21**
	Summer cereal	-0.11	0.10	1.04	0.29916	0.16	2	**SHDI-L**	**0.18**	**0.07**	**2.49**	**0.012834**	**1**	**21**
	p/a	-0.08	0.10	0.80	0.42378	0.08	1	**Maize phenology**	**-0.11**	**0.05**	**2.00**	**0.04594**	**0.96**	**20**
	SHDI-E	0.08	0.10	0.81	0.4163	0.07	1	Orchard	0.11	0.08	1.37	0.171541	0.54	11
	Maize phenology	0.08	0.10	0.77	0.44164	0.14	2	Non-crop habitat	-0.10	0.07	1.34	0.18059	0.35	8
	Winter cereal	0.07	0.10	0.68	0.4972	0.07	1	Alfalfa	0.10	0.07	1.32	0.187083	0.28	6
	Alfalfa	0.08	0.10	0.76	0.44877	0.07	1	p/a	0.06	0.05	1.07	0.285957	0.28	7
	SHDI-L	-0.06	0.10	0.58	0.56387	0.07	1	Fallow-winter cereal	-0.07	0.06	1.14	0.253781	0.17	4
								Summer cereal	0.04	0.13	0.30	0.761093	0.17	4
H. variegata	(Intercept)	0.58	0.22	2.61	0.00903			(Intercept)	0.02	0.03	0.75	0.453747		
	Prey	**-0.14**	**0.07**	**2.02**	**0.04374**	**1**	**13**	**Maize phenology**	**-0.05**	**0.01**	**3.69**	**0.000222**	**1**	**16**
	Maize phenology	-0.15	0.11	1.28	0.20062	0.28	4	Prey	0.03	0.02	1.75	0.080755	0.78	12
	Non-crop habitat	-0.12	0.09	1.27	0.20277	0.23	3	SHDI-E	-0.02	0.01	1.47	0.142096	0.45	7
	Orchard	-0.11	0.09	1.21	0.22645	0.22	3	Orchard	-0.02	0.01	1.40	0.162412	0.28	4
	Edges	-0.10	0.09	1.04	0.30065	0.12	2	Summer cereal	0.02	0.01	1.28	0.201567	0.18	3
	Summer cereal	0.09	0.09	0.99	0.32131	0.07	1	Forest	0.01	0.02	0.89	0.37391	0.14	3
	SHDI-E	0.08	0.09	0.91	0.36329	0.06	1	Fallow-winter cereal	0.01	0.01	0.77	0.438942	0.05	1
	p/a	-0.08	0.09	0.90	0.36806	0.06	1	Alfalfa	0.01	0.01	0.54	0.590857	0.04	1
	Forest	-0.08	0.09	0.87	0.38272	0.06	1	Non-crop habitat	-0.01	0.01	0.48	0.632022	0.04	1

Appendix B

2. Most parsimonious model results of the best models explaining herbivores abundance (log10(x+1) transformed). All variables present in the best models (ΔAIC < 2) are presented; significant *p* values are in bold characters. Abundance was calculated as average of three traps by field, 6 fields in 2015 and 23 fields in 2016 and 2017. All explanatory variables are standardised (mean-centred and scaled).

	Spring season							**Summer season**						
Specie/Group	**Variables best model**	**Estimate**	**SE**	**z**	**Pr(>|z|)**	**Relative importance**	**N containing model**	**Variables best model**	**Estimate**	**SE**	**z**	**Pr(>|z|)**	**Relative importance**	**N containing model**
F. occidentalis	(Intercept)	2.59	1.23	2.05	0.0404			(Intercept)	2.14	0.70	3.04	0.00234		
	Predator	**0.64**	**0.25**	**2.55**	**0.0107**	**1**	**6**	**Alfalfa**	**0.24**	**0.09**	**2.66**	**0.00782**	**1**	**4**
	SHDI-E	-0.32	0.17	1.88	0.0602	0.76	4	**Edges**	**-0.24**	**0.11**	**2.19**	**0.02827**	**1**	**4**
	Summer cereal	-0.24	0.17	1.35	0.1769	0.53	4	**Predator**	**0.91**	**0.10**	**8.68**	**< 2e-16**	**1**	**4**
	Alfalfa	0.22	0.17	1.28	0.2012	0.42	3	**Maize phenology**	**-0.51**	**0.10**	**4.92**	**8.70E-07**	**1**	**4**
								SHDI-E	**0.41**	**0.10**	**4.11**	**3.94E-05**	**1**	**4**
								SHDI-L	**-0.25**	**0.13**	**2.00**	**0.04505**	**1**	**4**
								Fallow-winter cereal	**-0.18**	**0.09**	**2.01**	**0.04491**	**1**	**4**
								p/a	0.16	0.09	1.75	0.08052	0.62	2
								Non-crop habitat	0.17	0.12	1.37	0.17199	0.44	2
Other Thripidae	(Intercept)	3.39	0.97	3.44	0.000584			(Intercept)	0.12	0.37	0.32	0.74777		
	Maize phenology	**-0.67**	**0.16**	**3.95**	**7.69E-05**	**1**	**15**	**Alfalfa**	**0.17**	**0.07**	**2.35**	**0.01895**	**1**	**4**
	Alfalfa	**0.46**	**0.17**	**2.56**	**0.010429**	**0.96**	**14**	**Predator**	**0.61**	**0.09**	**6.89**	**< 2e-16**	**1**	**4**
	Forest	-0.33	0.17	1.82	0.068755	0.51	7	**Maize phenology**	**-0.36**	**0.08**	**4.24**	**2.25E-05**	**1**	**4**
	Predator	0.40	0.26	1.49	0.13644	0.39	6	**SHDI-E**	**0.17**	**0.08**	**2.10**	**0.03559**	**0.84**	**3**
	SHDI-L	0.23	0.17	1.35	0.177258	0.27	4	**SHDI-L**	**-0.18**	**0.09**	**1.95**	**0.05114**	**1**	**4**
	Non-crop habitat	0.24	0.17	1.38	0.166606	0.23	3	**Fallow-winter cereal**	**-0.21**	**0.08**	**2.73**	**0.00637**	**1**	**4**
	p/a	0.20	0.17	1.13	0.257585	0.17	3	Non-crop habitat	0.10	0.10	1.02	0.3097	0.23	1
	Orchard	-0.28	0.20	1.38	0.16715	0.08	2	Summer cereal	-0.05	0.08	0.64	0.52573	0.17	1
Z. scutellaris	(Intercept)	2.27	0.84	2.63	0.00861			(Intercept)	2.24	0.56	3.95	7.70E-05		
	Edges	**0.47**	**0.17**	**2.75**	**0.00591**	**1**	**14**	**Edges**	**-0.32**	**0.14**	**2.21**	**0.0272**	**1**	**3**
	Predator	**0.60**	**0.26**	**2.22**	**0.02679**	**1**	**14**	**Predator**	**0.49**	**0.15**	**3.27**	**0.00106**	**1**	**3**
	Winter cereal	**-0.41**	**0.17**	**2.30**	**0.02172**	**0.64**	**8**	**Orchard**	**0.29**	**0.13**	**2.30**	**0.02173**	**1**	**3**
	Maize phenology	0.30	0.17	1.73	0.08386	0.62	8	**p/a**	**0.29**	**0.13**	**2.32**	**0.02061**	**1**	**3**
	Orchard	**0.42**	**0.21**	**1.91**	**0.05649**	**0.51**	**8**	**Maize phenology**	**-0.57**	**0.14**	**4.11**	**3.99E-05**	**1**	**3**
	Alfalfa	0.31	0.19	1.58	0.11535	0.18	3	**SHDI-E**	**0.26**	**0.13**	**2.00**	**0.04536**	**0.77**	**2**
	Summer cereal	-0.22	0.16	1.28	0.19988	0.16	2	Fallow-winter cereal	0.10	0.15	0.69	0.48807	0.23	1
	Forest	0.25	0.19	1.32	0.18616	0.14	2							
	p/a	0.19	0.18	1.04	0.29868	0.11	2							
L. striatellus	(Intercept)	0.62	0.83	0.72	0.4703			(Intercept)	1.41	0.34	4.12	3.73E-05		
	Predator	**0.56**	**0.23**	**2.32**	**0.0201**	**1**	**8**	**p/a**	**0.20**	**0.08**	**2.54**	**0.01122**	**1**	**33**
	Maize phenology	**0.39**	**0.16**	**2.44**	**0.0149**	**1**	**8**	**Maize phenology**	**-0.37**	**0.09**	**4.26**	**2.07E-05**	**1**	**33**
	Edges	0.28	0.15	1.81	0.0703	0.76	6	**Predator**	**0.25**	**0.09**	**2.73**	**0.00625**	**0.92**	**30**
	SHDI-E	0.19	0.15	1.24	0.2148	0.23	2	**Non-crop habitat**	**-0.25**	**0.11**	**2.22**	**0.02615**	**0.81**	**29**
	Summer cereal	0.18	0.15	1.14	0.2557	0.1	1	**Summer cereal**	**-0.30**	**0.12**	**2.51**	**0.01208**	**0.67**	**22**
	SHDI-L	-0.17	0.16	1.06	0.2898	0.1	1	**Orchard**	**0.28**	**0.13**	**2.06**	**0.03908**	**0.61**	**20**
	Non-crop habitat	-0.15	0.15	0.97	0.3312	0.1	1	SHDI-L	0.18	0.11	1.67	0.09474	0.59	20
	Orchard	-0.14	0.15	0.88	0.381	0.09	1	SHDI-E	-0.13	0.09	1.42	0.15645	0.44	16
								Forest	-0.15	0.09	1.69	0.09165	0.43	13
								Alfalfa	0.15	0.10	1.48	0.13884	0.3	10
								Fallow-winter cereal	-0.08	0.11	0.74	0.46008	0.14	5
								Edges	-0.07	0.09	0.80	0.42317	0.02	1
E. vitis	(Intercept)	1.86	0.43	4.28	1.87E-05			(Intercept)	0.86	0.34	2.51	0.012		
	Non-crop habitat	**0.57**	**0.21**	**2.59**	**0.00953**	**1**	**7**	**Predator**	**0.40**	**0.10**	**4.18**	**2.95E-05**	**1**	**23**
	Maize phenology	**-0.35**	**0.16**	**2.16**	**0.03058**	**1**	**7**	**p/a**	**0.20**	**0.09**	**2.31**	**0.0208**	**1**	**23**
	SHDI-L	**-0.44**	**0.21**	**2.03**	**0.04265**	**1**	**7**	SHDI-E	-0.15	0.09	1.70	0.0896	0.73	16
	Summer cereal	-0.25	0.16	1.48	0.13832	0.26	1	Edges	-0.16	0.10	1.67	0.0942	0.67	15
	Forest	-0.20	0.16	1.20	0.23113	0.22	2	Maize phenology	-0.12	0.09	1.31	0.1891	0.45	11
	Winter cereal	0.23	0.17	1.35	0.17606	0.17	1	Forest	0.12	0.09	1.29	0.1968	0.32	7
	Predator	0.29	0.24	1.17	0.24329	0.13	1	Orchard	0.07	0.08	0.91	0.3612	0.23	7
	p/a	0.20	0.17	1.11	0.26518	0.12	1	Summer cereal	-0.06	0.08	0.79	0.4301	0.09	3
Aphididae	(Intercept)	2.96	0.43	6.72	<2e-16			(Intercept)	1.02	0.13	7.63	<2e-16		
	Maize phenology	**-0.97**	**0.17**	**5.70**	**<2e-16**	**1**	**16**	**Maize phenology**	**-0.14**	**0.06**	**2.33**	**0.02**	**1**	**15**
	SHDI-E	-0.28	0.17	1.67	0.0952	0.6	10	**Alfalfa**	**0.13**	**0.06**	**1.96**	**0.0504**	**0.83**	**12**
	SHDI-L	0.21	0.17	1.16	0.2463	0.6	10	Non-crop habitat	0.13	0.08	1.54	0.1245	0.38	5
	Edges	-0.29	0.17	1.67	0.0945	0.58	9	SHDI-L	-0.12	0.08	1.57	0.117	0.2	3
	Summer cereal	-0.26	0.17	1.49	0.137	0.46	7	Orchard	-0.10	0.09	1.09	0.2752	0.16	3
	Predator	-0.20	0.18	1.04	0.2966	0.09	2	SHDI-E	-0.06	0.06	1.03	0.3052	0.13	2
	Winter cereal	0.16	0.16	0.96	0.3372	0.08	2	p/a	0.05	0.06	0.79	0.4301	0.11	2
	Alfalfa	0.14	0.17	0.81	0.4207	0.04	1	Forest	0.05	0.06	0.74	0.4624	0.1	2
								Summer cereal	-0.13	0.08	1.62	0.1055	0.06	1
								Predator	0.04	0.07	0.60	0.5485	0.05	1
								Edges	-0.04	0.07	0.59	0.5573	0.05	1

Chapter 3

Early planting, management of edges and non-crop habitats reduce potyvirus infection in maize

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Early planting, management of edges and non-crop habitats reduce potyvirus infection in maize

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Abstract

Viruses are a limiting factor in maize production areas around the world. The knowledge of the interactions between agroecosystems and the virus-vector-host system is limited, but a landscape-scale approach could help fill this gap. In this study, we show how the use of multiple spatial scales, i.e., 200, 500 and 1000 m, is a novel methodology for explaining the incidence of two closely related potyviruses: maize dwarf mosaic virus and sugarcane mosaic virus. To determine the factors involved in virus incidence, we recorded the proportion of surrounding crops and non-crop habitats at the landscape scale and, at the field scale, we recorded the planting date, the maize field area, the crop rotation and the weed diversity in the edges. In addition, we estimated the numbers of aphids with sticky yellow traps. Virus incidence in maize and in alternative grass hosts was determined by DAS-ELISA. Generalised linear mixed models were fitted using the multimodel inference method. The results showed that the most predictive model for the incidence of both potyviruses was at a scale of 200 m, but for the aphid abundance, it was at a scale of 500 m. Maize dwarf mosaic virus incidence was most affected by field management, and sugarcane mosaic virus by landscape variables. The **p**lanting date and the weed diversity in the edges were the field variables with the highest positive effects on both potyviruses. Moreover, both viruses were positively related to the abundance of aphids, and maize dwarf mosaic virus was only related to the cover of Johnsongrass in the edges. Non-crop habitats had negative effects on potyvirus incidence at all spatial scales, showing that biodiversity in the landscape decreases the incidence of viruses. Here we show that **t**he early planting, the management of edges and the presence of non-crop habitats are key factors.

Keywords: Maize virus; Aphids; Planting date; Alternative host; Non-crop habitats; Agricultural landscape; Sustainable crop protection.

1. Introduction

Many factors have driven the emergence of diseases in plants: human demographics and behaviours, the global trade, the increase in the agricultural surface worldwide (i.e., ecological changes, economic development and land use), the introduction of invasive pathogens and climate change. Viruses account for 47% of emerging infectious diseases in plants and are the second most important group of plant pathogens that cause high losses, mainly in intensive agricultural crops (García-Arenal and McDonald 2003; Anderson et al. 2004). With technification in agriculture systems, insect pests, fungi or weeds can be controlled by management programs, but viral diseases are more difficult to control because there is no direct product against viruses. Moreover, the oversimplification of crop diversity, reduced genetic diversity, intensive farming systems and the increasing use of phytosanitary products have reduced the ecological functions of agroecosystems and could promote changes in the epidemiology of diseases (Stukenbrock and McDonald 2008).

The host plant, vector and virus are interdependent components of a complex pathosystem. The effect of biodiversity on the ability of viruses to infect their host plant and cause disease is a major question in plant pathology that is central to understanding the emergence of infectious diseases and developing strategies for their management (Pagán et al. 2012). Keesing et al. (2006) postulated that reduced biodiversity can increase disease incidence as a result of the increased abundance of susceptible major hosts, thus facilitating disease spread, which is known as the “Dilution Effect” hypothesis. The spread of infectious diseases is inherently a spatial process often embedded in physically complex landscapes (Biek and Real 2010). However, little is known about the linkage between spatial processes at the landscape scale, the ecology of vector colonisation and the virus transmission rate in the epidemiological disease process (Meentemeyer et al. 2012). In agroecosystems, crop viruses need to persist locally in a host plant with long life history stages or in an alternative weed host to ensure the temporal availability of inoculum in the landscape (Malmstrom et al. 2011). Thus, the local abundance of long-lived hosts, the host range, and the movement of vectors are the key factors controlling infection risk (Borer et al. 2010; McLeish et al. 2017). Specifically, the behaviour and biology of vectors determine the incidence of viruses within geographical areas in the following manners: (1) the abundance of vectors coincides with virus-infected plants (crop or alternative weed hosts), (2) a moderate abundance of vectors coincides with a large number of virus-infected plants, or (3) large numbers of both vectors and virus-infected plants coincide.

Since the 1980s, maize fields in Spain have been subject to severe losses, highlighting viruses as one of the main causes limiting their production. Maize dwarf mosaic virus (MDMV) is endemic in the Ebro Valley (Spain)(Achon et al. 1994), and the occurrence of sugarcane mosaic virus (SCMV) has increased since its detection in 2002 (Achon and Alonso-Dueñas 2009). MDMV and SCMV are included in the sugarcane mosaic virus subgroup (*Potyvirus* genus, Fam. Potyviridae) and the nucleotide sequences of isolates detected in Spain differed from each other by 31% (Achon et al. 2007). Both viruses are transmitted in a non-persistent manner by more than 15 species of aphids (Ford et al. 1989; Teakle et al. 1989) and by seeds at a low rate (<0.5%). The host range of MDMV and SCMV is constrained to Poaceae, including maize and sorghum, the crops with the highest economic importance. Despite the large number of grasses reported as experimental hosts, alternative hosts in natural conditions are limited (Ford et al. 1989; Teakle et al. 1989; Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). *Sorghum halepense* (L.) Pers. (Johnsongrass) is the perennial reservoir for MDMV in Spain, and *Setaria verticillata* (L.) and *Digitaria sanguinalis* (L.) Scop. are annual summer grasses infected with this virus in the field (Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). To date, *Setaria verticillata* has been the only alternative host detected for SCMV in Spain (Achon and Alonso-Dueñas 2009). No winter reservoirs have been found for SCMV, although the potential capacity of species of the genera *Bromus*, *Cynodon* and other winter annual grasses has been demonstrated under field conditions (Hohmann et al. 1998; Oertel et al. 1999).

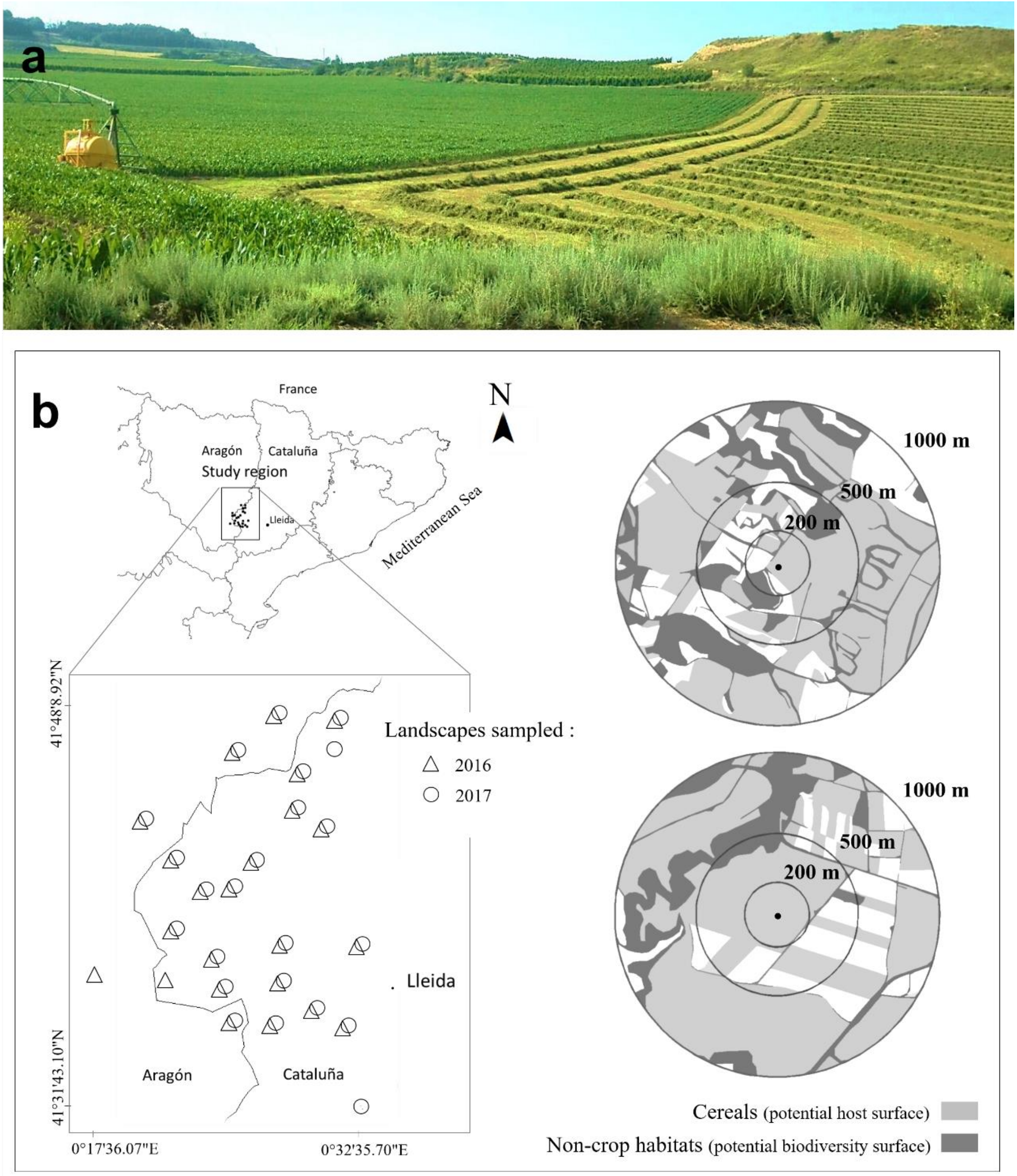
In our study area, Ebro Valley, the number of aphids colonising maize is closely linked to migrations of these species from winter cereals (Pons et al. 1994). Thus, increasing the amount of winter cereal might directly increase aphid abundance due to the resource concentration effect (Root 1973), especially in landscapes dominated by cereals. The amount of virus host habitats and their connectivity may influence the global infection pressure in certain areas. However, knowledge of larger-scale interactions among host spatiotemporal heterogeneity, environmental conditions, and the rates at which pathogens disperse through and among fragmented host populations is limited until now (Meentemeyer et al. 2012). We take into account this perspective and conducted our study under a landscape perspective in combination with field variables of crop management. During two consecutive years, we selected 46 commercial maize fields located in areas with different proportions of cereals in the landscape each year. We quantified the landscape composition at three spatial scales (i.e. 200 m, 500 m and 1000 m) within concentric cycle buffers. To further extend the knowledge of infection risk drivers in northeast Spain, we asked the following questions: (1) what are the main drivers of maize infection risk by MDMV and SCMV under different landscape and field variables? (2) Does the main driver of infection risk vary over different landscape scales? (3) What is the best explanatory spatial scale to elucidate the infection risk of two closely related potyviruses?

2. Materials and methods

2.1. Study area

This study was carried out during 2016 and 2017 in the Ebro Basin in NE Spain (41°48'12.20"N, 0°32'45.77"E; 120–346 m altitude; 200–400 mm rainfall, Tmin: 8º-24º C and Tmax: 18º-38º C) (Fig. 1a). The agroecosystem has been classically dominated by field crops; alfalfa rotates with winter (from December to June) and summer cereals (from April to November) mainly maize. Recently, commercial demand has led to an increase in the stone fruit orchard surface in some areas, leading to an intensive-production agroecosystem in this region. Crops are interspersed with scattered patches of non-crop habitats (non-productive areas, long fallows, semi-natural habitats and repopulated forest). Common pest management practices in cereals include pre- and post-emergence herbicide applications and cereal seed treatment with both insecticides and fungicides. The management of alfalfa consists of 5/6 cuttings during the productive period (March–October), and the crop is in the field for 4-5 years.

Figure 1. a. Agricultural landscape in northeastern Spain. b. Landscape sampled in 2016 and 2017. The proportion of cereals (grey) and non-crop habitats (black) vary among the scale chose in the study (radii of 200 m, 500 m and 1000 m).



2.2. Factors measured at the field level

2.2.1. Maize field variables

During the two years of the study, we selected 46 maize fields with a gradient of winter and summer cereal proportions in the surrounding landscapes. Some of the selected maize fields were not the same each year due to crop rotations. The size of the maize fields where virus incidence was measured varied between 0.9 and 13.68 ha, and they were separated from each other by at least 2 km. The agricultural landscape covered by the selected fields was 700 km^2 (Fig. 1b). The following explanatory maize field variables were included in the analysis: maize field surface (ha), planting date (number of weeks from January) and rotation/ not rotation (with winter cereal).

2.2.2 Maize surveyed

The survey for virus incidence was conducted at maize anthesis following the scheme described in Achon and Sobrepere (2001). In each field, we systematically collected 30 maize plants following a W-shaped pattern. The distance between plants varied according to maize field size. In addition, we collected at least two grass plants reported in the literature as potential virus hosts that were located inside of the maize field. Maize samples consisted of the two youngest leaves of the plant, and grass samples consisted of the leaves or the entire plant. In each field, each sample was placed in a separate plastic bag, grasses were identified at the species level, and maize and grasses were examined for virus-like symptoms or no symptoms. All samples were stored at -80°C until virus identification.

2.2.3. Edge surveys for weeds and grass collection

Floristic surveys were conducted in the edges of the 46 maize fields surrounded by crops or non-crops areas during May-June in the two years. To determine the abundance and composition of plant species in the edges, especially the species of grasses, we carried out surveys in edge areas when the maize was at an early growth stage or recently sown. For each sampling point, the cover-abundance of weed species was recorded using the Braun-Blanquet scale (1979) in three rectangular plots (2×5 m^2) along the edges. The number of edges surveyed in each landscape was between 2 and 6 but depended on the number of different crops and non-crop habitats close to the sampled maize field. For instance, in very diverse landscapes, we sampled six edges: maize-orchard, maize-alfalfa, orchard-alfalfa, maize-maize, orchard ground cover, and non-crop habitats. Then, the cover-abundance values were transformed into the mean value of the percent cover of each field, and the Shannon index (H) was calculated:

$$\mathrm{H} = -\sum_{i=1}^{46} \pi_i \times ln\pi_i$$

where ‘π’ is the proportional abundance of species, and ‘i’ is the number of observations. Johnsongrass plant cover and H were the explanatory field variables in the models.

In addition, for information about the cover plants and diversity groups of the edges, we used floristic surveys to transform the cover abundance of species into the mean value of the percent cover according to six types of edges sampled to calculate the Shannon index and grouped the recorded plant species as dicotyledons or monocotyledons (Fig. 2a). These variables were only descriptive and are not included in the analysis.

Furthermore, to detect edge grasses as an alternative host of virus inoculum, we collected samples in the surveyed edge plots mentioned above according to the following criteria: (1) two samples of the most abundant grass, (2) one sample of the second most abundant grass, (3) two samples of the least frequent grass species, and (4) if present, one Johnsongrass plant exhibiting virus-like symptoms (leaf mosaic). In each field, each sample was placed in a separate plastic bag, identified at the species level, and examined for virus-like symptoms or no symptoms. All samples were stored at -80°C until virus identification.

2.2.4. Virus detection

Virus identification of maize and grass leaf samples were performed by the double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Adams and Clark 1977) using polyclonal antisera against MDMV and SCMV (Loewe GmbH). Commercial antisera were used at the dilution and in the buffers recommended by the manufacturer. Samples were extracted (1:20 g/ml of fresh tissue and 1:100 of died tissue) by grinding with a mortar and pestle. Extracts from healthy maize and Johnsongrass plants were used as negative controls, and extracts of MDMV-Sp and

SCMV-Sp were used as positive controls. Samples were considered positive when the A_{405nm} values were three-fold higher than the negative controls on the same plate.

2.2.5. Aphid sampling

Aphids were collected in the field between the maize phenological stages V3 (vegetative growth) to VT (reproductive development-anthesis) using yellow sticky traps (30 ×25 cm, Serbios, Badia Polesine, Italy). In each field, we placed 3 traps on stakes at the crop canopy height along a transect perpendicular to the nearest edge (approx. 30 m). The traps were separated from each other by 15 m and left for 7 days. Then, the traps were collected and stored at 6-8^{0}C until insect identification and recording. The number of aphids caught on each trap was counted under binocular conditions in the lab.

2.3. Factors measured at landscape scales

Data on the landscape composition were obtained for both years from Instituto Geográfico Nacional (IGN) and Declaració única agrària (DUN) of Generalitat de Catalunya, Spain. ArcGIS software was used to identify four types of land use: orchard, cereals, alfalfa and non-crop habitats. Then, the proportions of each type of land in the landscape surrounding the central point of each maize field within radii of 200 m, 500 m and 1000 m were calculated (Fig. 1b). Autocorrelation can be a problem for classical statistical tests, which rely on independently distributed errors, as it may lead to erroneous conclusions on the significance of covariates in studies of species-environment relationships. Thus, the correlations among the four land use variables in all the fields were assessed using Spearman rank correlation coefficients. These analyses showed that the proportions of cereals and orchards in the landscape were negatively correlated in the three spatial scales (Spearman’s rho ≥ 0.71); therefore, the proportion of orchards was excluded to build the models according to the criteria of Campbell and Swinscow (2009).

2.4. Data analysis

We used multimodel inference (MuMIn package, Bartoń 2018), a procedure that fits models using all possible combinations of predictors and weights them using the Akaike information criterion (AIC) (dredge function). This method allows the data-based selection of a “best” model and the ranking and weighting of the remaining models in a pre-defined set. This procedure generated AIC values and Akaike weights for each candidate model. Model averaging was performed on the set of ΔAICc < 2 criteria. The selection of a best approximating model represents an inference from the data and tells us what “effects” (represented by parameters) can be supported by our data.

First, we used Moran’s I statistic for the spatial autocorrelation (measure of the correlation of a variable with itself through space) of the incidence of MDMV, SCMV and aphid abundance. The results indicated that there was no significant spatial autocorrelation (MDMV Moran’s I=-0.015, P=0.92; SCMV Moran’s I= -0.007, P= 0.83; aphid Moran’s I= -0.014, P= 0.89). Second, the landscape and field metrics for each model were standardised (mean centred and scaled). Third, to analyse the relationships between the incidence of MDMV, SCMV, and aphid abundance with the field and landscape variables, we used a generalised linear mixed model (GLMM) in R within the lme4 package. After that, models were fitted following the different spatial scales mentioned above: 200, 500 and 1000 m from the selected maize fields. We used the percentage of viral incidence in each field, including the weight of the variable (number of maize samples per field), to analyse the effects. In the virus (percentage of vital incidence) and aphid (vector abundance) models, the planting date, maize field area, crop rotation, H in the edges, percentage of Johnsongrass plants in the edges, and proportions of alfalfa, cereals and non-crop habitats were included as fixed factors, and in the virus models, the sum of aphids was also included. The year was included as a random factor in all models. The models of viruses were fitted using glmer (for the binomial distribution), and the abundance of aphids was fitted using glm.nb (for the negative binomial distribution) using the R package MASS (Ripley 2019). Then, models of virus incidences residuals were graphically inspected with qqplot and histogram graphics to ensure there was no violation of normality and homoscedasticity assumptions. Finally, in the virus models, the relative importance of each predictor variable was plotted to check the weight of the variables included in the best model.

3. Results and discussion

3.1. Incidence of MDMV and SCMV in maize fields

Virus incidence in the maize fields was determined using serological analyses of 1,324 maize plants collected in the systematic surveys. Virus incidence varied significantly between the two years for both viruses, that is, MDMV ($F_{1,45} = 5.09$, $p = 0.03$) and SCMV ($F_{1,45} = 7.10$ $p = 0.01$). The highest incidence of MDMV and SCMV was observed in 2016 (24% and 28%, respectively). In 2017, the incidence decreased notably, with values of 7% for MDMV and 6% for SCMV. Moreover, the highest incidences were detected in fields sown later in the year (from May to end of June) with values of 22% of MDMV and 23% of SCMV compared with early sown (from March to end of April) 10 % of MDMV and 12% of SCMV. In the study period compared with previous years, the overall incidence of SCMV in the Ebro Valley increased by 13.8%, and the MDMV remained at a similar level (Achon et al. 2001; Achon and Alonso-Dueñas 2009). The increasing incidence of SCMV in the last years is in concordance with the predictions of Achon and Alonso-Dueñas 2009 from the first increasing detection during 1997-1999 (Achon and Sobrepere 2001). Albeit other factors could not discard, the increased incidence of SCMV may be the result of the greater susceptibility of the current maize varieties grown in the study area (Achon and Alonso-Dueñas, unpublished results). In addition, we found a high correlation between the incidence of both viruses within the same year (R^2: 0.94, p = <0.001; df = 45).

The grass species found and collected within the maize field were Johnsongrass, *Setaria* spp., *Cynodon dactylon* (L.) Pers., and *Echinochloa crus-galli* (L.) P.B. Although these samples were not considered in the virus incidence models, a total of 66 grass samples were analysed using DAS-ELISA. Only Johnsongrass was infected with MDMV (39.29% of samples in 2016 and 57.14% of samples in 2017), and unexpectedly, one sample was infected with both SCMV and MDMV in 2016. These results confirm that Johnsongrass continues to be the main perennial reservoir of MDMV, as Achon and Sobrepere (2001) reported, but may also be an inoculum source of SCMV, a role that has not been reported before in our area. Thus, the perennial character of Johnsongrass is important to the role of this weed as a virus host as virus infection risk increases with increasing local abundance of the perennial grass (Borer et al. 2010).

3.2. Plant diversity and alternative hosts of MDMV and SCMV in maize edges and surrounding habitats

A total of 203 plant species were identified in the 504 sampling points in the edge surveys. The maximum plant cover and H were detected in the edges of non-crop habitats (Fig. 2a), but none plant collected in this habitat resulted infected with the two viruses. On the other hand, the proportion of monocotyledons, the only potential virus reservoirs, was highest in edges between maize-maize fields (Fig. 2a). Of the 203 plants sampled, 12% of the species identified were grasses, among which the most abundant species were *Hordeum murinum* L., *Cynodon dactylon*, *Bromus diandrus* (L.), *Poa annua* L., Johnsongrass, *Avena sterilis* L., *Bromus catharticus* Vahl. and *Lolium rigidum* Gaudin.

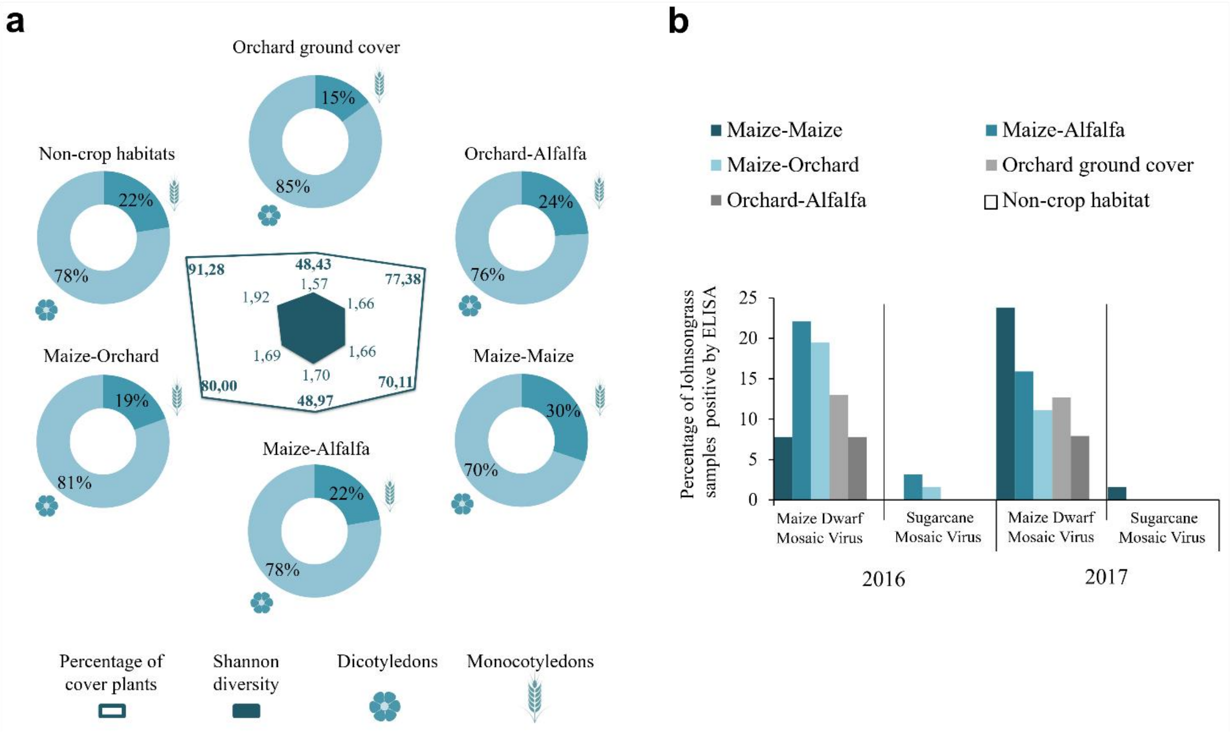


Figure 2. a. The composition of plant species in edges was estimated by the Braun-Blanquet scale. The cover-abundance values were transformed into the mean value of the percent cover according to the six types of edges sampled. The radar graph represents the mean percentage of the plant edge cover in sampled maize fields and H according to the field edge of the neighbouring crop. Circles represent the flora grouped into dicotyledons and monocotyledons. b. Percentage of Johnsongrass samples positive with maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV) antisera by DAS-ELISA in maize field edges and surrounding habitats.

During the edge survey, we collected a total of 641 grasses belonging to 25 species reported as a host, possible host or potential anecdotic host that were analysed by DAS-ELISA for MDMV and SCMV (Table 1). Specifically, high abundances of Johnsongrass were found in all surveyed edges, in alfalfa fields around sprinklers, and in the ground cover of orchards. Although the management of edges includes herbicide treatments and/or mechanical labour, during samplings in the study we observed that Johnsongrass was particularly present and frequently exhibited mosaic virus symptoms in the edges and the base of sprinklers. A total of 110 samples of Johnsongrass were positive with MDMV (approximately 75% of the samples), although there were variations among edges and years (Fig. 2b). Although Johnsongrass was abundant around alfalfa sprinklers and hosted abundant aphids, only 1 of the 9 Johnsongrass samples collected in this situation was infected with MDMV. In addition, 1 of the 69 samples of *C. dactylon* and 1 of the 37 samples of *B. catharticus* were positive for MDMV (Table 1); these species have not been reported as MDMV hosts until now (Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). This is a remarkable result for the virus epidemiology given that both species are particularly abundant and multiannual, increasing the host range in our agroecosystem (McLeish et al. 2017).

Concerning SCMV, we found 4 positive samples of Johnsongrass, representing 0.8% and 2% of the samples in 2016 and 2017, respectively; these percentages were much lower than those observed for MDMV. Moreover, three samples with mixed MDMV and SCMV infections were detected (4% of Johnsongrass samples in 2016) (Table 1, Fig. 2b). No previous Johnsongrass samples positive for SCMV had been detected in our area, but this species is among the most persistent weeds (Peerzada et al. 2017), and it has been positively detected as an SCMV host in another Mediterranean country (Moradi et al. 2017). Although Achon and Alonso-Dueñas (2009) reported positive samples of *Setaria verticillata* with SCMV, no evidence of grass hosts for SCMV other than Johnsongrass was found in this study when we analysed 641 grass samples belonging to 25 species. This could be because the edge areas we sampled in spring, *Setaria* spp. showed a low cover because it is a summer grass.

Table 1. Relation of grasses collected in edge surveys and analysed by DAS-ELISA. Data in the ‘host’ column were taken from the literature. *** host, ** possible host, *anecdotic species; A: annual species, P: perennial species. The three right columns show the number of plants that reacted with antisera of the plants collected for analysis. The numbers in parentheses represent the percentages of ELISA-positive samples for MDMV and SCMV.

Year	Grass species collected	Host	Growth habitat	Reacterd with anthisera		
				MDMV	SCMV	Double infection
2016	*Avena sativa* L.	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Avena sterilis L.	**	A	0/58 (0)	0/58 (0)	0/58 (0)
	Brachypodium phoenicoides (L.)	**	P	0/27 (0)	0/27 (0)	0/27 (0)
	Bromus catharticus Vahl.	**	P	0/17 (0)	0/17 (0)	0/17 (0)
	Bromus spp.	**	A	0/32 (0)	0/32 (0)	0/32 (0)
	Cynodon dactylon (L.) Pers.	**	P	1/45 (2.22)	0/45 (0)	0/ 45 (0)
	Dactylis glomerata L.	*	P	0/5 (0)	0/5 (0)	0/5 (0)
	Hordeum murinum L.	**	A	0/58 (0)	0/58 (0)	0/58 (0)
	Koeleria phleoides (Vill.)	*	A	0/2 (0)	0/2 (0)	0/2 (0)
	Lepturus repens (G.Forst.)	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Ligeum spartum (L.) Kunth	*	P	0/1 (0)	0/1 (0)	0/1 (0)
	Lolium rigidum Gaudin	**	P	0/14 (0)	0/14 (0)	0/14 (0)
	Mellica celiata L.	*	P	0/3 (0)	0/3 (0)	0/3 (0)
	Oryzopsis miliacea (L.)	*	P	0/9 (0)	0/9 (0)	0/9 (0)
	Phalaris arundinacea L.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Phalaris minor Retz.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Poa annua L.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Poa pratensis L.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Polygonon sp.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Setaria pumila (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria verticillata (L.)	**	A	0/2 (0)	0/2 (0)	0/2 (0)
	Setaria viridis (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Sorghum halepense (L.)	***	P	54/77 (70.13)	3/77 (3.9)	3/77 (3.9)
2017	*Avena barbata* Pott	**	A	0/3 (0)	0/3 (0)	0/3 (0)
	Avena sterilis L.	**	A	0/33 (0)	0/33 (0)	0/33 (0)
	Brachypodium phoenicoides (L.)	**	P	0/10 (0)	0/10 (0)	0/10 (0)
	Bromus catharticus Vahl.	**	P	1/20 (5)	0/20 (0)	0/20 (0)
	Bromus diandrus Roth	*	A	0/16 (0)	0/16 (0)	0/16 (0)
	Bromus madritensis L.	*	A	0/4 (0)	0/4 (0)	0/4 (0)
	Bromus spp.	**	A	0/7 (0)	0/7 (0)	0/7 (0)
	Cynodon dactylon (L.) Pers.	**	P	0/24 (0)	0/24 (0)	0/24 (0)
	Echinochloa crus-galli (L.) P.B.	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Eragrostis spp.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Hordeum murinum L.	**	A	1/44 (0)	0/44 (0)	0/44 (0)
	Lolium rigidum Gaudin	**	P	0/18 (0)	0/18 (0)	0/18 (0)
	Oryzopsis miliacea (L.)	*	P	0/6 (0)	0/6 (0)	0/6 (0)
	Phalaris minor Retz.	*	P	0/3 (0)	0/3 (0)	0/3 (0)
	Phleum paniculatum Huds.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Poa annua L.	*	A	0/6 (0)	0/6 (0)	0/6 (0)
	Poa pratensis L.	*	P	0/10 (0)	0/10 (0)	0/10 (0)
	Polygonon sp.	*	P	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria pumila (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria verticillata (L.)	**	A	0/4 (0)	0/4 (0)	0/4 (0)
	Setaria viridis (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Triticum spp.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Sorghum halepense (L.)	**	P	51/63 (81)	1/63 (1.6)	0/63 (0)
	Total samples			105/641 (16.4)	4/641 (0.62)	3/641 (0.46)

However, the results of our random edge survey to find Johnsongrass plants positive with SCMV and the high incidences observed on maize in our study suggest that the long duration of the life history stages of this specie make it a potential alternative host that ensures the temporal availability of inoculum in the landscape. Although it has been reported in other countries that species of the genera *Bromus*, *Cynodon* and other winter annual grasses could act as hosts in the absence of maize, many samples of these genera in this study were negative for SCMV. Thus, the low occurrence of the winter host of SCMV continues to be the bottleneck in the epidemiological knowledge of this potyvirus. These results suggest more powerful detection methods, such as next-generation sequencing (NGS) tools, should be used in future research.

3.3. Effects of landscape and field variables on the vectors of MDMV and SCMV

Aphids are one of the primary pests in the cultivation of maize in Spain, with variable abundances seasonally and spatially (Pons et al. 1994; Asín and Pons 1999). During the two-year study, a total of 240 traps were placed in 46 maize fields where 2,684 aphids were recorded. The abundance of aphids varied significantly between years ($F_{1,45} = 15.23$, $p = <0.001$). Aphids were notably more abundant in 2016 than in 2017 (2,390 and 294 aphids, respectively). Moreover, the highest densities of aphids in June coincidence with the highest incidence of MDMV and SCMV in maize fields sown later **(**since the week number 25) (Fig. 3b, graph aphid abundance).

The most parsimonious model relating the aphid abundance with the landscape and field variables is shown in Table 2. Only significant variables of the best model are shown. Although the model at 500 m was slightly more predictive than the model at 200 m, the two scales can be considered valid because the differences between their AIC values were less than 2. At the scale of 500 m, the aphid abundance on maize was also found to relate to some landscape variables in a study carried out recently in the area (Clemente-Orta et al. 2020). Moreover, in the model with a 200 m scale, an important relationship was found between the proportion of cereals in the landscape and the maize aphid abundance, although this effect was not detected at the two higher scales (i.e., 500 and 1000 m). These results obtained at the landscape scale confirm that the colonisation of maize is closely linked to migrations of these species from nearby winter cereals, as Pons et al. (1994) reported. Thus, the presence of winter cereal surfaces could lead to increased aphid abundances on maize because of a possible concentration effect (Root 1973) in early seasons at small landscape scales. This trend was also reported by Gilabert et al. (2017), who showed that aphid populations increase in homogeneous landscapes dominated by cereals. Although the effect of non-crop habitats on the abundance of herbivorous insects has been found to be inconsistent (Chaplin-Kramer et al. 2011), the proportion of non-crop habitats had a positive effect in this study on the early-season aphid abundance at the three scales. The lack of infected grasses, as found in this study, as well as the higher species diversity in non-crop habitats than in other habitats, suggest that these are a source of aphids in the early season, although likely not viruliferous.

3.3. Effects of landscape and field variables on maize potyvirus incidence

It has been suggested that common single-scale analyses can underestimate the impact of humans on biodiversity, diseases, and the environment (Cohen et al. 2016). In fact, we used an approach based on the proportion of cereals, alfalfa, and non-crop habitats surrounding the sampled fields at three spatial scales to determine whether a high proportion of cereals in the landscape contribute to the risk of viral diseases. The most parsimonious models relating MDMV and SCMV incidences with the landscape and field variables are shown in Table 2. Only significant variables of the best model are shown. The most predictive model according to the AIC value for both viruses was at the 200 m scale. This small spatial scale mostly involves close field edges. These results are in concordance with those reported by Borer et al. (2010), who showed that local context provides the strongest explanation of disease risk variation in generalist viruses. Overall, the incidence of MDMV was most influenced by field effects, whereas the SCMV incidence was most affected by landscape factors.

Field variables related to field management had strong effects on both viruses as Fig. 3a. shows. All field variables used in the analysis had strong positive effects on MDMV, but only the planting date, the aphid abundance and the weed diversity of edges had positive effects on SCMV. Concretely, the planting date was the first and the weightiest field variable linked positively to the virus incidence in both virus models especially, in later planting dates (since week number 25), (Fig. 3b). The strong effect of late sowing maize resulted from spatial-temporal encounters of high aphid populations and high inoculum pressure. By contrast to the early planting where the only source of viruses is grass reservoirs, in late showing, source of viruses included also infected-maize planting earlier. This result is particularly relevant in our area and in other areas where maize is sown late after winter cereals have been harvested. We therefore note the necessity to review the adequacy of maize planting dates, especially for late sown maize. In addition, the important relationship between the plant species composition of edges and the potyvirus incidence indicates that edges are an important driver of infection at 200 m (Fig. 3b, graph of diversity of edges). Furthermore, when we grouped the information relating flora surveys by the type of edges, we found that the species diversity value was not different between edges, but plant cover was especially high in the edges of multiannual crops (for example, in the edges of alfalfa or in orchard ground covers) (Fig. 2a). This feature confirms that the importance of virus dispersal to maize fields could depend more on the cover and multiannual character of edge plant species cover than their diversity, especially in spring. Therefore, analyses of infection risk by potyviruses in the future must include the cover of non-abundant grass.

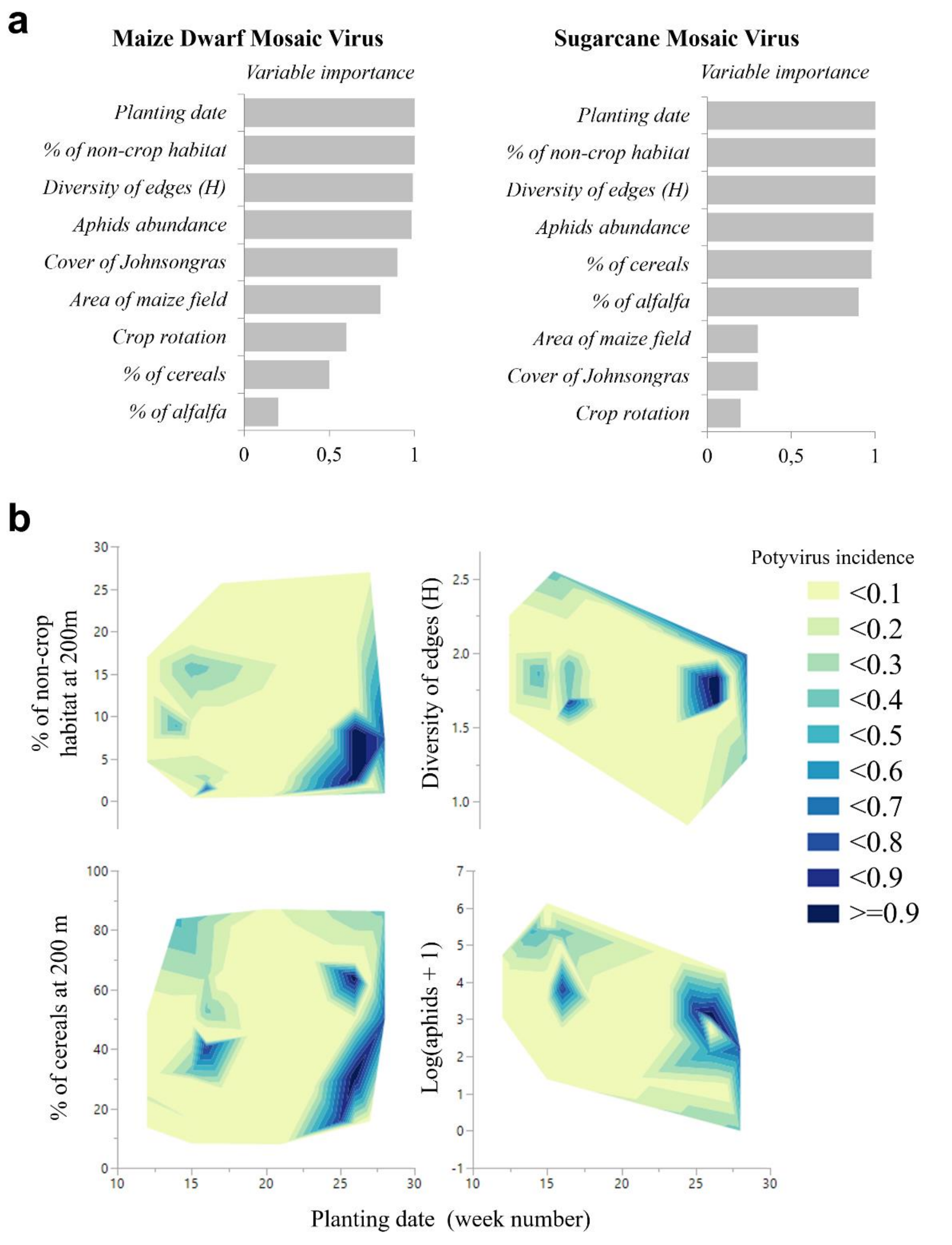
On the other hand, the percentage of non-crop habitats was a landscape variable that was very negatively related to the incidence of both viruses in all models, especially at 200 m (Fig. 3b, graph of non-crop habitat and Table 2). Thus, increased levels of human management that is associated with decreased habitat species diversity result in increased virus infection risk, as stated by Pagán et al. (2012) for virus epidemics. However, although biodiversity in non-crop habitats has been reported as a factor determining disease risk (Keesing et al. 2006; Pagán et al. 2012), few studies have focused on host plant-virus systems. Our results seem to follow the “dilution effect” hypothesis (Keesing et al. 2006), which means that an increase in plant species diversity in the landscape could decrease the overall disease risk by increasing the possibility that vectors will feed on noninfected plants.

The study area was a landscape dominated by winter and summer cereals, mainly maize (the maximum proportions for all sites were 87.05 at 200 m, 86.26 at 500 m and 73.60 at 1000 m), with the relevant presence of non-crop habitats in some areas. Although at 200 m the percentage of cereals had positive effects on SCMV, in contrast to our expectations and as suggested by Rodríguez-Nevado et al. (2017), the high proportion of cereals did not amplify the virus incidence of MDMV and SCMV at large spatial scales (Fig. 3b, graph of % of cereals). The positive relationship between the percentage of alfalfa in the landscape with both viruses at 1000 m and with SCMV at 200 m suggests that the durability and presence of grasses in the edges and within this crop result in a broad source of host plants of multiannual species, particularly Johnsongrass, as mentioned above.

Table 2. Generalised linear mixed models used in multimodel inference to select the best effects model on aphid abundance, MDMV and SCMV incidence relating the influence of landscape and field variables. Models were fitted at three spatial scales from 200 to 1000 m around the sampled fields. Only significant variables in the best models (ΔAIC < 2) are presented. AIC values indicate little differences in support from data model.

		200 m			**500 m**			**1000 m**		
Scale	**Variables**	**Estimate**	**z value**	**p-value**	**Estimate**	**z value**	**p-value**	**Estimate**	**z value**	**p-value**
Aphid abundance										
Local	(Intercept)	3,46	5,45	<0.001	3,45	5,15	<0.001	3,45	5,15	<0.001
	Planting date (weeks)	-0,56	3,16	0,002	-0,48	3,42	0,001	-0,48	3,42	<0.001
	Area maize field (ha)									
	Rotation (winter/summer cereal)									
	H' in the edges									
	Johnsongrass plant cover									
Landscape	Percentage of cereals	0,24	1,73	0,058						
	Percentage of alfalfa									
	Percentage of non-crop habitats	0,30	2,13	0,033	0,49	2,87	0,004	0,37	2,86	0,004
	Akaike information value (AIC)	436,33			**434,21**			441,64		
MDMV incidence										
Local	(Intercept)	-2,47	2,89	0,004	-2,30	3,77	<0.001	-2,24	4,34	<0.001
	Planting date (weeks)	0,97	8,93	<0.001	0,97	8,84	<0.001	0,97	8,25	<0.001
	Area maize field (ha)	0,39	2,90	0,004	0,20	2,17	0,030	0,29	2,90	0,004
	Rotation (winter/summer cereal)	0,27	2,02	0,044				0,44	3,10	0,002
	H' in the edges	0,79	6,83	<0.001	0,51	4,99	<0.001	0,61	5,44	<0.001
	Johnsongrass plant cover	0,37	2,84	0,005				0,29	2,36	0,018
	Aphid (sum)	0,44	3,22	<0.001	0,34	3,02	0,003			
Landscape	Percentage of cereals				-0,38	3,76	<0.001	-0,27	2,67	0,008
	Percentage of alfalfa							0,55	6,26	<0.001
	Percentage of non-crop habitats	-0,98	8,47	<0.001	-0,90	6,23	<0.001	-0,32	3,67	<0.001
	Akaike information value (AIC)	**485,41**			538,71			537,15		
SCMV incidence										
Local	(Intercept)	-2,54	2,35	0,019	-2,35	3,00	0,003	-2,15	2,87	0,004
	Planting date (weeks)	0,97	10,33	<0.001	0,97	10,29	<0.001	0,97	10,40	<0.001
	Area maize field (ha)									
	Rotation (winter/summer cereal)									
	H' in the edges	0,96	8,30	<0.001	0,80	7,03	<0.001	0,70	6,29	<0.001
	Johnsongrass plant cover									
	Aphid (sum)	0,39	3,43	<0.001	0,39	3,74	<0.001			
Landscape	Percentage of cereals	0,36	3,43	<0.001	-0,50	5,04	<0.001	-0,20	2,10	0,036
	Percentage of alfalfa	0,30	2,71	<0.001				0,52	6,17	<0.001
	Percentage of non-crop habitats	-0,98	8,52	<0.001	-0,87	7,56	<0.001	-0,27	3,42	<0.001
	Akaike information value (AIC)	**523,98**			561,16			584,29		

Figure 3. a. Graphs of relative importance of each predictor variable (sum of Akaike weights of the best models in which each variable appears) on virus incidence models at 200 m. In the best models at 200 m for both viruses, the percentage of non-crop habitats, the maize planting date and the diversity of edges were strong predictors. b. Contour plots show the response values and desirable operating conditions. The contour plot contains the following elements: predictors on the X (planting date) and Y (% of non-crop habitats and % of cereals at 200 m, aphid abundance and H of edges) axes. Contour lines connect points that have the same adjusted response value.



* % represents the proportion of surrounding crops and non-agricultural habitats in the landscape in a 200 m buffer.

4. Conclusions

Our results show for the first time the main drivers of potyvirus infection in maize crops by using a novel analysis methodology considering landscape and field variables at different spatial scales. We show that infections by the two potyviruses follow different patterns that are more predictive at a small spatial scale (200 m). The fact that the best spatial scale for both viruses is 200 m means that maize fields itself and close edges, that is, the local context is the strongest predictor of the risk of infection. While MDMV infection risk is more linked to field management than SCMV, infection risk of SCMV is more dependent than MDMV on the close field edges measured in this study as landscape variables. In addition, infection risk demonstrates a strong dependency on the proportion of non-crop habitats, the maize planting date, and the diversity of weeds in the edges. Moreover, Johnsongrass is the main driver of infection by the two viruses, especially in maize fields shown late in coincidence with the more abundant flights of vectors. On the other hand, the use of more powerful tools to detect infected samples by SCMV could improve our understanding of the role of minor multi-annual grasses in the epidemiology of the virus, especially in grasses growing in edges between alfalfa and cereal fields.

Overall, we report that in areas where generalist viruses are transmitted in a non-persistent manner, the local context is the most appropriate context to prevent virus infection. Thus, we recommend the following measures: (1) avoid late maize planting dates as much as possible to minimise infection risk, (2) integrate or keep non-crop habitats in the landscape in order to increase plant biodiversity, and (3) confirm the convenience of the eradication of grass weeds, particularly Johnsongrass, within the field and in maize edges.

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Contributions
G.C.O. contributed to collect the landscape information, the insect abundance, grass and maize samples, analysed of the data, interpreted the results, and drafted the article. R.A. contributed to the design of the work, the collect insect data and drafted the article. M.A. contributed to the design of the collect maize and grass samples, and revised the final manuscript.

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Chapter 4

Maize planting date determines which landscape and field variables are drivers in the epidemiology of Maize Rough Dwarf disease

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Maize planting date determines which landscape and field variables are drivers in the epidemiology of Maize Rough Dwarf disease

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Abstract

Maize rough dwarf virus (MRDV) is one of the main yield-limiting factors of maize in the Mediterranean. An understanding of its epidemiology is crucial to control this disease. However, there is limited knowledge about the interactions between the agroecosystem and the virus-vector-host relationship. MRDV moves through the agricultural landscape via *Laodelphax striatellus* and grass species act as sources of the virus inoculum and as breeding and feeding vector. Understanding the movement of the vector and the role of landscape elements is of key importance and in doing so, the landscape-scale and field management are variables that influence MRDV epidemiology can be identified. Results of the generalized linear mixed models and multi-model inference method showed that the planting date has an important influence on the variables involved in the epidemiology of MRDV. Including this information into prediction models could improve decision support systems that will rationalize the decision-making process towards more integrated control of the disease. These findings provide new insights into the causes and limitations of maize production and offer some guidance to consider reducing losses by MRDV with the combination of early planting dates, the management of grasses at edges, and the non-overlapping of maize and winter cereals.

Keywords: Maize virus; MRDV, Crop rotation system; Landscape composition; Local context; *Laodelphax striatellus*.

Introduction

World agriculture is evolving in response to human population growth, a growing demand for different food commodities, climate change, and new issues related to agriculture, such as biofuels, agro-pharma and CO_2 absorption. Thus, global agriculture can be the world's single largest driver of global environmental change if it combines sustainable practices and meets human needs[1]. Viruses are the second most important group of plant pathogens that cause high losses, mainly in intensive agricultural crops[2,3]. While the management of agricultural habitats offer solutions to reduce yield loss due to pests[4], in the case of viral diseases, the oversimplification of crops and genetic cultivar diversity, the intensive farming systems and the increasing use of phytosanitary products have interfered with the ecological functions of agroecosystems and have altered the epidemiology of plant diseases[5].

The host plant, vector and virus are interdependent components of a complex pathosystem. Thus, it has been suggested that the spread of infectious diseases is inherently a spatial process often embedded in physically complex landscapes[6]. However, few studies have dealt with the linkage between spatial processes at the landscape scale, the ecology of vectors in crop colonization and the virus transmission in the disease epidemiological process[7].

Maize rough dwarf disease (MRDD) is one of the most damaging viral diseases found in the maize growing areas of Europe, Asia and South America. Spain and other areas of Mediterranean basin are affected by maize rough dwarf virus (MRDV), a member of group 2 of *Fijivirus* (Fam. Reoviridae), and other areas are affected by other virus species of this group[8,9,10,11,12]. In Spain, MRDV was first reported in the 1960s[13], and a later outbreak of this virus was observed in 1999 in the northeast region of the country[14]. Intensive surveys conducted from 2001 to 2006 in the main maize growing regions of Spain revealed that MRDV was the most widespread virus infecting maize crops, and its coverage was estimated in 68% of the Spanish maize surface area[15]. MRDV is transmitted in a persistent propagative manner by the planthopper *Laodelphax striatellus* Fallén (Delphacidae, Fulgoroidea), which is a unique natural vector for MRDV in Spain that contributes to an increase in virus inoculum[16,17,18]. Overwintering nymphs carrying MRDV survive in weed grasses and rice, and then the adults move into maize and infect maize when feeding on plants[19,20,21]. Early infections lead to severe plant stunting and premature death when the maize plants are most susceptible[22,17]. Maize is the most affected crop in Spain[15], and the MRDV host range is limited to Gramineae, with lower proportions in species such as *Digitaria sanguinalis* (L.) Scop, *Echinochloa crus-galli* (L.) P.B., *Cynodon dactylon* (L.)[13,19,16], and *Lolium perenne* (L.); however, it is very occasionally found in wheat crops with a low occurrence[17]. Although winter cereals have been shown to act as winter reservoirs for other *Fijivirus*[23,24,25], the role of these crops in MRDV epidemiology in Spain has not yet been defined[15,17].

It is widely accepted that the epidemiology of the MRDD is strictly linked to the abundance and distribution of its vector[16]. In Spain, the population dynamics of *L. striatellus* on maize shows abrupt seasonal fluctuations, with two peaks during the season one in June and another in September[16,17]. These studies determined that the incidence of MRDV was correlated with the first captures in maize fields during the first development stages of the crop. However, several additional factors must be analysed to optimize management strategies. In this sense, the planting date also varies between maize-growing areas[26,27,28] according to the climate conditions, and the expected length of the growing season where the maize is produced and the optimal date for planting vary greatly[29]. In the irrigated area of Spain, the maize growers sowed maize from March to April; however, in the last years, growers have delayed the planting date, likely as a result of milder springs and earlier winter cereal harvesting allowing to sow maize after the winter cereal[30,31].

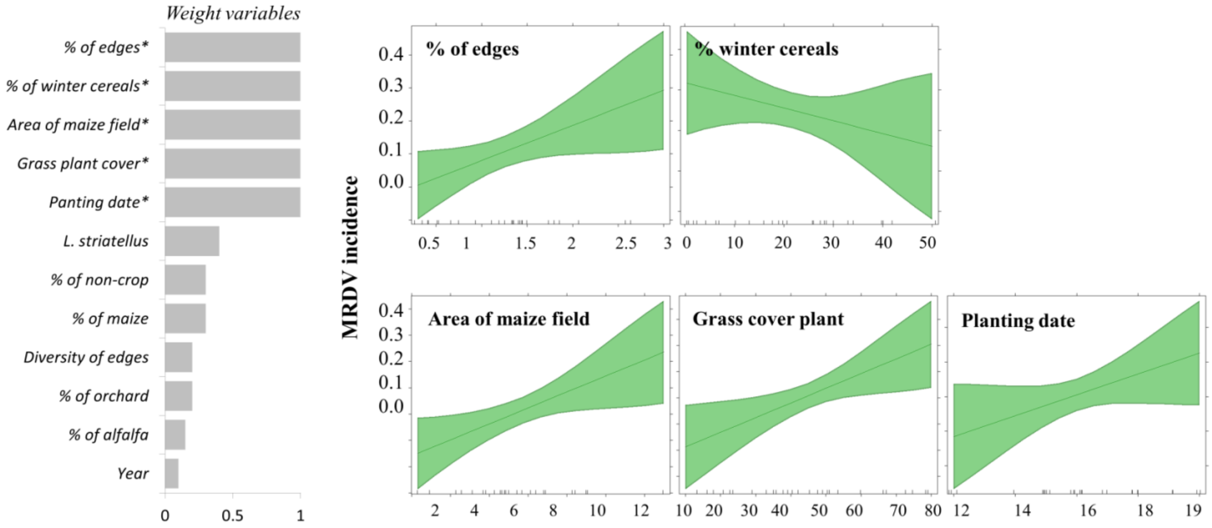
This study aimed to identify which landscape and field factors are mainly involved in the MRDD epidemiology in our area. To further extend the knowledge of infection risk drivers, we worked under the following questions: (1) can we elucidate, from a landscape perspective, the main epidemiological factors driving the incidence of an endemic virus? (2) What are the landscape and field variables involved in maize infection risk by MRDV? (3) Are the same factors involved in early and late maize sown fields?

Results

MRDV incidence in maize fields. A total of 1,324 maize plants were analysed during two consecutive years. The average of virus incidence registered was 12.90% in 2016 and 9.45% in 2017, with no significant differences between years ($F_{1,45}$ =1.04, p =0.3). However, we found significant differences between sowing months ($F_{3,39}$ =4.25, p =0.011). Specifically, the average incidence was higher in the fields sown in May (13%) and lower in those sown in March (1.3%). These results helped to set the two planting periods used in the next analysis.

Effects of field and landscape variables on MRDV incidence. The most parsimonious model relating the incidence of MRDV with the field and landscape variables in maize in early planting is shown in Fig. 3.a, and that in late planting is shown in Fig. 3.b. In grey bars, we show the relative importance of each predictor variable (sum of Akaike weights of the models in which each variable appears in the best models) in the best virus incidence models (ΔAIC < 2). In both figures, only significant variables of the best models are shown in green graphs. The most significant variables affecting MRDV incidence varied in the two planting periods analysed. In both planting periods, the grass cover at the edges was positively related with the virus incidence, but the other significant variables varied with the planting date. For the early planting date, the surface area of maize fields, the proportion of edges and the planting date (number of weeks in the year) were positively related with the MRDV incidence, while the proportion of winter cereals in the landscape was negatively related. For the late planting date, the vector abundance and the proportions of both orchards and fallow-winter cereal in the landscape were the variables positively related with MRDV incidence. In contrast, with early planting, the proportion of edges was negatively related with the virus incidence.

a. Early planting



b. Late planting

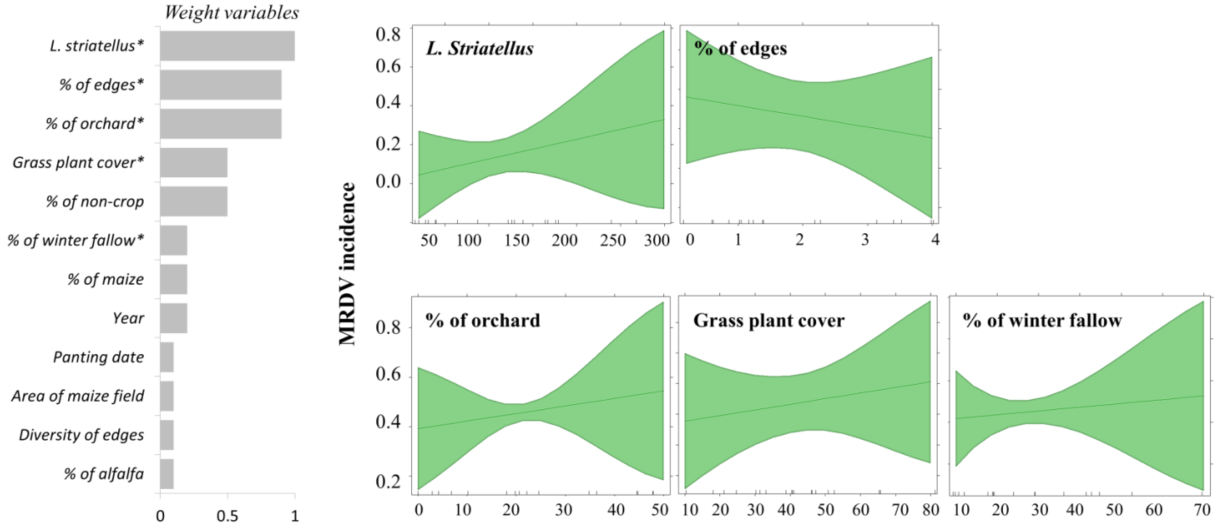
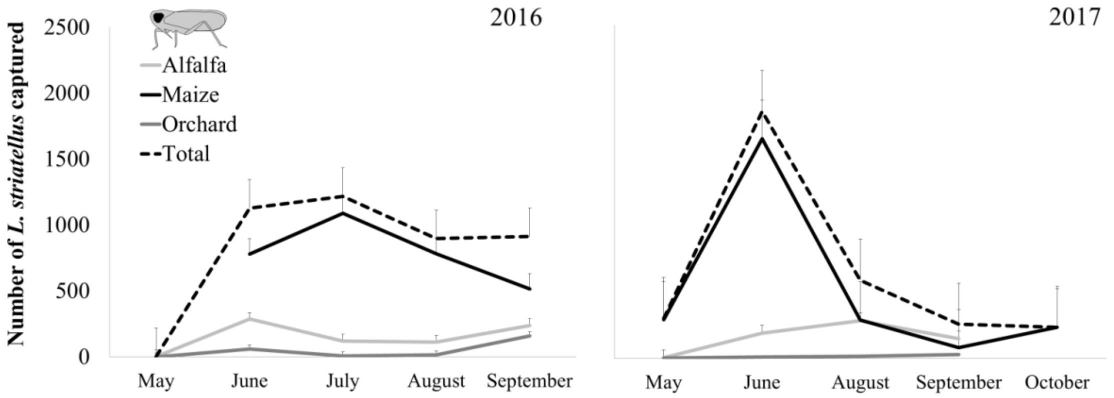


Fig. 3. Effects of landscape and field variables on MRDV incidence in a. early and b. late planting. Generalized linear models (GLMs) using a binomial distribution were used in multi-model inference to select the best effects model on MRDV incidence. The grey bars shown the relative importance of each predictor variable (sum of Akaike weights of the models in which each variable appears in the best models) in the best model virus incidence models (ΔAIC < 2). In the best models, only the significant variables (*) are represented in the green graphs.

Influence of phenology of *L. striatellus* flights on MRDV incidence. The population dynamics of the MRDV vector monitored with yellow sticky traps (from March 2016 and from May 2017) is shown in Fig. 2. A total of 7,451 *L. striatellus* individuals were caught. This number was higher in 2016 than in 2017 (4,223 and 3,228 respectively). Furthermore, we found differences between the months in which the vector populations were monitored in both 2016 ($X^2 = 218.4$, df = 5, $p < 0.001$) and 2017 ($X^2 = 95.83$, df= 4, $p < 0.001$). Vectors in 2016 were more abundant from June to September than in March and May (Dunn test, $p < 0.001$), and in 2017, vectors were more abundant in June and October than in May, August and September (Dunn test, $p < 0.001$).

Moreover, we recorded more *L. striatellus* in maize fields (3,170 and 2,538 in 2016 and 2017, respectively) than in alfalfa (793 and 630 in 2016 and 2017, respectively) or orchards (260 and 60 in 2016 and 2017, respectively) (Table 1). The models showed that the incidence of MRDV was positively related with the abundance of *L. striatellus* in May to the captures in maize fields, in June to the captures in the maize, alfalfa and orchards fields, and in July to the captures in orchard and maize fields.



2016	May	June	July	August	September
Alfalfa	25-45 cm	blooming	cutting	50-70 cm	blooming
Maize	V3-V6 *VE	V7-V10 *V3-V6	V13-V16 *V7-V10	VT-R1 *V13-V16	R2-R6 *VT-R1
Orchards	cover growth	harvest	cover moving	harvest and dry cover	dry cover

2017	May	June	August	September	October
Alfalfa	25-70 cm	blooming	cutting or 20-40cm	blooming and 50-70 cm	
Maize	V3-V7 *VE	V12-V16 *V4-V7	VT-R2 *V8-V12	R3-R6 *V13-V16	R6 *VT-R2
Orchards	cover growth	15-25 cm of cover	harvest and with cover		dry cover

Fig. 2. Abundance of *L. striatellus* during maize growing season. The table shows different phenology and management of sampled crops.

Table 1. Phenology of *L. striatellus* flights on MRDV incidence. The captures of vectors were located in alfalfa, maize and orchard fields during the maize growing season. The models relating MRDV to *L. striatellus* abundance captured in crops in sampling months were analysed using a generalized linear mixed model (GLMM) for binomial distribution.

May			
	Estimate	z value	*p* value
(Intercept)	-2.06	-8.56	< 0.001
Alfalfa	-0.02	-0.21	0.83
Orchard	0.08	0.79	0.43
Maize	0.27	3.63	**< 0.001**
June			
	Estimate	z value	*p* value
(Intercept)	-2.12	-9.31	< 0.001
Alfalfa	0.20	2.88	**< 0.001**
Orchard	0.17	2.27	**0.02**
Maize	0.41	4.69	**< 0.001**
July			
	Estimate	z value	*p* value
(Intercept)	-2.11	-23.57	< 0.001
Alfalfa	-0.10	-1.14	0.26
Orchard	0.41	5.90	**< 0.001**
Maize	0.32	4.82	**< 0.001**

Margin-covering species and grasses at edges as virus reservoirs. In the goal to determine and characterize the cover weeds species, a total of 203 plant species were identified in the 504 sampling points during the edge surveys in both years. In Table 2, we show the values of plant cover and diversity of sampled edges. Overall, the edges of non-crop habitats showed the highest plant cover (91.3%) and H’ value (1.92), while the H’ value of the remaining edges did not differ significantly between them. The orchard ground cover showed the lowest coverage and diversity (48.4% and 1.57, respectively). In addition, edges between perennial crops and cereals showed a high cover (80% in cereals-orchard and 77.3% in orchard-alfalfa).

A total of 64 grasses samples identified as *Avena sterilis* L., *Avena sp.* (fallow), *Brachypodium phoenicoides* (L.), *Bromus diandrus* Roth, *Bromus catharticus* Vahl., *Cynodon dactylon* (L.) Pers., *Dactylis glomerata* L., *Echinochloa crus-galli, Eragrostis* spp., *Hordeum murinum* L., *Lepturus* spp., *Lolium rigidum* Gaudin, *Oryzopsis miliacea* (L.), *Phalaris minor* Retz., *Phleum paniculatum* Huds., *Poa pratensis* L., and *Polygonum* spp. were collected and analysed (Table 2). None of these samples exhibited the MRDV-like symptoms and no genomic segments of the virus were detected.

Table 2. Types of edges sampled using Braun-Blanquet scale. The composition of plant species, the cover-abundance and the H' according to the field edges of maize-neighbouring crops. It shows the most abundant grass (≥ 20% of plant cover) and species analysed by selective isolation of dsRNA in each type of edge.

Type of edge	**% of soil covered**	**Shannon Index**	**Grasses more abundant ≥ 20%**	**Species analysed**	**Nº samples analysed**
Ground cover of orchards	48.43	1.57	*H. murinum*	*A. sterilis*	2
			P. annua	*B. diandrus*	2
			C. dactylon	*B.phoenicoides*	1
				E. crus-galli	1
				P. paniculatum	1
Maize-Alfalfa	48.97	1.70	*S. halepense*	Avena sativa	9
			A. sterilis	*A. sterilis*	3
			B. diandrus	*B. diandrus*	1
			H. murinum	Lepturus sp.	1
			C. dactylon	*L.rigidum*	1
			L.rigidum	*B.catharticus*	1
			P. annua	Polygonum sp.	1
			B.phoenicoides	*O. miliacea*	1
				Eragrostis sp.	1
Maize-Maize	70.11	1.66	*S. halepense*	*P. pratensis*	1
			C. dactylon	Avena (ricio)	2
				A. sterilis	2
				P. minor	2
Alfalfa-Orchards	77.38	1.66	*H. murinum*	*A. sterilis*	5
			C. dactylon	*B. diandrus*	2
			B. diandrus	*B.phoenicoides*	1
			S.halepense	*H. murinum*	1
				B.catharticus	1
Maize-Orchards	80.00	1.69	*H. murinum*	*A. sterilis*	8
			S. halepense	*B.catharticus*	4
			C. dactylon	*B.phoenicoides*	1
			P.annua	*L.rigidum*	3
				P.pratensis	1
Non-crop habitats	91.28	1.92	**D. glomerata*	*O. miliacea*	1
			**H. murinum*	*A. sterilis*	2
			**A.sterilis*	*D. glomerata*	1
				TOTAL	64

* Cover < 15 %

Discussion

Since 1999, maize rough dwarf disease has been the most serious constraint in maize production in Spain. Attempts to understand the main factors involved in the disease outbreaks have revealed that the introduction of new crop practices and MRDV population are involved in these disease episodes[16,17,12]. Although these studies have modified cultural practices and reduced MRDD incidence, several questions remain unanswered, probably because the studies have been conducted at field and not landscape scales. Given that the spread of infectious diseases is inherently a spatial process embedded in a physically complex landscapes[6], this study was conducted by considering the structure of the landscape surrounding the maize fields in the 500-m buffer. We analysed how landscape composition and field characteristics and management influenced MRDV incidence.

We found that both field management and landscape composition were implicated in the virus incidence, but they varied with planting date (Fig. 4). The effects of planting date on virus incidence have been reported by Achon *et al.*[16,17] for MRDV and by Wang *et al.*[25] for other Fijivirus. Aiming to identify criteria to choose an optimal planting date as a function of the epidemiology of MRDV, we separated the analysis into two periods according the planting date of each field. In this way, we expected to have more information about ecological processes involved in the MRDV epidemiology, an approach recommended by Chaplin-Kramer et al.[32] for landscape studies. The choice of these two periods is also meaningful from the perspective of MRDV epidemiology, given that the changing planting dates and the coincidence of the first peak of the vector population were already known in the area. The differences reported in this study showed a 3% reduction in virus incidence in early planting compared to that in late planting, representing an important production benefit for growers.

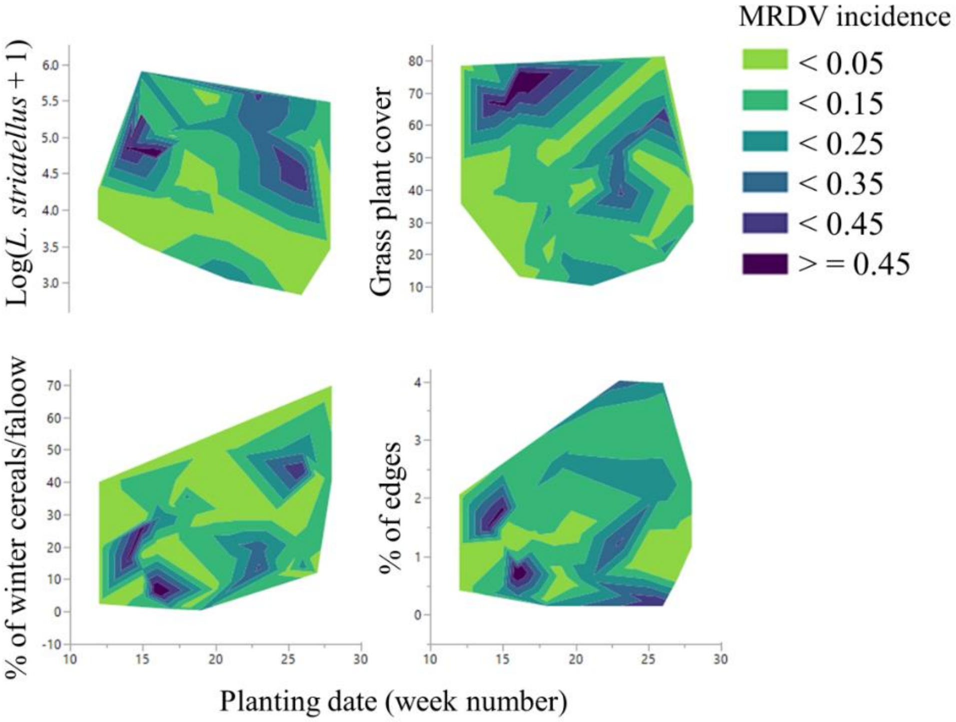


Fig. 4. Pattern of main MRDV drivers. Contour plot contains the following elements: Predictors on the X (planting date) and Y (abundance of *L. striatellus*, proportion of winter cereals/fallow, proportion of edges in the landscape and percentage of grass cover plant at the edges). Contour lines connect points that have the same adjusted response value.

In the landscape analysis, the fact that the MRDV incidence was related to grass cover in both planting periods and to edge proportion and winter cereals in early planting confirms that there are overwintering adults feeding and breeding in these hosts[33,18], particularly when in close proximity to gramineous patches[34]. In addition, virus incidence in early vs. late planting maize fields was negatively vs. positively related respectively to the proportion of winter cereals in the landscape, suggesting that the first peak of vector flights occurs in the area by June-July[16,17]. Before that, vectors breed in winter cereals, and vector migration to maize fields is rather low as long as winter cereals remain as a suitable host. This pattern is why more winter cereal fields in the landscape cause a lower proportion of vector adults to move to grasses[35] or maize plants early in the season when they are looking for Gramineae to feed and reproduce later[25]. Moreover, as the season progresses, winter cereals mature and finally are harvested, increasing the number of vectors that leave winter cereals to colonize maize[36,37]. In late planted maize fields, the relationship between MRDV incidence and the proportion of winter cereal fields (mostly fallow with potential MRDV-susceptible grasses) becomes positive because adult vectors coming from cereals migrate to grasses and maize, a phenomenon reported by Achon *et al.*[16]. In addition, Achon *et al.*[17] reported that winter cereals can only occasionally be a source of inoculum of the virus when the vector moves to maize in late planting fields.

On the other hand, the proportion of edges in the landscape was related to the virus incidence in maize, but in an opposite sense according to the planting date. Although the relationship was positively related in early planting, it was negative in late planting fields. The positive influence of proportion of edges on virus incidence in the early season was probably a consequence of the role of edges in the landscape as a source of vectors and MRDV inoculum. In addition, the high dispersal capacity of *L. striatellus*[38] and the propagative type of transmission of the virus likely allow the vector to retain the infection capacity for longer than that of non-propagative viruses. In the case of non-propagative maize viruses such as maize dwarf mosaic virus (MDMV), the role of the maize field edges was more important than in the present virus, as remarked by Clemente-Orta *et al.*[39]. Later in the season, the vectors are more abundant and maize plants are young and more attractive for the vector, and the role of edges as an alternative reservoir is irrelevant, particularly when many edges in the landscape are dry, burned or treated with herbicides by growers. Note that the composition of winter grass changes with the season. Moreover, in the early season, grasses could provide the resources needed by the vector for overwintering, while in the late season, grasses in irrigated orchard ground cover can remain greener than those at the edges and be a suitable host for vector reproduction as remarked by Clemente-Orta *et al.*[35] in the area. These habitats were characterized by a higher cover of *H. murinum* and *C. dactylon* acting as potential virus and vector resources.

Among field variables, maize field surface area and planting date (number of weeks in the year) in the early planting date were variables influencing MRDV incidence. Insect preference for larger fields is a phenomenon that may have several causes; however, during host-plant habitat colonization by herbivorous insects, the amount of resources for feeding and reproducing is a major stimulus[40,41,42] affecting habitat selection. Later, when an initial population has already been established, field size is a secondary field characteristic as reflected by its non-significant relationship with virus incidence in late planting fields.

The population patterns of *L. striatellus* flights on maize were similar in the two study years and affected the seasonal occurrence of this insect reported previously in Spain[16,17]. In addition, these authors reported that the variation in virus incidence was mostly a function of few viruliferous insects that are required during the early development stages of a crop. These results suggest that a higher virus incidence was registered in fields sown later and corresponded mostly to vector immigration for the colonization of maize in comparison with the low number of insects caught in March, April and May. As expected, the abundance of vectors in alfalfa or orchard fields was much lower than that in maize. However, in spite of the low number of vectors in orchards, the virus incidence in the later planting period was positively related to insect catches in orchards and those captured in maize in that period. Clemente-Orta *et al.*[35] reported that the abundance of *L. striatellus* was related to the proportion of orchard in the landscape in the late season. It is known that different crop management techniques in the agroecosystem affect the pattern of vector abundance and vary between years, especially with overwintering adults[43,44]. It is also known that the patterns of movement and abundance of the species in agricultural landscapes is highly complex (temporal and spatial), and this complexity hinders its interpretation and comparison amongst studies[45].

Although we realized a high sampling effort to find reservoir grasses in the landscape, the non-detection of MRDV in any of the analysed weeds confirms the reduced number of alternative hosts of this virus as well as their reduced susceptibility[13,19,15,17]. Most of the grasses found infected by these authors were summer or late spring grasses, as sampling was performed in very late spring or summer, while our sampling was done when summer grasses were rather scarce and sampling was focused on the most abundant grasses. On the other hand, the sensibility of the method used for virus detection has affected these results. In this sense, the preliminary results obtained using a next-generation sequencing (NGS) approach confirmed that *Avena* spp. is a host of MRDV.

The results obtained in this study provided, for the first time, the relevance of surrounding crops and their management in the epidemiology of MRDD. We report important information about the higher incidences registered at the late planting dates and identify the main variables implicated in the MRDV incidence. In addition to the strong influence of maize planting date on MRDV incidence, the vector abundance, the high grass plant cover at the edges and the proportion of winter cereals/fallows in the landscape are the main factors involved in the epidemiology of MRDV (Fig. 4). The weight of the factors that determine virus incidence strongly depends on the crop planting date. For the early planting date, the presence of edges is the main factor to consider, while for the late planting dates, the increase in vector abundance in these months increases the risk of infection. In addition, our results show that *L. striatellus* is related to MRDV in the late planting dates, which has not been previously reported in our area and contrasts to the results of Wang *et al.*[25] but agree with the results of Conti[33].

Thus, these results contribute to our knowledge of crop management and should be considered when selecting planting dates to minimize the virus incidence in maize crop areas. Finally, a number of recommendations can be issued from this study to reduce the risk of the infection by MRDV, which is responsible for hard losses in maize in our area:

(1) Late maize planting dates should be avoided as much as possible to minimize the risk of infection by MRDV; from this point of view, March and April could be suitable planting months.

(2) We should prevent the coincidence of planting maize fields in the vicinity of winter cereals as much as possible, especially in cereal harvesting periods.

(3) The application of herbicides at the edges could be optimized to minimize the grass cover at both the planting period and at the first stage of crop development. Grass species act as sources of the virus inoculum and as breeding and feeding vectors. However, it should be considered that edges can be also a reservoir of natural enemies to colonize maize fields and prevent outbreaks of insect pests.

Methods

Study area. The study was carried out during 2016 and 2017 in the Ebro Basin in NE Spain (41°48'12.20"N, 0°32'45.77"E; 120–346 m altitude; 200–400 mm altitude; 200–400 mm rainfall, Tmin: 8º-24ºC and Tmax: 18º-38ºC). The agroecosystem has been classically dominated by alfalfa in rotation with winter (mainly wheat and barley, from December to June) and summer (mainly maize, from March to November) cereals. Recently, commercial demand has led to an increase in stone fruit orchard surface in the area, leading to a more intensive agricultural landscape that is interspersed with scattered patches of non-crop habitats (non-productive areas, long fallows, semi-natural habitats and repopulated forest by *Pinus halepensis* (Mill)) (Fig. 1.a). Common pest management efforts in these crops in our area include the following: (1) cereals: pre- and post-emergence herbicide applications, cereal seed treatment with both insecticides and fungicides; (2) alfalfa: consists of 5/6 cuttings during the productive period (March–October), and the crop is in the field for 4-5 years[46]; (3) orchards: management includes an average of 7-14 chemical sprays (insecticides, fungicides and bioregulators), herbaceous cover mowing (approximately once per month), herbicide application (mainly glyphosate), and tree fertilization[47].

Variables sampled in maize fields. Forty-six fields were selected in 2016 and 2017 in areas with a different gradient of cereal proportion in the surrounding landscapes. A few fields changed in the two years due to the rotation. The size of the fields varied between 0.9 and 26.13 ha. The sampled maize fields were separated by at least 2 km so that the study spanned an agricultural landscape of 700 km^2 (Fig. 1.b). The maize field variables considered by the analysis were: maize field surface area (ha) and planting date (number of weeks in the year).

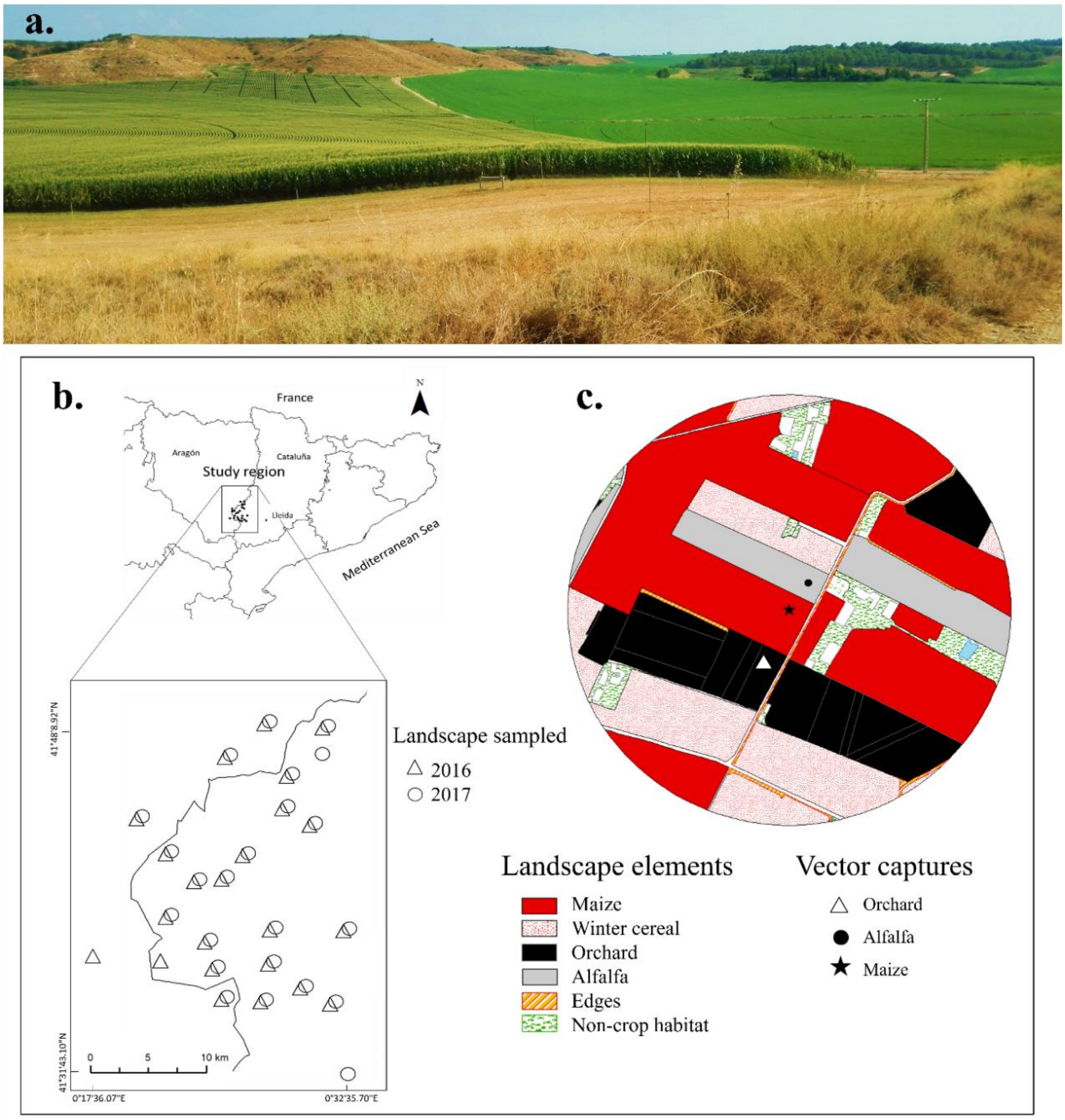


Fig. 1. a. Study region in the Ebro Basin in north-eastern Spain b. Landscape sampled in 2016 and 2017. c. The star, the circle and the triangle indicate the middles of the sticky yellow traps in the sampled fields used to collect MRDV vectors.

Maize survey. A random survey for MRDV incidence was conducted at maize anthesis following the scheme described in Achon and Sobrepere[14] in July. In each field, we randomly collected the three upper leaves of approximately 30 maize plants following a W-shaped pattern. The distance between plants varied according to the maize field size.

In each of the fields, each sample was placed separately in a plastic bag and stored at –80ºC until virus identification.

Edge surveys for weeds and grass collection. Floristic surveys were conducted at the edges of the 46 maize fields surrounded by crop or non-crop areas during May-June in the two years. To determine the abundance and composition of plant species at the edges, especially grass species, we carried out surveys in edge areas when the maize was in the early growth stage. For each sampling point, the cover-abundance of weed species was recorded using the Braun-Blanquet scale[48] in three rectangular plots (2×5 m^2) along the edges. The number of edges surveyed in each landscape was between 2 and 6 but depended on the number of different crop and non-crop habitats close to the sampled maize field. For instance, in very diverse landscapes, we sampled 6 edges: maize-orchard, maize-alfalfa, orchard-alfalfa, maize-maize, orchard ground cover, and non-crop habitats. Then, the cover-abundance values were transformed into the mean value of the percent cover of each field, and the Shannon index (H') was calculated (Eq. (1)):

$$\mathrm{H} = -\sum_{i=1}^{46} \pi_i \times ln\pi_i$$

where 'π' is the proportional abundance of a species, and 'i' is the number of observations. H' and the grass cover proportion were the explanatory field variables in the models.

In addition, to provide information about the cover plants and diversity groups of the edges, we used floristic surveys to transform the cover abundance of species into the mean value of the percent cover according to six types of edges sampled to calculate the Shannon index. These variables were only descriptive and were not included in the analysis.

Furthermore, to detect edge grasses as an alternative host of the virus, we collected samples in the surveyed edge plots mentioned above according to the following criteria: (1) two samples of the most abundant grass, (2) one sample of the second most abundant grass, and (3) two samples of the least abundant grass species. In each field, each sample was placed in a separate plastic bag, identified at the species level, and examined for virus-like symptoms or no symptoms. All samples were stored at -80°C until virus identification.

Virus detection. Maize and grass samples were examined for MRDV symptoms; additionally, the virus infection of symptomatic maize samples was verified by selective isolation of dsRNA genomic segments of MRDV using the mini-prep modified method of DePaulo and Powell[49]. Briefly, dsRNA was isolated from 40 mg of fresh tissue by the sodium dodecyl sulphate (SDS)/KOAc procedure, fractionated by chromatography on non-ionic cellulose (CF-11), eluted in 30 µl of RNAase-free water and separated on 0.8% agarose gels to observe the presence of the MRDV genomic segments. This method was also used to detect virus infection in grass samples with or without symptoms.

***Laodelphax striatellus* data collection.** To determine the contribution of *L. striatellus* to the different crops in the landscape, samplings were performed in maize fields, alfalfa and orchard fields. *L. striatellus* was captured using yellow sticky traps (30 × 25 cm, Serbios, Badia Polesine, Italy). Five samplings were performed monthly using 3 traps per field (3-9 traps per locality), and traps remained active for 7 days during the maize growing season. A total of 1,812 traps were placed in the fields over the two years. In maize fields, the traps were placed on a stake at canopy height (until V12) or at ear level (from V15 onwards) depending on the growth stage, and they were arranged in a transect perpendicular to the edge, with a separation distance of 15 m (the first one was placed 15 m from the edge)[50]. In alfalfa fields, traps were placed on a stake at the canopy level, with a height of 1 m, in a transect perpendicular to the edge, and traps were separated by 12 m from each other, with the first trap located 12 m from the edge[51]. In orchards, traps were placed on a stake at a height of 2 m within tree lines and were separated by 30 m from each other starting 30 m from the edge. Once collected, traps were kept at 4°C until processing. The number of *L. striatellus* caught on each trap was counted under the binoculars and identified at species level using the key of Holzinger *et al.*[52].

Variables at the landscape level. The maize fields were selected based on the proportion of cereals in the landscape using aerial photography in a circular buffer of 500 m surrounding the maize fields. The landscape composition was characterized by the proportion of the different landscape elements embedded in the circular buffer surrounding the maize fields. To incorporate the seasonal variation in the proportion of cereals in early and late spring in the landscape, its composition was measured in the two periods coinciding with early and late maize planting dates. The landscape composition was described each year by direct field observations, by an orthophoto of Plan Nacional de Ortografan Aérea (PNOA), and by geographical information maps of the Instituto Geográfico Nacional of Spain. Then, we quantified the proportions of the landscape elements using ArcGIS software 10.3.1[53]. Next, the 34 landscape elements initially identified in the study were grouped into seven categories: orchards, maize, winter cereals, winter cereal/fallow, alfalfa, non-crop habitats and edges (Fig. 1.c).

Data analysis. Data of virus incidence in maize fields were not normally distributed and were transformed by (log x+1). To identify the influence of the planting month on virus incidence, we analysed the number of plants infected by MRDV in each field with a two-way ANOVA, including the month and year as factors, while the number of maize samples per field used to analyse virus presence and the area of maize fields were used as covariates. The month × year interaction was not significant and it was removed from the analysis.

We used multi-model inference (‘MuMIn’ package[54], a procedure that fits models using all possible combinations of predictors and then weights them by the Akaike information criterion (AIC) (dredge function). This method allows the data-based selection of a “best” model and a ranking and weighting of the remaining models in a pre-defined set. This procedure entailed generating AIC values and Akaike weights for each candidate model. Model averaging was performed on the set to $\Delta AICc < 2$[55]. The selection of a best approximating model represents the inference from the data and tells us what “effects” (represented by parameters) can be supported by the data. First, we used Moran’s I statistic[56] to determine whether there was spatial autocorrelation (measure of the correlation of a variable with itself through space) regarding the incidence of MRDV and *L. striatellus* abundance. The results indicated there was no significant spatial autocorrelation (MRDV Moran’s I = 0.11, $p = 0.14$; *L. striatellus* Moran’s I = -0.07, $p = 0.6$). Moreover, the landscape and field metrics for each model were standardized (mean centred and scaled) using the ‘caret’ package[57]. Then, the relationships between the incidence of MRDV and the field and landscape variables were analysed using generalized linear models (GLMs) with the ‘lme4’ package[58] (for binomial distribution) by each planting date (early: March and April; late: May and June). We used the percentage of viral incidence in each field including the weight of the variable (number of maize samples per field) to analyse the effects. Models of MRDV included the following fixed factors: planting date (number of weeks in the year); area of maize field (ha); diversity of edges (Shannon index); proportions of alfalfa, maize, winter cereals/fallow, orchard, edges, and non-crop habitats; and year and sum of *L. striatellus.* Then, model residuals were graphically inspected with qqplot and histogram graphics to ensure there was no violation of the normality and homoscedasticity assumptions[59]. Finally, in the MRDV models, the relative importance of each predictor variable was plotted to check the weight of the variables included in the best models.

Data on *L. striatellus* abundance captured on the landscape showed no homogeneity of variances, and we used a Kruskal-Wallis test for analysis. We compared the vector abundance among months in 2016 (March, May, June, July, August and September) and 2017 (May, June, August, September and October). Further differences were analysed using the Dunn test.

Finally, the models relating MRDV incidence to *L. striatellus* abundance captured by crop and by month (May, June and July) were analysed using a generalized linear mixed model (GLMM) for binomial distribution, including the year as a random factor with the 'lme4' package. All analyses were performed using R software[60].

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Author contributions
GCO contributed to collect the landscape information, the insect abundance, collected grass, maize samples, analysed of the data, and drafted the article. RA contributed to the design of the work, the collect insect data and drafted the article. IB collected the insect data. MA contributed to the design and to collect maize and grass samples, and revised the final manuscript.

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General discussion

In this thesis, we have worked under the general hypothesis that insects and viruses that affect maize crops in the Ebro Valley are subject to the effects of the surrounding landscape structure. Our specific hypotheses have been based on the results found so far in this area of study for both insects and viral epidemiology. To elucidate the effects of the agricultural landscape on the abundance of herbivores, natural enemies (NE) and the main viruses in maize, several studies were conducted introducing novel methodologies of spatial analysis, statistical analysis, variables of landscape structure and field management, taking into account temporal variability.

Biological control (BC) studies have undergone evolution in recent years due in large part to the emergence of new spatial analysis methodologies and statistical packages. This has led to a cascade of numerous studies focused on extrapolating and comparing methodologies and results obtained in BC from the laboratory to a broader spatial scale, such as the landscape or agroecosystem. The growing demand for food and services from agriculture with the subsequent intensification of agricultural production has caused a fragmentation of natural habitats, one of the main causes of the very important loss of biodiversity of species in ecosystems. Certain habitats provide resources or protection to species, helping to increase the biodiversity and abundance of NEs and thus maintain one of the main ecosystem services, the natural BC of pests in agroecosystems. Although most of the pioneering works in the area focused on demonstrating that patches of natural habitats had positive effects on the NE, at present and after years of scientific publications, it has been observed that the ecological functionality of the patches often has more effects on the species than certain non-cultivated habitats. These response patterns of the species are supported by the "resource-habitat" theory. Although species of NE have been the ones that have reported the most results, the growing scientific literature of macro studies at the landscape scale has brought to light the lack of homogeneity in the effects or patterns of response. In this sense, some of the causes of this heterogeneity in the results may be the use of different methodologies to measure BC, the use of averaged data, the limited description of the agroecosystems studied, and the lack of analyses that consider temporal and spatial variability, among others. In addition, to all this is added the scarcity of studies with species of herbivores (the trophic basis of the web, since the arrival of NEs in the crop depends on these) and the inclusion of field management variables in the analyses. All the anterior points out this makes it so that there are many causes for which BC in agroecosystems is not as successful as it has been suggested (Chapter 1).

In our case, we used species of herbivores and NE to establish a cause-effect relationship between trophic interactions and landscape structure in the maize crops of the Ebro Valley. Using sticky yellow traps, we selected the most representative species of insects following Albajes et al. (2013). In addition, Comas et al. (2015) had documented sticky yellow traps as good estimators of the abundance of various species of arthropods in maize, and thus we rely on this method to cover a wider study area. Statistical models were developed for two different seasons, spring and summer, as a consequence of the change that occurs in the landscape due to crop rotation. The use of new statistical packages such as multimodel inference analysis helped us to analyse a multitude of variables of a different nature in the same analysis. Our results showed that the recent and growing surface of fruit trees in the landscape produced negative effects on the main species of NE of the surrounding maize (Chapter 2). Although some effects were not statistically significant, they pointed to a pattern towards a negative effect of fruit orchards and the abundance of NE. Some authors suggest that the negative effects of intensive management of orchards could be masked by the contribution of insects that come from surrounding crops, so it is necessary to delve into this question (Markó et al. 2017). However, it could also happen that the NE that use cover resources in summer are being affected by the management and the intensive treatment of the covers, notably affecting their populations, which is not the case of the populations of herbivores since these are more abundant. In addition, we found a positive relationship between the surface of orchards in the landscape and the abundance of the most abundant species of herbivores, such as thrips, or other homoptera vectors of viruses in maize, such as *Laodelphax striatellus*. This positive relationship between herbivores and the surface of orchards could be a result of keeping alive and under irrigation the ground covers in summer, just when the rest of the non-crop habitat of the agricultural landscape (edges, semi-natural habitat or understory) is practically dry as a consequence of the scarcity of rain. This relationship between orchard to herbivores and NE must be taken into account, as the presence of ground covers could provide the trophic network with new efficient taxa of NE, which may help to maintain balanced herbivore populations (Álvarez et al. 2019).

On the other hand, the presence of alfalfa crops showed positive results in the abundance of NE, as other authors had previously pointed out in the area (Núñez, 2002; Pons et al., 2005; Ardanuy et al., 2018). Moreover, we found that herbivore species present in the maize crop also had positive effects related to the presence of alfalfa in the landscape, these results had not been obtained until now. It follows that the alfalfa serves as a resource for both herbivores and NE that live in maize crops during maize growth. These results suggest that the presence of alfalfa in the landscape is essential for the establishment of trophic networks in the surrounding crops in the Ebro Valley area.

Contrary to the majority of the results obtained in studies upon agroecosystems at landscape scale in Europe (Thies and Tscharntke, 1999; Tscharntke et al. 2005, 2012; Bianchi et al. 2006; Rusch et al. 2010; Landis 2017), the semi-natural habitats, the forest and the diversity of the landscape (measured with the Shannon index) in our study did not have great effects on the abundance of insects in maize crops. This could be a consequence of the difference between the patches of natural habitats in Northern Europe and Spain. Non-crop plant species diversity in our study area was mainly composed of anthropized species related with agroecosystems. Furthermore, the absence of rain makes these habitats dry zones during most of the year.

On the other hand, the presence of edges in the landscape, in general, did not have large effects on the insect species. Interestingly, as other authors previously reported in the study area (Ardanuy et al., 2018), we found that *Orius* spp. and *Zyginidia scutellaris* were the species most strongly linked to edges. These is of great importance due to the fact that *Z. scutellaris* inhabits the edges before or during the first stages of the crop, especially within grass species (Nickel 2003) attracting *Orius* spp. to these habitats and subsequently to the crop (Pons et al. 2005; Albajes et al. 2011).

Surprisingly, the introduction of local variables provided great information about the weight of these landscape effects on all species and the close relationship between the type of resource exploited by the species and the growth stage of the crop. Both herbivore species and NE responded to the growth stage of maize with a pattern dependent on the stage of crop development. In addition, we observed that the models were normalized when introducing the prey-predator relationship as one of the study variables. This variable showed the strong relationship between herbivores and NE in maize. Other variables measured at the field level, such as the diversity of weeds or field size, did not have large effects on insect species.

Although there is a large literature on the effect of BC and NE in agroecosystems at the landscape scale, the same does not apply to the case of viruses. While it has been shown that habitat management can help to increase and conserve the biodiversity of arthropod species (Landis et al. 2000), this does not occur in the case of viruses because the pathosystem is a very complex system of interrelations between the plant, the virus and the vector. Moreover, given that there are no treatments with which to treat the affected plants, the use of non-resistant varieties, agricultural intensification, crop homogeneity and the use of phytosanitary treatments, which have altered the agroecosystem, have caused changes in the epidemiology of viruses, making these patterns much more difficult to understand. Our results suggest that the change in management practices, especially the planting date and to some extent the phenology of the winter cereal, are the variables that most affect the endemic viruses of the area: the MDMV, SCMV and MRDV (Chapter 3 and 4). Especially, the epidemiology of the 3 viruses are strongly affected by the edges because these habitats are essential for the persistence of the viruses. The viruses that affect maize are confined to grasses and require a vector for transmission. It is important to note that the edges of our study area have a high coverage of grasses with not high species diversity, which can cause an increase in insects that need this resource, especially the vectors that grow, reproduce and overwinter in these habitats in the absence of focal crop. In the case of potyviruses, the high presence and abundance of the Johnsongrass, *Sorghum halepense,* in the landscape (its main alternative host) makes the transmission of the virus, even if non-persistent, to reach high incidences some years, especially in late planting dates when the Johnsongrass with mosaic in the landscape is very abundant (Chapter 3). In the case of MRDV, although we did not find grasses positive for the virus, the coverage of grasses at the edges was a variable very important (Chapter 4). These results indicate the need to use more powerful and sensitive tools for virus detection in weeds. It is clear that despite our initial hypothesis, a landscape dominated by maize did not increase the viral incidence of maize-specific viruses, but other variables such as the planting date are key because the vector, the virus, and the host coincide over time.

It is interesting to note that, although we did not find large effects of semi-natural habitats on insects, for the case of potyviruses, we found that they are negatively affected by the presence of these habitats in the three study scales used (200, 500 and 1000 m). However, the MRDV was not influenced by these habitats. These results suggest that the difference between the effects found in the viruses under study is due to the type of vector and its mode of transmission. The specific MRDV vector *Laodelphax striatellus* can travel and move around for several km, being able to transmit the virus throughout its lifetime, as well as its offspring (Syobu et al. 2011). In the case of aphids, the vectors of MDMV and SCMV, they can also travel many km in the landscape, although, as a non-persistent transmission, the time elapsed between the tasting and the transmission to host plant are a few minutes. Furthermore, we found that aphids that are related to the viral incidence of maize fields were mainly and positively affected by the landscape at 200 m. This result confirms that the vectors of potyviruses that infect maize come mainly from the edges close to maize and not so much from other habitats.

Here, we present results and patterns that occur throughout the development of maize crops based on the effects that the elements of the agricultural landscape have on the abundance of the main species of insects, such as in the epidemiology of vector-borne viruses in maize. We can conclude that field management is the variable with the greatest weight both in the abundance of insects and in the viral incidence in the cultivation of maize, although it is not detached from the landscape structure. NE species appear to come from alfalfa more than from semi-natural habitats, and in the case of viruses, edges are highly potential areas for harbouring the viruses from one year to the next. Therefore, it is essential to adapt the planting dates both to decrease the presence of high population peaks of vectors and high viral incidences. We mainly suggest that the rotations that delay maize planting in May and June should be avoided in this area. Moreover, we insist that there is an urgent need to increase semi-natural habitat areas and their diversity as a basis for the improvement and establishment of an effective BC programme. These results strongly impact the current IPM plan but aim to improve agricultural production in the area, which is ultimately the justification for this thesis.

For more sustainable pest management, future efforts should contemplate developing tools that inform farmers when their land-use decisions represent a win-win among (1) multiple ecosystem services, (2) the landscape effects modulated by local field management, and (3) the biology of herbivores and their NE or infectious diseases. In the future, research directions will also include models that incorporate the key variables of landscape structure, diversity predictors, and local farming practices as well as the species dynamic. Trophic networks will be used to account for biotic interactions in NE and herbivores relationships and their effect on the BC efficacy. Finally, the sensitivity of NGS sequencing will be used to increase our understanding of the ecology of infectious diseases in the agroecosystems.

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Conclusions

CONCLUSIONS

The results of this thesis show the effect of both field management and agricultural landscape on the abundance of insect species and viral incidence in maize crops in northeastern Spain. These results are of great importance since they help to establish a reference framework for the evaluation of the effects of changes in cultural practices in the current programme of integrated pest management (IPM). Our results open a broad framework in the future towards the use of new statistical and spatial methodologies, as well as the creation of new focus points of studies in this area.

1. Models that study trophic and viral epidemiology relationships at scales greater than the field itself should consider both landscape and local structure variables, as well as introduce the temporality of ecological processes determined by the area of study and the cultivation itself.

2. The effects of landscape are strongly modulated by the effects of field management. Future efforts in IPM programmes should develop tools to inform farmers and their advisors on how herbivore populations, natural enemies and viral epidemiologies are affected by the management of the crop locally.

3. The growing surface of fruits negatively affects the abundance of natural enemies (NE) in maize as a consequence of intensive management in agricultural practices. However, the plant cover of these plants in summer can cause a greater presence of herbivores in maize.

4. Alfalfa is a crop that is a resource for both predatory and herbivorous species in maize. In intensive agricultural landscapes, this crop plays a more important role in the abundance of species in maize than semi-natural habitats.

5. The presence of edges does not have great effects on NE but does on the viral epidemiology of MDMV, SCMV and MRDV. This is due to the low diversity of species at the edges, the abundance of alternative hosts that are the source of inoculum and the management of edges, especially during the maize planting season.

6. Seminatural habitats, forest and landscape diversity do not positively affect the abundance of NE in maize crops. However, the presence of these areas decreases the viral incidence of the two potyviruses studied.

7. Changes in crop management, especially the rotation of winter and spring cereals and the delay of maize planting, increase the viral incidence of the 3 main viruses in our study area.

8. Contrary to our initial hypothesis, landscapes dominated by cereals do not increase the viral incidence but other crops such as fruit trees offer in summer, thanks to irrigation, a more important resource for virus vectors.

CONCLUSIONES

Los resultados de la presente tesis muestran el efecto que tienen tanto el manejo del campo como el paisaje agrícola en la abundancia de especies de insectos y en la incidencia viral en cultivos de maíz del nordeste de España. Estos resultados son de gran importancia ya que ayudan a establecer un marco de referencia para la evaluación de los efectos que tienen los cambios en las prácticas culturales en el actual programa de control integrado de plagas (CIP). Nuestros resultados abren un amplio marco de trabajo en el futuro hacía el uso de nuevas metodologías estadísticas y espaciales, así como la creación de nuevos focos de estudios en esta área.

1. Los modelos que estudian las relaciones tróficas y de epidemiologia viral a escalas mayores que el propio campo deben contemplar tanto variables de estructura del paisaje y locales, así como introducir la temporalidad de los procesos ecológicos determinada por el área de estudio y el propio cultivo.

2. Los efectos del paisaje están fuertemente modulados por los efectos del manejo del campo. Futuros esfuerzos en programas de CIP deben desarrollar herramientas que informen a los agricultores y a sus asesores sobre cómo las poblaciones de herbívoros, de enemigos naturales y las epidemiologias virales están afectados por el manejo que se haga localmente en el cultivo.

3. La creciente superficie de frutales afecta negativamente a la abundancia de los EN en maíz como consecuencia de un manejo intensivo en las prácticas agrícolas. Sin embargo, las cubiertas vegetales de estos en verano pueden causar una mayor presencia de herbívoros en maíz.

4. La alfalfa se presenta como un cultivo que es recurso tanto para las especies de depredadores como para los herbívoros en el maíz. En paisajes agrícolas intensivos este cultivo juega un rol más importante en la abundancia de especies en maíz que los hábitats semi-naturales.

5. La presencia de márgenes no tiene grandes efectos en los EN pero sí en la epidemiología viral del MDMV, SCMV y MRDV. Esto es consecuencia de la poca diversidad de especies en los márgenes, la abundancia de huéspedes alternativos que son fuente de inóculo y el manejo de los márgenes especialmente en la época de siembra del maíz.

6. Los hábitats semi-naturales, el bosque y la diversidad del paisaje no afectan positivamente a la abundancia de EN en el cultivo del maíz. Sin embargo, la presencia de estas áreas disminuye la incidencia viral de los dos potyvirus estudiados.

7. Los cambios de manejo de los cultivos, especialmente la rotación de cereales de invierno y primavera, retrasan las fechas de siembra del maíz aumentado la incidencia viral de los 3 principales virus en nuestra área de estudio.

8. En contra de nuestras hipótesis, paisajes dominados por cereales no incrementan la incidencia viral sino que otros cultivos como los frutales ofrecen en verano, gracias al regadío, un recurso más importante para los vectores de virus.

Había un lenguaje en el mundo que todos entendían. Era el lenguaje del entusiasmo, de las cosas hechas con amor y con voluntad, en busca de algo que se deseaba o en lo que se creía.

El Alquimista, Paulo Coelho

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La influencia del paisaje agrícola en el control biológico desde una perspectiva espacial

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La intensificación agrícola modifica y simplifica el paisaje agrícola alterando los servicios ecosistémicos que la biodiversidad proporciona a los agroecosistemas, especialmente el control biológico de plagas. Con el objetivo de ofrecer una perspectiva general sobre la influencia que el paisaje agrícola puede tener sobre el control biológico, en la presente revisión se recopilan diversos artículos que analizan los efectos del paisaje desde una perspectiva de complejidad y composición espacial. Encontramos que existe una creciente literatura científica, que sugiere que la presencia de hábitats naturales beneficia a los enemigos naturales en los agroecosistemas. Sin embargo, la baja eficacia del control biológico sigue siendo uno de los principales retos en estos estudios. Entender los patrones de abundancia y movimiento de las especies de enemigos naturales y de herbívoros en los paisajes agrícolas es altamente complejo (espacial y temporalmente), lo que dificulta su interpretación y comparación entre estudios. Aunque el uso de redes tróficas todavía es muy escaso en la literatura, su aplicación en este tipo de estudios supone un desarrollo prometedor.

Palabras clave: enemigos naturales; paisaje; escalas del paisaje; ecología del paisaje; agroecosistema; complejidad del paisaje; composición del paisaje; hábitat natural; redes tróficas

Clemente-Orta, G., Álvarez, H.A. 2019. The influence of agricultural landscape in biological control from a spatial perspective. *Ecosistemas* 28(3):13-25. Doi.: 10.7818/ECOS.1730

Agricultural intensification simplifies and modifies the agricultural landscape, disturbing the ecosystem services that biodiversity provides to agroecosystems, particularly the biological control. In this review we gathered several articles that analyse landscape from the perspective of spatial composition and spatial complexity. Our aim was to present an overall view of the influence that an agricultural landscape may have on biological control. We found that there is an increasing scientific literature that suggest that the presence of natural habitats beneficiates natural enemies within agroecosystems. However, inefficient biological control supposes a great challenge in this type of studies. Understanding the patterns of movement and abundance of the species of herbivores and natural enemies in agricultural landscapes is highly complex (temporal and spatial) and this hinder its interpretation and comparison amongst studies. Although the use of a trophic network approach is still scarce in the literature, however, its application at different scales may entail a promising development in such research.

Key words: natural enemies; landscape; landscape scales; landscape ecology; agroecosystem; landscape complexity; landscape composition; natural habitat; food webs

Introducción

La pérdida de la biodiversidad y los cambios correspondientes en la composición de las especies alteran los servicios que los ecosistemas proporcionan a la humanidad (Cardinale et al. 2012). Concretamente en los agroecosistemas, la intensificación agrícola, los monocultivos, el uso continuo de productos fitosanitarios y la fragmentación de los hábitats naturales, ha resultado en la pérdida de uno de los servicios ecosistémicos más importantes para la producción agrícola: el control biológico (Eilenberg 2006). El control biológico se distingue de otras formas de control de plagas por actuar de una manera denso-dependiente, es decir, la población de enemigos naturales se incrementa y depredan o parasitan una gran proporción de presas cuando éstas incrementan su población en un cultivo (DeBach 1964; DeBach y Rosen 1991). En cualquier programa de control biológico, la conservación de los enemigos naturales es un elemento crítico. Esto implica que es necesario identificar el o los factores que limitan la cantidad y/o efectividad de los enemigos naturales en el agroecosistema. De manera que es preciso entender que los paisajes agrícolas son ecosistemas simplificados (agroecosistemas) donde se producen diversos recursos, pero también donde se establecen complejas interacciones ecológicas entre todos sus componentes.

El Paisaje

El paisaje como una unidad de organización

Existen varias definiciones aplicadas al paisaje, consecuencia de su evolución multidisciplinar y de la diversidad de perspectivas con las que se puede identificar este concepto (McGarigal y Cushman 2005). El Convenio Europeo del Paisaje (ELC) lo define como “un área, como la perciben las personas, cuyo carácter es el resultado de la acción e interacción de factores naturales y/o humanos”. Desde una perspectiva más ecológica, el paisaje está definido como “una unidad de organización mayor que el ecosistema” (Burel y Baudry 1999). Según la Teoría General de Sistemas, un paisaje, (1) no está necesariamente definido por su tamaño, sino por un mosaico de parches que interactúan entre sí, los cuales son relevantes para el fenómeno de estudio (McGarigal y Cushman 2005); (2) es un sistema abierto donde los flujos de energía se mueven hacia dentro o hacia fuera del mismo; y (3) está caracterizado por su heterogeneidad tanto espacial como temporal (von Bertalanffy 1993; Wagner y Fortin 2005; Martin et al. 2016).

Desde el laboratorio hasta el paisaje

Los estudios tradicionales de control biológico en ensayos de laboratorio desarrollaron medidas de control eficientes desde un enfoque del comportamiento del insecto (la herbivoría, el parasitismo, la colonización y la competencia). La extrapolación de estos resultados entre el laboratorio y el campo estaba bajo el supuesto de que las parcelas donde se obtenían las muestras de un experimento debían ser esencialmente iguales, asumiendo una homogeneidad en el espacio y el tiempo. Este hecho permitía controlar estadísticamente la variación ambiental y las relaciones entre diferentes variables (Wagner y Fortin 2005). Pero, los procesos ecológicos son inherentemente espaciales y las parcelas o zonas de estudio, son afectadas por la interacción local y el entorno circundante (“neighbouring units”, Levin 1992; y posteriomente “landscape context”, Pearson 2002) lo que da lugar a patrones entrelazados en múltiples escalas.

El desarrollo de herramientas en sistemas de información geográfica (SIG) y de paquetes estadísticos libres, propició una cascada de metodologías para abordar desde diferentes enfoques el control biológico. Pero no siempre se puede comparar y mantener la resolución de un estudio de laboratorio en uno de campo (Scherber et al. 2012). Este reto científico se puede abordar desde diferentes escalas: regional, paisaje o local (**Fig. 1**).

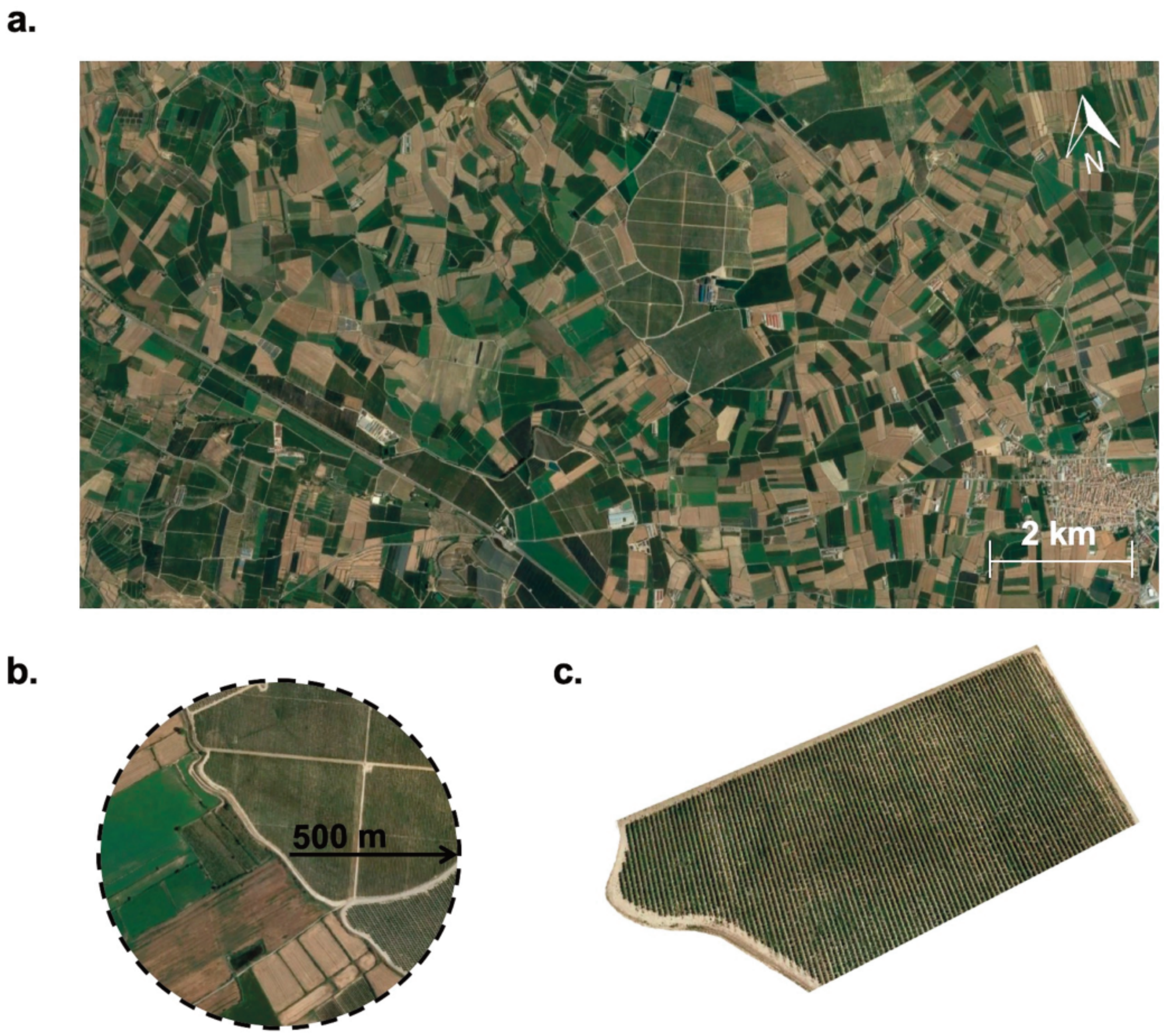


*Figura 1. Diferentes escalas de estudio en el agroecosistema. Escala regional (**a**), escala de paisaje basada en un área de influencia alrededor del campo de muestreo (**b**) y escala local a nivel de campo (**c**). Las escalas espaciales cambian dependiendo del tipo de organismos: pequeñas en plantas (primer nivel trófico) e intermedias en herbívoros (segundo nivel trófico). En cambio, la escala espacial en poblaciones de depredadores (tercer nivel trófico) es amplia y puede experimentar muchos cambios y depende del tamaño corporal y de la especialización de la especie (e. g. parasitoides especializados).*

*Figure 1. Different scales of study in the agroecosystem. Regional scale (**a**), landscape scale based on an area of influence around the sampling field (**b**), and local scale at field level (**c**). The spatial scales change depending on the type of organisms: small in plants (first trophic level) and intermediate in herbivores (second trophic level). In contrast, the spatial scale in populations of predators (third trophic level) is wide and can undergo many changes, which depends on the body size and specialization of the species (e.g., specialized parasitoids).*

Por otro lado, la estructura (configuración y composición) de la matriz agrícola ejerce una influencia tanto en insectos herbívoros y sus enemigos naturales, como en las interacciones entre estos (Tscharntke et al. 2005). Así, en un estudio ideal del agroecosistema, la parte experimental debería contemplar: (1) el establecimiento de un borde o limite, (2) fragmentos de distintos tipos de hábitats, (3) una caracterización de la composición y configuración de la matriz agrícola, (4) un registro de tratamientos fitosanitarios (en el cultivo y en los hábitat circundantes), (5) abundancias de herbívoros y enemigos naturales, (6) tasas de depredación y/o parasitismo y finalmente (7) una cuantificación de la producción final. Sin embargo, llegar a conseguir todas estas variables en muchos casos es complicado por razones de logística y de limitaciones económicas y humanas debido a que los estudios a escalas de paisaje cubren grandes áreas agrícolas, cuyos campos son manejados por diferentes agricultores. En estas circunstancias, donde existe una variabilidad tan alta, la cual es difícil de controlar, los estudios son establecidos en gradientes de complejidad y/o composición y configuración.

Ecología del paisaje

Históricamente, la definición de ecología del paisaje y el paisaje han evolucionado de manera conjunta y continua. El término ecología del paisaje mantiene una clara vinculación con la geografía (Vila Subirós et al. 2006). Troll (1939) fue el primero en utilizar la expresión “landscape ecology”, y la definió como “el estudio de toda la complejidad de relaciones causa-efecto que existen entre las comunidades de seres vivos y sus condiciones ambientales, en una sección específica de paisaje”. En general, la principal contribución que hace la ecología del paisaje es aceptar que: (1) la mayoría de los procesos ecológicos son inherentemente espaciales (Levin 1992), y (2) están limitados por las condiciones ambientales que varían en el espacio y el tiempo, así como por la interacción local con otros procesos a múltiples escalas (Wagner y Fortin 2005). La ecología del paisaje particularmente se ha desarrollado en los últimos años para establecer cuál es el efecto de la antropización sobre los ecosistemas y la repercusión sobre los servicios ecosistémicos, los cuales dependen del mantenimiento de una alta diversidad biológica y de sus interacciones (Altieri 1994; 1999) (**Fig. 2**).

El paisaje como una variable cuantitativa

El concepto base para llevar a cabo la interpretación de un paisaje es el mosaico, que puede ser aplicado desde una escala microscópica hasta una planetaria. El mosaico está compuesto a su vez por un conjunto de elementos (landscape-elements): los fragmentos (patches), los corredores (corridors) y la matriz (matrix). En lo que respecta a la “composición de un paisaje”, esta viene definida por los tipos de parches que coexistan en un paisaje y su abundancia relativa (Wagner y Fortin 2005). Estos parches, además, pueden ser de varias formas y tamaños y su disposición puede variar en el espacio (Steffan-Dewenter et al. 2002), por lo que “la configuración de un paisaje” describe la forma de los parches y la disposición de uno respecto al resto (Gustafson 1998). De manera que, para describir la heterogeneidad de un paisaje (también llamada estructura del paisaje), se pueden utilizar ambas aproximaciones: heterogeneidad de la composición y heterogeneidad de la configuración (Fahrig y Nuttle 2005). La existencia de “índices de paisaje” que resultan de la aplicación de métodos cuantitativos en ecología del paisaje, permiten comparar entre distintas composiciones y configuraciones espaciales en distintos momentos, tanto a nivel de fragmentos como de paisaje (FRAGSTATS, McGarigal y Marks 1995) (Botequilha et al. 2006; McGarigal et al. 2012).

Figura 2. *Manejo del paisaje agrícola: vistas aéreas y panorámicas de dos agroecosistemas en el norte de España. Paisaje moderadamente simplificado (izquierda). Paisaje altamente simplificado (derecha). La actividad humana destaca como una de las principales actividades que modifican la estructura espacial del paisaje. Una actividad moderada favorece la diversificación de formas en el paisaje mientras que, una actividad intensa aumenta la simplificación de este. Fuente: G. Clemente-Orta.*

Figure 2. *Agricultural landscape management: aerial and panoramic views of two agroecosystems in northern Spain. Moderately simplified landscape (left). Highly simplified landscape (right). Human activity stands out as one of the main activities that modify the spatial structure of the landscape. A moderate activity favors the diversification of forms in the landscape while, an intense activity increases the simplification of this. Source: G. Clemente-Orta.*

Funcionalidad de los elementos del paisaje

En los agroecosistemas, las prácticas agrícolas tienen efectos sobre la biodiversidad (Rusch et al. 2010). Estos efectos pueden ser observados tanto a escala local (el propio campo) como a escala de paisaje (hábitats circundantes) (Landis et al. 2000; Tscharntke et al. 2007). La fragmentación del hábitat natural ha sido documentada como una de las principales causas de la extinción y pérdida de la biodiversidad de las especies (Tilman et al. 2001; 2002). Por ejemplo, la cantidad, estructura y forma de la superficie de estos fragmentos (parches) genera efectos positivos o negativos sobre la abundancia y diversidad de los insectos (Bianchi et al. 2006; Tscharntke et al. 2012). Diversos autores sugieren que la respuesta de las especies a la forma y calidad del hábitat se puede entender desde un contexto de disponibilidad del recurso (Ries y Sisk 2004; Ries et al. 2004) y que a través de mecanismos como: (1) la distribución complementaria del recurso (Dunning et al. 1992; McCollin 1998; Fagan et al. 1999); (2) el desbordamiento (“spillover”) (Shmida y Wilson 1985); y (3) los hábitats mejorados (Cadenasso et al. 1997) pueden jugar un papel muy importante para predecir cómo los organismos se concentrarán en diferentes tipos de hábitats (Álvarez et al. 2016; 2017; Cotes et al. 2018). Esta disponibilidad de los recursos se traduciría en el desplazamiento de las especies: (1) entre hábitats no-cultivados, (2) desde el hábitat natural (como fuente de especies) al cultivo, y (3) desde el cultivo (como fuente de especies generalistas) al hábitat natural circundante (Tscharntke et al. 2007). Debido a esto, es posible que en muchos agroecosistemas se produzcan efectos de concentración (Root 1973) o de dilución de las poblaciones (Otway et al. 2005) y que las diferencias de abundancia de las especies se asocien a un determinado hábitat y/o recurso (Moreira et al. 2016). Estos patrones de respuesta de la abundancia de las especies a dicho recurso permiten establecer un criterio de calidad en los paisajes agrícolas a través de la identificación y cuantificación de la diversidad de grupos funcionales presentes como un estimador de la resiliencia del sistema (Bengtsson et al. 2003; Loreau et al. 2003).

En consecuencia, a lo largo de los años, los agricultores han aprendido a estimular las poblaciones de EN (depredadores y parasitoides) a través del manejo y la conservación de los agroecosistemas (Symondson et al. 2001; Rusch et al. 2010). Por ejemplo, en Europa el reconocimiento de la pérdida de la biodiversidad se ha traducido en programas agroambientales para mejorar la biodiversidad en diferentes cultivos, como lo es el uso de cubiertas vegetales (García et al. 2018) y de márgenes entre cultivos (Malavolta y Perdikis 2018) o entre invernaderos (Rodríguez et al. 2018; Cotes et al. 2018). Estas perspectivas se basan en la hipótesis de que el aumento de la abundancia y diversidad de enemigos naturales impacta directamente en las plagas, disminuyendo su abundancia y con ello las pérdidas en la producción (Rusch et al. 2010; Tscharntke et al. 2012).

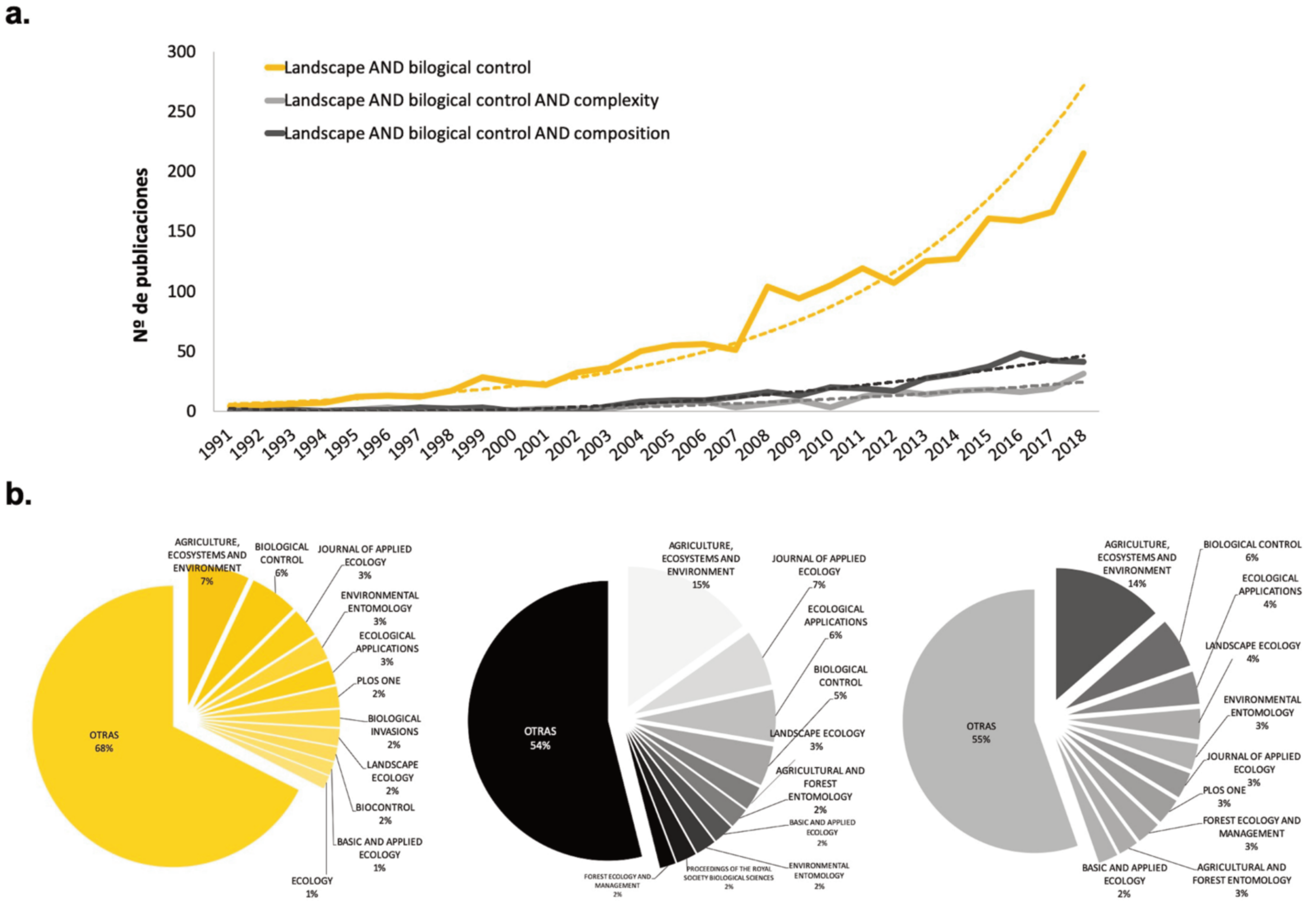
Relación entre la complejidad del paisaje y su función

Si bien algunos autores definen el paisaje en términos de complejidad del hábitat, midiendo los tipos de hábitats presentes en un área de influencia, área de estudio o región, este término ha sido más comúnmente utilizado como la cantidad o proporción de hábitat no cultivado, también definido como hábitat natural o hábitat semi-natural (variable de composición) en los agroecosistemas. Ésta es posiblemente la métrica más simple para caracterizar la complejidad de un hábitat y se usa ampliamente porque a menudo se correlaciona con los índices de diversidad de Shannon o de Simpson (Thies y Tscharntke 1999). Así, paisajes muy complejos (altos porcentajes de hábitat natural) normalmente presentan altos índices de diversidad. La **Figura 3** muestra la reciente evolución de los estudios que abordan la complejidad y composición del paisaje, así como las principales revistas en las que se han publicado estos resultados (tendencia basada en los resultados de búsquedas en la Web of Science, WoS). Estos gráficos ilustran que desde hace una década el marco de trabajo ha tomado relevancia y que son las revistas de corte ecológico las que un mayor número de publicaciones tienen.

El paradigma establece que los paisajes complejos incrementan la abundancia de enemigos naturales y que a consecuencia de este fenómeno se produce un efecto positivo en el control biológico de plagas (Bianchi et al. 2006) lo que se ha denominado como “la hipótesis del hábitat-complejo” (Álvarez et al. 2019). Así por ejemplo, Marino y Landis (1996) mostraron que la diversidad de especies de parasitoides en campos de maíz no variaba ni se veía influenciada por la cercanía del hábitat natural en paisajes simples o complejos (campos pequeños con márgenes y hábitat natural), pero que el porcentaje medio de parasitismo era significativamente mayor en paisajes complejos. Otros autores, mostraron que la presencia de márgenes y barbechos incrementaban la biodiversidad de enemigos naturales, las tasas de depredación y el parasitismo (Thies y Tscharntke 1999). Asociar la abundancia y la diversidad de enemigos naturales con el control biológico de plagas ha mostrado resultados positivos en la mayoría de los casos pero existen unos pocos estudios que muestran efectos neutros e incluso efectos negativos (Finke y Denno 2002; 2005).

Tylianakis y Romo (2010) apuntaban al hecho de que es necesario conocer mucha más información acerca de las presas para poder establecer un buen control biológico en los sistemas agrícolas. Por su parte Chaplin-Kramer et al. (2011) cuestionaban si una alta diversidad de enemigos naturales mejora la función del control biológico *per se,* por lo que realizaron un metanálisis con 46 estudios a nivel de paisaje. Estos encontraron que los enemigos naturales tenían una fuerte respuesta positiva a la complejidad del paisaje, siendo más fuerte esta respuesta en los enemigos naturales generalistas en todas las escalas medidas; sin embargo, los enemigos naturales especialistas respondieron con más fuerza a escalas más pequeñas. Como ya habían apuntado Chaplin-Kramer et al. (2011), la respuesta positiva de los enemigos naturales a la complejidad del paisaje no tenía por qué traducirse necesariamente en un control biológico más efectivo (Bianchi et al. 2006; Rusch et al. 2010), ya que puede ocurrir que la abundancia de plagas muestre una respuesta significativa a la complejidad del paisaje (Chaplin-Kramer et al. 2011). Concepción et al. (2012) en un estudio realizado con 232 campos ubicados en seis países, concluyen que el manejo del cultivo tenía efectos sobre la riqueza de las especies pero que era dependiente de la complejidad de cada agroecosistemas, siendo los más de efectivos los paisajes de complejidad intermedia (medido como km márgenes semi-naturales y % hábitat no cultivado). Otros estudios centrados en la abundancia y diversidad de polinizadores y enemigos naturales, sugieren que las prácticas de manejo y de la calidad de los hábitats naturales locales, especialmente de setos y márgenes, son las variables más importantes para muchas especies (Garratt et al. 2017).

Por otro lado, variables como la medición de dinámicas poblacionales (en lugar de los recuentos estáticos), no se están considerando en los estudios para poder caracterizar mejor la variabilidad de respuestas en relación con la complejidad del paisaje y el control biológico. Así, Chaplin-Kramer et al. (2013) midieron la abundancia semanal de enemigos naturales (larvas de sírfidos) y de pulgones en cultivos de brócoli durante tres años. Los resultados mostraron que la abundancia de larvas de sírfidos aumentó potencialmente con la proporción de hábitat natural disminuyendo la abundancia de los pulgones. Además, los autores señalan que cuando agregaron los datos en promedios anuales (una métrica común en las investigaciones dirigidas al control biológico) no se observó dicho efecto. Estos resultados sugieren que una resolución temporal más alta de los datos de los enemigos naturales y la dinámica de abundancia de las plagas puede revelar un control “top-down” en los agroecosistemas, que de otra manera puede estar enmascarado por la variación estacional e interanual en los factores ambientales (Plećaš et al. 2014). Raymond et al. (2015) encontraron que, aunque la eficiencia del control biológico parecía ser mayor en paisajes estructuralmente simples, los paisajes complejos mostraron una colonización más temprana de los enemigos naturales que podría



"Landscape AND biological control" "Landscape AND biological control AND complexity" "Landscape AND biological control AND composition"

Figura 3. *Evolución del número de publicaciones (**a.**) y porcentaje de revistas (**b.**) que estudiaron el paisaje junto con el control biológico de plagas, basado en búsqueda avanzada en la Web of Science. Se representan tres parámetros: (1) paisaje + control biológico; (2) paisaje + control biológico + complejidad; y (3) paisaje + control biológico + composición (categorías de refinamiento: Ecología, Entomología, Ciencias ambientales, Conservación de la biodiversidad, Agricultura multidisciplinaria, Ciencias multidisciplinarias, Ciencias de las plantas, Agronomía, Silvicultura, Biología, Estudios ambientales).*

Figure 3. *Evolution of the number of papers (**a.**) and percentage of journals (**b.**) that studied the landscape and biological control of pests, based on advanced search in the Web of Science. It is represented three parameters: (1) landscape and biological control; (2) landscape and biological control and complexity; and (3) landscape and biological control and composition (categories of refinement: Ecology or Entomology or Environmental Sciences or Biodiversity Conservation or Agriculture Multidisciplinary or Multidisciplinary Sciences or Plant Sciences or Agronomy or Forestry or Biology or Environmental Studies).*

facilitar y asegurar un control biológico temprano y eficiente sobre las poblaciones de pulgones. Recientemente Karp et al. (2018) en un análisis donde comparan 132 estudios realizados en 6759 parcelas concluyen que en la mayoría de los casos, los hábitats no cultivables circundantes a los cultivos no mejoraron el control biológico, y que este control sólo se observa en pocos cultivos con características muy específicas. Por lo que plantea si el hecho de no encontrar una relación positiva entre la diversidad de enemigos naturales y la regulación del control biológico podría deberse a que la mayoría de estudios espaciales no incluyen realmente la dinámica temporal como variable explicativa, además de que existen diversas metodologías para cuantificar el control biológico. De manera que investigar tanto la diversidad como la dinámica temporal de los diferentes gremios de enemigos naturales, podría ayudar a entender mejor la relación entre diversidad funcional y control biológico en los agroecosistemas (Ortiz-Martínez y Lavandero 2018; Álvarez et al. 2019). Otra posible explicación aportada por Tscharntke et al. (2016) es que el hecho de que los hábitats naturales incrementen la abundancia de enemigos naturales, pero no produzcan un control biológico dentro del agroecosistema puede ser explicado en un contexto de interacciones ecológicas y manejo humano (**Fig. 4**).

Aún con una larga lista de literatura científica al respecto, continua la variabilidad de los resultados obtenidos y el desconocimiento de un control biológico más efectivo, ver **Tabla 1**. Además, son escasos los estudios que puedan cuantificar en rendimientos económicos los beneficios aportados por la estructura del paisaje y el control biológico en los cultivos. Uno de los pocos estudios que cuantifica dicho efecto es el de Paredes et al. (2019) que muestran como la presencia de parches de hábitat natural en el agroecosistema del olivo aumenta el control biológico sobre *Prays oleae*, produciendo rendimientos por valor de 186.36 € / ha.

Relación entre la composición del paisaje y su función

A pesar del aumento reciente de las investigaciones científicas sobre la complejidad del hábitat y los enemigos naturales (**Fig. 3**), así como el poder predictivo que reflejan, se ha argumentado que la funcionalidad del hábitat (fuente/recurso) podría ser más acertada para una especie o grupo en concreto (Fahrig et al. 2011). Los hábitats pueden clasificarse en categorías de acuerdo con su potencial para proporcionar refugio, alimento, sitios de oviposición o algún otro beneficio a las especies de enemigos naturales (Östman et al. 2001). Por ejemplo, una aproximación a esta medida sería tener en cuenta todo el perímetro de los parches (Martin et al. 2016), el tamaño del campo muestreado (Bosem et al. 2017), o la métrica de coste-distancia (Perović et al. 2010).

Tabla 1. *Resumen de los efectos de la complejidad del paisaje en distintos estudios medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos así como el efecto sobre el control biológico (CB) en los agroecosistemas.*

Table 1. *Summary of the effects of the complexity of the landscape in different studies measured on abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in agroecosystems.*

Autores	**Escala espacial (m)**	**Taxón**	**Categoría**	**Variable**	**Efectos en:**			
					A	**D**	**P**	**CB**
Marino y Landis 1996	3200	Lepidoptera	Herbívoro	% HN	-			
		Hymenoptera	Parasitoide	% HN	+	+	+	+
Thies y Tscharntke 1999	1500	Coleoptera	Herbívoro	% semi-HN	-			
		Hymenoptera	Parasitoide	% semi-HN	+		+	+
Finke y Denno 2002	Jaula	Hemiptera	Depredador	% HN	+			+
		Araneae	Depredador	% HN	+			0
Finke y Denno 2005	Invernadero	Araneae	Depredador	% HN	+	+		+
		Coleoptera	Depredador	% HN	+	+		+
		Hemiptera	Depredador	% HN	+	+		+
		Araneae	Depredador	% HN	+	+		+
Chaplin-Kramer et al. 2013	500, 100 y 1500	Diptera	Depredador	% HN	+			+
Plećaš et al. 2014	1000 a 6000	Hemiptera	Herbívoro	% HN	+			
	500 a 2000	Hymenoptera	Parasitoide	% HN	+		+	0
Raymond et al. 2015	500	Coleoptera	Depredador	% HN	+	+		+
		Coleoptera	Depredador	% HN	+	+		+
Garratt et al. 2017	500	Hymenoptera	Polinizador	% semi-HN	+			
		Araneae	Depredador	% semi-HN	+			+
Ortiz-Martínez y Lavandero 2018	500	Hemiptera	Herbívoro	% HN	-			
		Hymenoptera	Parasitoide	% HN	-		-	0
		Hymenoptera	Parasitoide	Int. agrícola	+		+	+
		Coleoptera	Depredador	% HN	+	+		+
Paredes et al. 2019	1000	Lepidoptera	Herbívoro	% HN	-			
		Hemiptera	Depredador	% HN	+			+

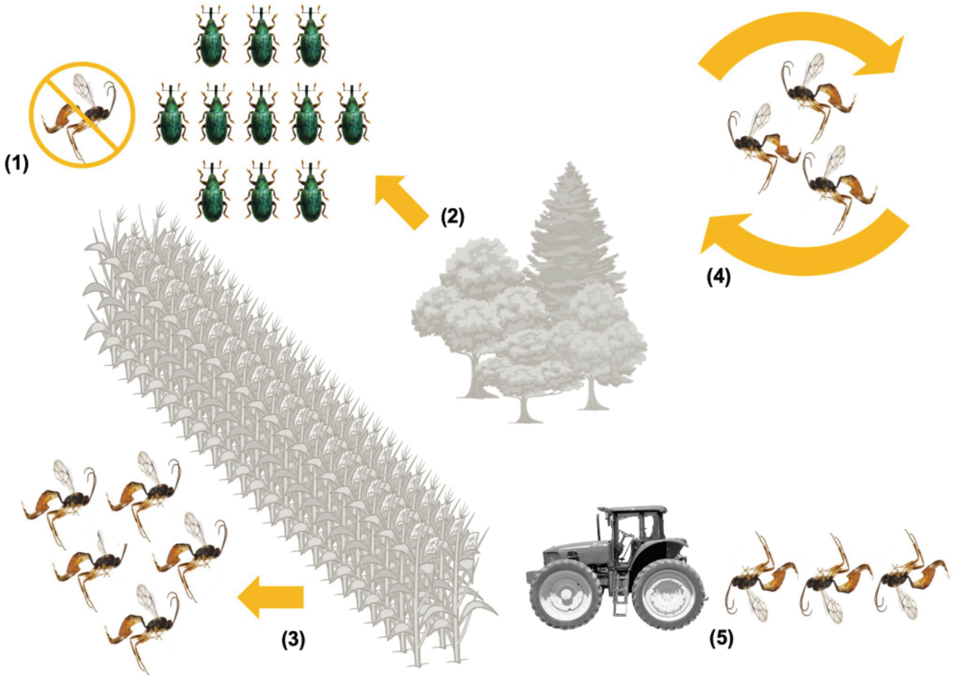


Figura 4. *Procesos por los cuales el hábitat natural no provee un control biológico de plagas efectivo. (**1**) Las plagas no tienen enemigos naturales efectivos en la región. (**2**) El hábitat natural es un "recurso-fuente" mayor para las plagas. (**3**) Los cultivos proveen recursos más importantes para los enemigos naturales. (**4**) El hábitat natural es insuficiente para generar poblaciones de enemigos naturales. (**5**) Las prácticas agrícolas contrarrestan el establecimiento de los enemigos naturales (adaptado de Tscharntke et al. 2016).*

Figure 4. *Processes by which natural habitat fail to provide an effective biological pest control: (**1**) Pest populations have no effective natural enemies in the region. (**2**) Natural habitat is a greater source of pests. (**3**) Crops provide more important resources for natural enemies. (**4**) Natural habitat is insufficient to provide natural enemy populations. (**5**) Agricultural practices counteract natural enemy establishment (adapted from Tscharntke et al. 2016).*

La composición y organización espacial del agroecosistema son dos aproximaciones importantes para determinar la dinámica poblacional de los enemigos naturales (Rusch et al. 2010). Además, en este tipo de estudios es más común encontrar variables locales ya que, factores como la elección del cultivo, la fecha de siembra y prácticas de fertilización o los tratamientos fitosanitarios pueden modificar las interacciones entre las plagas y los cultivos (en el tiempo o en el espacio) (Médiène et al. 2011). Así, en estos análisis, la cantidad de variables que se generan con datos espaciales y locales es alta y necesitan ser optimizadas y simplificadas (Zuur et al. 2010; Dormann et al. 2013; Pasher et al. 2013), ver **Tabla 2**.

Maisonhaute et al. (2010) estudiaron si la estructura del paisaje era la variable que explicaba la mayor parte de la variación en especies de escarabajos depredadores en comparación con las prácticas agrícolas y el ambiente local. Ellos encontraron que el hábitat natural y la heterogeneidad del paisaje tuvieron una influencia positiva tanto en la abundancia como en la diversidad de escarabajos depredadores, aunque la estructura del paisaje fue el factor principal. Holzschuh et al. (2010) encontraron diversas respuestas en función de las especies, de manera que las abejas fueron más sensibles a altos porcentajes de hábitat natural en el paisaje; las avispas dependieron de altas densidades de márgenes; y que los parasitoides estuvieron fuertemente ligados a sus huéspedes. Ellos concluyeron que la conversión de hábitat cultivable en no cultivable no era una estrategia lo suficientemente exitosa para mejorar las poblaciones de estos himenópteros porque son más afectados por el aislamiento que por la pérdida del hábitat. Otras especies como los carábidos (depredadores generalistas) en cambio pueden verse beneficiadas en paisajes agrícolas simplificados. En ese sentido, los autores resaltan que este hecho no implica necesariamente un mejor control biológico de plagas en estos ambientes, puesto otros factores como que algunas especies de enemigos naturales pueden competir entre ellos (depredación intragremial), podría limitar su capacidad para controlar las plagas (Caballero-López et al. 2012). Ardanuy et al. (2018) encontró que la abundancia de *Orius* spp., uno de los depredadores generalistas más importantes en el maíz, no respondía a la composición del hábitat, sino que presentaba una fuerte relación positiva con la abundancia de su principal presa y con la densidad de márgenes en el paisaje.

La diversidad de enemigos naturales junto con los rendimientos en los cultivos, podrían mejorar si se optimizan los efectos de distintos parámetros del paisaje, especialmente la configuración y diversidad del paisaje a diversas escalas de estudio (Martin et al. 2016). En línea con esto, Maisonhaute et al. (2017) señalan que el control biológico de los pulgones de la soja podría mejorar si se reduce la proporción de soja en el agroecosistema, se aumenta la riqueza de cultivos y se conservan los bosques naturales. También, Bosem et al. (2017) muestran (por primera vez) que la abundancia de pulgones de cereal podría ser reducida en el agroecosistema si se optimizará la composición (diversificación de cultivos), la configuración (mantener pequeños campos con márgenes); y añaden que la heterogeneidad temporal (rotación) se muestra como un factor clave dentro del mosaico de cultivos del agroecosistema.

En estos estudios de estructura del paisaje la elección, simplificación y agrupación de las variables no es sencilla. Por ejemplo, Janković et al. (2017) muestran que la superficie de cultivo no tiene ningún efecto en los enemigos naturales pero que al separar en pequeñas categorías los distintos tipos de hábitat natural, la variable correspondiente a los setos tuvo un papel importante, tanto para los enemigos naturales como para las plagas. Este patrón no se podría haber revelado si se hubiesen sumado todos los tipos de hábitats naturales del paisaje. Lo anterior sugiere que considerar un enfoque funcional del agroecosistema está intrínsecamente ligado con las características propias de las especies que se vayan a contemplar en los estudios de paisaje. Kebede et al. (2018) encontraron que, aunque la abundancia de especies de parasitoides y moscas parásitas no estaba influenciada por el tipo de margen, los campos más pequeños y con más bordes podían soportan densidades de enemigos naturales relativamente más altas. Además, señalan que la proporción de un monocultivo puede anular todos los factores de manejo y gestión a nivel del campo, por lo que para el manejo de ciertas plagas es necesario considerar un enfoque a escalas de paisaje amplias, por ejemplo, en el caso los barrenadores del maíz. Por su parte, Martin et al. (2019) en un análisis con datos de 49 estudios en 1515 paisajes, muestran que la interacción entre la composición (% de hábitats) y la configuración (densidad de márgenes en el paisaje) aumentan la polinización y la abundancia de enemigos naturales, mejorando finalmente el control biológico concretamente en los agroecosistemas europeos. No obstante, la reciente literatura científica parece estar enfocada en estudiar los efectos de las superficies de cultivos de frutales en las especies. Estos estudios están sugiriendo que el manejo de estos cultivos puede estar afectando negativamente a la colonización (Aviron et al. 2016) y a la abundancia de los enemigos naturales (Samnegård et al. 2018; Yang et al. 2018; 2019), y cuyo efecto no se ha observado en frutales ecológicos (Happe et al. 2019). Markó et al. (2017) muestran que los efectos obtenidos podrían estar enmascarados por la continua inmigración de enemigos naturales desde cultivos herbáceos hasta los frutales, determinado fuertemente por un patrón estacional. Asimismo, proponen que otros cultivos podrían estar actuando como un recurso más importante para los enemigos naturales que ciertos hábitats semi-naturales. Además, sugieren que el uso intensivo de pesticidas en los agroecosistemas podría estar enmascarando los efectos positivos esperados de los hábitats semi-naturales (Ricci et al. 2019). Sin embargo, para que haya una reducción del uso de estos productos debe de producirse una mejora de estos hábitats naturales que garantice un control biológico natural efectivo.

Una tendencia emergente: las redes tróficas

En los últimos años, los estudios ecológicos se mueven cada vez más hacia enfoques basados en rasgos funcionales para entender con más detalle los servicios ecosistémicos que presta la biodiversidad e impulsar sus efectos positivos en los agroecosistemas. Como ya hemos visto, aunque los patrones de los enemigos naturales y su papel en el control biológico están fuertemente ligados a factores intrínsecos del paisaje (Tscharntke et al. 2012; 2016; Veres et al. 2013; Karp et al. 2018), dichos patrones son también afectados por las interacciones tróficas entre los organismos en diferentes nichos y hábitats (Bohan et al. 2013; Massol y Petit 2013).

El enfoque de redes tróficas tiene un alto potencial para añadir valor a las investigaciones en materia de control biológico (Tylianakis y Binzer 2014). Una red describe la interacción entre los componentes de un sistema dado, en forma de enlaces (Bohan et al. 2013). La teoría de redes ecológicas (Strogatz 2001) tiene como objetivo entender cómo las propiedades de una red y sus enlaces se relacionan con los sistemas ecológicos. Así, las redes tróficas describen una serie de interacciones tróficas en una comunidad biológica. Dentro de las redes tróficas, y dependiendo de la naturaleza del objeto de interés (individuos, poblaciones, especies o hábitats), las más utilizadas son las redes de interacciones antagonistas e interacciones mutualistas (Bohan et al. 2013).

Recientemente, los patrones de respuesta de los enemigos naturales y sus efectos sobre las plagas en los agroecosistemas han sido revisados y detallados bajo un contexto de redes ecológicas y redes tróficas (Woodward y Bohan 2013; Tilyanakis y Binzer 2014). Por ejemplo, en su revisión de los efectos de los cambios ambientales sobre el control biológico y las redes tróficas parasitoide – hospedador, Tilyanakis y Binzer (2014) investigan como las redes parasitoide – hospedador afectan directamente al control biológico en los agroecosistemas. Ellos sugieren que la intensificación agrícola tiende a producir redes parasitoide – hospedador de una baja complejidad y donde la fuerza de las interacciones es desigual, lo que en teoría podría diezmar la efectividad del control biológico.

Tabla 2. *Resumen de los efectos de la composición del paisaje en distintos estudios medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos así como el efecto sobre el control biológico (CB) en los agroecosistemas. La integración de las variables locales (VL) son más comunes en este tipo de análisis.*

Table 2. *Summary of the effects of the composition of the landscape in different studies measured on the abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in agroecosystems. The integration of local variables (VL) are more common in this type of analysis.*

Autores	Escala espacial (m)	Taxón	Categoría	Variable	Efectos en:				VL
					A	D	P	CB	
Perović et al. 2010	3000	Hemiptera	Herbívoro	% Pastos	+				
	1500	Coleoptera	Depredador	% HN	+			+	
	120	Araneae	Depredador	% HN	+			+	
	750	Hymenoptera	Parasitoide	% Algodón	+			+	
Maisonhaute et al. 2010	200 y 500	Coleoptera	Depredador	% No cultivo	+	+		+	x
Holzschuh et al. 2010	500	Hymenoptera	Polinizador	% No cultivo	+				x
		Hymenoptera	Polinizador	% semi-HN	+				x
		Hymenoptera	Parasitoide	% semi-HN	+		+	+	x
Caballero-López et al. 2012	2000	Hemiptera	Herbívoro	% Pastos	+				
		Coleoptera	Depredador	% Pastos	+			+	
		Araneae	Depredador	% Pastos	+			0	
		Coleoptera	Depredador	% Pastos	+			0	
		Hymenóptera	Parasitoide	% semi-HN	+			+	
Aviron et al. 2016	100, 200 y 300	Hemiptera	Depredador	% semi-HN	+			+	x
		Hemiptera	Depredador	% Frutales	-			-	x
Martin et al. 2016	100 a 1000	Hemiptera	Herbívoro	Manejo IMP y configuración	+				x
		Hymenoptera	Parasitoide	Manejo OR / Configuración	+ / +	+ / +		+ / +	x
		Diptera	Depredador	Manejo OR / Configuración	+ / +	+ / +		+ / +	x
		Araneae	Depredador	Tipo de cultivo	+				x
		Coleoptera	Depredador	% semi-HN	+			+	x
		Coleoptera	Depredador	Configuración	+	+		+	x
		Hymenoptera	Depredador	Manejo OR / Configuración	+ / +	+ / +		+ / +	x
Bosem et al. 2017	1000	Hemiptera	Herbívoro	% semi-HN y diversidad cultivos	-				
		Hymenoptera	Parasitoide	% semi-HN	+		+	+	
		Diptera	Depredador	% semi-HN	+			+	
		Araneae	Depredador	% semi-HN	+			+	
		Neuroptera	Depredador	% semi-HN	+			+	
		Coleoptera	Depredador	% semi-HN	+			+	
Janković et al. 2017	1000	Hemiptera	Herbívoro	semi-HN / Manejo intensivo	+ / +				
		Hymenoptera	Parasitoide	semi-HN / Manejo intensivo	- / -			- / -	
		Hymenoptera	H-parasitoide	semi-HN / Manejo intensivo	+ / +			+ / +	
		Coleoptera	Depredador	% Cultivos	+	-		+	
		Hemiptera	Depredador	% Cultivos / semi-HN	- / -			- / -	
Maisonhaute et al. 2017	1500	Hemiptera	Herbívoro	Diversidad cultivos	-				x
		Coleoptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Neuroptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Neuroptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hemiptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hemiptera	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Araneae	Depredador	% Soja / % HN	- / +	- / +		- / +	x
		Hymenoptera	Parasitoide	% Soja / % HN	- / +	- / +		- / +	x
		Hongo	Depredador	% Soja / % HN	- / +	- / +		- / +	x

Continuacion Tabla 2.
Table 2 Continuation

Autores	Escala espacial (m)	Taxón	Categoría	Variable	Efectos en:				VL
					A	D	P	CB	
Markó et al. 2017	1000	Hemiptera	Herbívoro	Insecticidas	-				
		Coleoptera	Depredador	% Urbano / % HN / Arables	+			+	
		Coleoptera	Depredador	% Urbano / % HN / Arables	+			+	
		Coleoptera	Depredador	% HN / Arables	- / +			- / +	
Ardanuy et al. 2018	500	Hemiptera	Herbívoro	% semi-HN	+			+	
	1000	Hemiptera	Herbívoro	% semi-HN / % Cereals	- / +			+	
		Hemiptera	Depredador	% semi-HN y presa	+			+	
Kebede et al. 2018	Parcela	Lepidoptera	Herbívoro	% Maíz	+				x
		Dermaptera	Depredador	Diversidad cultivos	+			+	x
		Coleoptera	Depredador	Diversidad cultivos	+			+	x
		Hymenoptera	Depredador	Diversidad cultivos	+			+	x
		Coleoptera	Depredador	Diversidad cultivos	+			+	x
Samnegård et al. 2018	1000	Hemiptera	Herbívoro	Manejo IMP	-				x
		Lepidoptera	Herbívoro	Manejo IMP	-				x
		Hymenoptera	Polinizador	Manejo OR / Vegetación adyacente	+	+			x
		Diptera	Polinizador	Manejo OR / Vegetación adyacente	+	+			x
		Dipteros	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Dermaptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Coleoptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Coleoptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Hemiptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Neuroptera	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
		Opiliones	Depredador	Cubierta / Manejo OR	- / +	- / +		- / +	x
Yang et al. 2018	500 y 2000	Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
		Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
		Coleoptera	Depredador	% Urbano / % semi-HN	+ / +			+ / +	
Happe et al. 2019	1000	Araneae	Depredador	Manejo OR	+			+	x
		Coleoptera	Depredador	Manejo OR	+			+	x
		Dermaptera	Depredador	% HN / Manejo OR	- / +			+	x
		Diptera	Depredador	Manejo OR	+			+	x
		Hemiptera	Depredador	Cubierta / Manejo OR	- / +			+	x
		Opiliones	Depredador	Manejo OR / % HN	- / +			+	x
Ricci et al. 2019	1000	Depredacion pulgones en suelo	Depredador	Insecticidas / % No cultivo / Diversidad cultivos	- / + / +			- / + / +	x
		Depredacion pulgones en el cultivo	Depredador	% Prados / % HN	+ / +			+ / +	x
		Depredacion presa centinela	Depredador	Insecticida / Cultivo / semi-HN	- / - / +			- / - / +	x
		Depredacion semillas en suelo	Depredador	Cultivo / Manejo	- / -				x
Yang et al. 2019	500,1000, 1500 y 2000	Lepidoptera	Herbívoro	% Non-crop / % Maiz y algodón	- / +				
		Hymenoptera	Parasitoide	Campos pequeños / % Maíz	+ / +		+ / +	+ / +	

Sin embargo, estos autores, encuentran pocos estudios que liguen el control biológico con la estructura de las redes parasitoide – hospedador. También, sugieren que no hay patrones claros que muestren que a mayor complejidad del paisaje se genere una mejor estructura en las redes parasitoide – hospedador. De acuerdo con lo anterior, Derocles et al. (2014) utilizan datos moleculares y evalúan el nivel de compartimentación entre las redes tróficas de pulgones y parasitoides en márgenes y áreas de cultivos. Ellos encuentran que la contribución de los márgenes como fuente de enemigos naturales para el control biológico es muy limitada y proponen que se necesita ampliar este tipo de estudios a escalas temporales y espaciales más grandes.

Si bien, se ha comenzado a integrar el estudio del control biológico con redes tróficas, estudios que utilicen metodologías espaciales y análisis de redes tróficas son muy escasos. Para ejemplificar esto nosotros realizamos una búsqueda dentro de la base de datos en la WoS. Específicamente, nuestro objetivo era encontrar artículos científicos que estudiaran a los enemigos naturales en agroecosistemas y que integraran a la par metodologías de análisis de redes tróficas y análisis espaciales por medio de áreas de influencia (buffers). Para ello, en el buscador avanzado de la WoS se introdujeron como criterios de búsqueda: paisaje (Landscape), trófico (trophic), redes (networks), y redes (webs), dando énfasis a las palabras paisaje y trófico (*). Se pidió específicamente buscar artículos científicos en idioma inglés que hayan sido publicados entre los años 1990 y 2019, dentro de los índices: SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH, BKCI-S, BKCI-SSH, ESCI, CCR-EXPANDED, IC.

Se obtuvieron 46 artículos que integraban alguno o varios de los criterios de búsqueda. Se separaron los artículos que se enfocaban en enemigos naturales o comunidades de insectos, dentro de agroecosistemas, y que en sus metodologías se especificara la integración de las metodologías de nuestro interés. Como resultado sólo 3 artículos mostraron las características deseadas, (ver **Tabla 3**):

McFayden et al. (2009) investigaron en 20 áreas de estudio (farms) bajo manejo ecológico (orgánico) y convencional, si las diferencias en la estructura de las redes tróficas afectaban al control biológico. Ellos caracterizaron la composición del paisaje basada en cada uno de los componentes del paisaje y colectaron plantas, pulgones y parasitoides para crear una red trófica de tres niveles. La interacción planta- hospedador -parasitoide les permitió calcular índices cualitativos y cuantitativos de dichas redes tróficas. Sus análisis sugieren que la estructura de las redes tróficas es diferente según el manejo y que la riqueza de especies en los tres niveles tróficos es mayor en las áreas con manejo ecológico. Más aún, ellos muestran que los pulgones en las áreas de estudio con manejo ecológico son atacados por más especies de parasitoides. Sin embargo, no encontraron diferencias significativas en la proporción de parasitismo de las redes tróficas entre ambos manejos.

Gacic et al. (2012) investigaron los efectos de la complejidad del paisaje sobre las redes tróficas de pulgón - parasitoide - híperparasitoide en campos de trigo. Ellos encontraron que la intensificación agrícola es importante para la estructura de dichas redes tróficas y para el control biológico. Además, la abundancia de pulgones y el híperparasitismo, fue mayor en campos con menor intensificación agrícola. Sorprendentemente, sus datos muestran que la complejidad de las redes tróficas tiende a ser mayor con la intensificación agrícola y con una variabilidad temporal alta.

Ye et al. (2017) por su parte, muestran resultados similares a Gacic et al. (2012) pero ellos integran a la red pulgón - parasitoide - híperparasitoide el efecto de bacterias endosimbiontes en pulgones. Ellos investigan si la endosimbiosis facultativa confiere protección contra los parasitoides y si ésta es afectada por la complejidad del paisaje. Sus resultados sugieren que la complejidad del paisaje no tiene ningún efecto significativo positivo sobre la endosimbiosis facultativa, pero la tendencia del patrón muestra que las tasas de endosimbiosis facultativa (infección) en las momias de pulgones son menores en campos fertilizados que en campos no fertilizados.

Tabla 3. *Resumen de los efectos de la estructura del paisaje en estudios de redes tróficas medidos sobre la abundancia (A), diversidad (D) y parasitismo (P) de diferentes artrópodos así como el efecto sobre el control biológico (CB) en los agroecosistemas. Integración de las variables locales (VL).*

Table 3. *Summary of the effects of landscape structure in trophic network studies measured on abundance (A), diversity (D) and parasitism (P) of different arthropods as well as the effect on biological control (CB) in the agroecosystems Integration of local variables (VL).*

Autores	Escala espacial (m)	Taxón	Categoría	Variable	Efectos en:					Estructura del paisaje	VL
					A	D	P	CB	RT		
Macfadyen et al. 2009	Farm	Diptera	Herbívoro	Manejo (orgánico)		+	+		+	Composición (Orgánico vs Convencional)	x
		Hymenoptera	Parasitoide			+		≈	+		
		Lepidoptera	Herbívoro			+	+		+		
Gagic et al. 2012	500	Hemiptera	Aphididae	Intensificación agrícola	-				+	Complejidad (Orgánico vs Convencional)	
		Hymenoptera	Parasitoide		+ / -		-	≈	+		
		Hymenoptera	Híper-parasitoide		-		-		-		
Derocles et al. 2014	Parcela	Hemiptera	Aphididae	Márgenes	+	+				Complejidad (cultivo vs márgenes)	
		Hymenoptera	Parasitoide				+	+ / -	-		
Ye et al. 2017	500	Hemiptera	Aphididae + endosimbionte	% Habitats semi-naturales + fertilización	+ / -					Complejidad (HN)	x
		Hymenoptera	Parasitoide				+ / -	-			
		Hymenoptera	Híper-parasitoide				+		+		

Conclusiones

El estudio del paisaje, así como su efecto sobre la abundancia y diversidad de enemigos naturales, y su relación con el control biológico, ha tenido un gran crecimiento en los últimos años. Sin embargo, es posible que en muchas investigaciones cierta información se esté perdiendo debido a que los enemigos naturales responden a diversos y complejos tipos de variables como: dinámicas temporales; la composición y configuración del paisaje; interacciones tróficas; o el manejo del cultivo. Los estudios de carácter funcional donde se estudia la composición del paisaje han demostrado que las especies de enemigos naturales necesitan de hábitats específicos, pero que otras variables como son los efectos locales del cultivo también pueden afectar a las dinámicas de los enemigos naturales y las plagas con más fuerza. Consideramos que los futuros esfuerzos realizados en las investigaciones de paisaje necesitan abordar el establecimiento de metodologías o protocolos en común, para simplificar y facilitar la comparación entre estudios. Así también, es necesario desarrollar modelos dinámicos que puedan abordar la interacción entre heterogeneidad espacial y los procesos ecológicos que causan los efectos en las especies. Finalmente, y en base a los resultados recabados en esta revisión cabe destacar que urge la necesidad de promover y fomentar paisajes agrícolas que garanticen niveles mínimos de biodiversidad y sostenibilidad como base inicial en el desarrollo de programas de control biológico a múltiples escalas espaciales.

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Changes in landscape composition influence the abundance of insects on maize: The role of fruit orchards and alfalfa crops

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ABSTRACT

The traditional agricultural landscape of Ebro Basin (NE Spain), which is mainly composed of alfalfa and cereal crops, has undergone changes in recent years, mainly consisting of an increase in the area occupied by intensively managed irrigated orchards. Recently, it has been reported that the presence of a higher proportion of orchards in the landscape and their management negatively affect the abundance and diversity of natural enemies. Two hypotheses are tested in this study: (1) the increased orchard surface has led to a reduction in natural enemies in neighbouring maize crops, and (2) the higher alfalfa proportion of agricultural land enhances the predatory fauna on maize. Maize fields were selected across a landscape gradient created by orchards and field crops (alfalfa and maize) in a buffer of 500 m. The abundance of 17 insect taxa in each maize field was estimated by means of 3 yellow sticky traps per season over three years. The insect abundance was related to the landscape structure (proportions of landscape elements and landscape diversity) and local variables (maize phenology, perimeter/area, weed diversity of the maize edges and abundance of the potential predators or potential prey). Our results show that the proportion of orchards in the landscape had negative effects on the main predators, and alfalfa had positive effects on herbivores and their predators. Semi-natural habitats (non-crop habitats and forest) and landscape diversity had low effects on insect abundance. However, variables at the local level included more significant effects than landscape structure; maize growth stages and abundance of potential prey or predators on the crop were the most influential variables at a local level. Here we show the interplay between different land uses types and local management and their impact on natural enemies and herbivores in maize crops in the Mediterranean area.

1. Introduction

Agroecosystems are not static systems over time but are linked to market demand for different food commodities, among other factors. Insects exploiting such agroecosystems and their associated natural or semi-natural habitats need to be able to find the resources provided by the different cover types in ephemeral and disturbed environments (Rusch et al., 2010; Schellhorn et al., 2014). Thus, herbivores and their natural enemies must move among habitats, resulting in spatial or temporal emigrations (Landis et al., 2000; Rand et al., 2006; Tscharntke et al., 2012; Bianchi et al., 2013). The combination of many trophic level interactions, the landscape structure (i.e., its composition and configuration), the management of the crop fields (i.e., tillage, irrigation, pesticide inputs, harvesting/cutting or rotation) and the constant changes in agricultural policy make it difficult to understand and predict the changing patterns of insect abundance in particular agricultural habitats. Recently, studies have been performed to understand the negative and positive effects of agricultural land use on the conservation of biodiversity and its relation to ecosystem services, with a landscape perspective (Tscharntke et al., 2005). The spatial scale that best predicts the natural enemy density and population dynamics may depend on the specialisation, dispersal capability, and trophic level of a particular natural enemy (Perović et al., 2010; Chaplin-Kramer et al., 2011).

Most of the literature on landscape structure and insect abundance relationships has been devoted to the natural enemies of insect pests with the objective of managing habitats for cost-effective pest control (Symondson et al., 2002; Bianchi et al., 2006; Rusch et al., 2010; Tscharntke et al., 2012). By contrast, herbivore responses to landscape variables are much less conclusive in the literature than the data on

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natural enemies (Bianchi et al., 2006); this is a knowledge gap that should be filled to allow the design of better forms of biological control of crop pests.

In the Ebro Basin (NE Iberian Peninsula), in the last 25 years, the authors have studied the composition and abundance of arthropods in winter cereals, maize, and alfalfa in irrigated arable crop rotations. In this area, agricultural landscapes are traditionally dominated by arable crops that are managed by the rotation of winter and summer cereals and alfalfa. In these landscapes, small separate areas of fruit orchards are cultivated. In addition, natural or semi-natural habitats are scattered within the agricultural matrix, shaping the agricultural landscape. More recently, changes in market demand have led to modifications to the composition of agricultural landscapes in the region, with the most significant being an increase in the area of stone fruit orchards (National Bureau of Statistics of Spain, 2017), which have led to the transformation of a landscape dominated by arable fields to an orchard-field crop mix landscape. These changes can modify the abundance of pests and their natural enemies that occur on the crops that make up the landscape.

The low economic threshold of stone fruit pests has led to intensive crop management and repeated pesticide treatments, which are considered a main cause of natural enemy reduction in the landscape because pesticides affect their behaviour and habitat recolonisation (Rusch et al., 2010). Consequently, landscapes dominated by stone fruit orchards have been reported to negatively affect the richness of beneficial arthropod species (Samnegård et al., 2018). In contrast, alfalfa fields in this area have been reported to be important reservoirs of natural enemies (Núñez, 2002; Pons et al., 2005; Ardanuy et al., 2018), from which predators show bidirectional movement between neighbouring alfalfa and maize fields (di Lascio et al., 2016; Madeira et al., 2014, 2018; Madeira and Pons, 2016). Additionally, the cover and the composition of herbaceous plants in hedgerows surrounding maize fields may provide resources and shelter for natural enemies of maize pests (Ardanuy et al., 2018).

The aim of the present work is to disentangle the influence of the actual agricultural landscape on the composition and abundance of insect fauna in maize fields. Based on the preliminary results obtained by authors in this area, we present two hypotheses: (1) the intensive chemical spraying that is usually practised in orchards in this area has negative consequences for the biological control functions in surrounding maize crops, and (2) alfalfa can act as a reservoir of natural enemies in intensive agricultural landscapes. To test these two hypotheses, we analysed the influence of the landscape structure and local variables on herbivore and predatory insect abundance on maize. A total of 52 maize fields over three years were sampled to determine the abundance of 17 insect groups, 11 predators and 6 herbivores. The abundance of these insect groups was related in spring and summer in an agricultural landscape in a circle of 500 m around the sampled maize fields.

2. Methods

2.1. Study area

This study was carried out in 2015, 2016 and 2017 in the Ebro Basin in north-eastern Spain (41°48′12.20″N, 0°32′45.77″E; 120–346 m altitude; 200–400 mm rainfall, Tmin: 8°-24 °C and Tmax: 18°-38 °C) (Fig. 1A). Most of the crops in this region are irrigated, and crop fields are interspersed with patches of non-crop habitats (non-productive areas, longer fallows, natural habitats and wetland) and forest repopulated by *Pinus halepensis* (Mill). Crop rotation mostly includes winter (mainly wheat and barley) and summer (mainly maize) cereals and alfalfa. Traditionally, pome fruit orchards and field crops are grown in separate areas. Recently, the surface area of the stone fruit orchards (mainly peaches) has grown exponentially, leading to a mixed landscape characterised by orchards and field crop plots with different shapes and sizes. Pest management in the cereals includes pre- and post-emergence herbicide applications, treatment of seeds of winter cereals with fungicides, and treatment of maize with both insecticides and fungicides. Management of alfalfa consists of 5/6 cuttings during the productive period (March–October), and the crop is in the field for 4–5 years (Madeira et al., 2014). In orchards, management includes from 7 to 14 chemical sprays (insecticides, fungicides and bioregulators), herbaceous cover mowing (approximately once per month), and herbicide and tree fertilisation (Cantero-Martínez, 2013).

2.2. Landscape structure variables

During the 3-year study, 52 maize fields were selected according to the initial gradient of the orchard and field crop proportion in the landscape using aerial photography in a circle buffer of 500 m surrounding the maize fields. Due to crop rotation, some of the sampled maize fields changed in this period; thus, we selected 6 maize fields in 2015 and 23 in 2016 and 2017. The size of the maize fields varied between 0.9 and 13.68 ha, and these fields were located at least 2 km apart from each other. The agricultural landscape covered was 700 km^2 (Fig. 1B) (Appendix A.1).

The landscape composition was characterised by the proportion of the different landscape elements embedded in a circle buffer with a 500 m radius surrounding the maize fields. In addition, spring and summer characterisations of the landscape composition were conducted to incorporate the seasonal variations of the proportions of cereals in spring and winter cereal-fallows in summer. The landscape composition was described each year by direct field observations, an orthophoto from the Plan Nacional de Ortografía Aérea (PNOA), and geographical information maps of the Instituto Geográfico Nacional of Spain. Then, we quantified the proportions of the landscape elements using ArcGIS software 10.3.1 (ESRI, 2015). Next, the 34 landscape elements initially identified in the study were grouped into eight categories: orchards, summer and winter cereals, winter cereal-fallow, alfalfa, non-crop habitats, forest and edges (Table 1 and Fig. 1B) (Appendix A.2).

The landscape configuration was characterised by landscape diversity (hereinafter SHDI-L). SHDI-L was calculated as a function of the proportional abundance of each landscape element type, *Li,* using FRAGSTAT (McGarigal et al., 2012) as follows:

$$\text{SHDI}-\text{L}= -\sum_{i=1}^{34} L_i \times lnL_i$$

2.3. Local variables

Local variables included the maize phenology, perimeter to area of the maize fields, Shannon index in maize field edges (hereinafter SHDI-E), and abundance of potential predators (for the study of herbivore species) and potential prey (for the study of predators) (Appendix A.3). In recent years, maize is variably sown in the early (March-April) or late season (at the end of June); consequently, we sampled both early (17 fields in 2016 and 18 fields in 2017) and late sown maize fields (6 fields in 2015 and 2016 and 5 fields in 2017). Maize phenology was recorded at each sampling date according to Ritchie et al. (1992). The perimeter to area of the maize fields was calculated using ArcGIS software. The SHDI-E index was calculated from flora surveys carried out in the edges between the maize and neighbouring fields (orchards, alfalfa or maize) during May and June in 2016 and 2017. In addition, for each sampling point, the cover-abundance of weed species was recorded using the Braun-Blanquet, 1979 in three rectangular plots (2 × 5 m^2) along the edges. Then, the cover-abundance values were transformed into the mean value of the percent cover according to each field, and we calculated the Shannon index as a function of the proportional **weed** species abundances, E_i:

$$\text{SHDI}-\text{E}= -\sum_{i=1}^{52} \text{E}i \times lnE_i$$

In addition, we used floristic surveys of the edge cover compositions to transform the cover abundance of species into the mean value of the percent cover according to three types of edges (maize-orchard, maize-

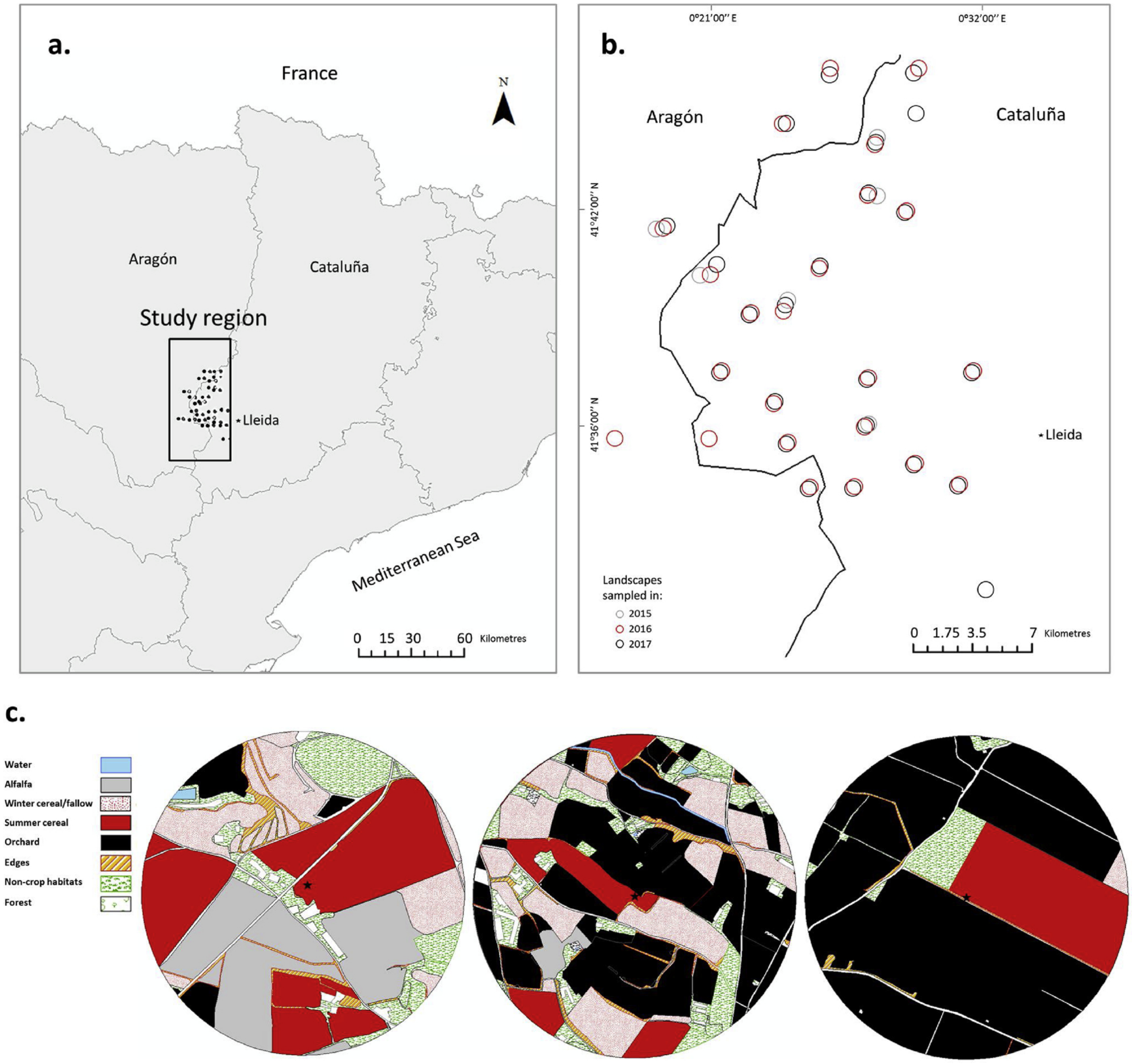

Fig. 1. A. Study region in the Ebro Basin in north-eastern Spain. B. Landscape sampled (2015, 2016 and 2017). C. The star point indicates the middle sticky trap in the maize field. Additionally, the different orchard proportions are shown in the landscapes.

alfalfa and maize-maize), calculated the Shannon index (hereinafter H’), and grouped the recorded plant species as dicotyledons or monocotyledons.

Autocorrelation can be a problem for classical statistical tests, such as regression, which rely on independently distributed errors (Legendre, 1993), as it may lead to erroneous conclusions regarding the significance of covariates in studies of species-environment relationships (Wagner and Fortin, 2005). Therefore, the degree of correlation

Table 1
Landscape structure and local variables used in this study.

Variables	Categories	Description
Landscape structure	Winter cereals	Proportion of winter cereal (mainly wheat and barley)
	Winter cereal-fallow	Proportion of fallow when winter crop is end (fields under no crop rotation)
	Summer cereals	Proportion of summer cereal (mainly maize)
	Orchard	Proportion of fruits orchards, figs, citrus, dried fruit, vineyard and olive
	Alfalfa	Proportion of alfalfa
	Edges	Proportion of the margin strip (see Marshall and Moonen, 2002)
	Non-crop habitats	Proportion of no productive areas, longer fallows, natural habitat and waterland
	Forest	Proportion of forest repopulate of *Pinus halepensis*
	SHDI-L	Shannon diversity index calculated as landscape diversity in the buffers
Local environment	SHDI-E	Shannon diversity index calculated in edges between maize and neighbouring crops*(Marshall and Moonen, 2002)
	Maize phenology	Stage of maize development (Ritchie et al, 1986)
	Perimeter/area	Perimeter to area ratio of the sampled maize field (m $^{-1}$)
	Prey/Predator	Abundance of mainly prey and predator by each group of insect

between variables was assessed through a Spearman rank correlation between landscape composition, landscape configuration and local variables (Appendix A.4). According to Campbell and Swinscow (2009), some variables were weakly to moderately correlated (Spearman's rho < 0.59), but they were not excluded to build the models as done by Schmidt et al. (2019).

2.4. Yellow trap catches of herbivores and predators

The abundance of insects in maize fields was estimated using yellow sticky traps (30 × 25 cm, Serbios, Badia Polesine, Italy). Samplings were conducted once a month, and the traps were left active for 1 week. In each field, we placed 3 traps on stakes at the crop canopy height, depending on the growth stage, along a transect perpendicular to the nearest edge (approx. 30 m), with the traps 15 m away from each other (Albajes et al., 2013). The traps were then collected and conserved at 6 − 8 °C until insect identification. Individuals were identified at the family, genus or species level depending on their state of conservation. Vouchers of individuals identified at species level were deposited in the laboratory of Entomology of the University of Lleida.

2.5. Statistical analyses

The effects of the landscape structure and local variables on the insect abundance on maize were analysed separately for each of the two seasons—spring and summer. We used a linear mixed-effects model with the 'year' as the random structure for each mode using the 'nlme' package (Pinheiro et al., 2018) for R software (R Development Core Team, 2018). For each field and sampling date, the mean number of each insect taxa selected for identification per trap was log transformed [log10(x + 1)] to achieve, as much as possible, a normal distribution of the model residual. In addition, we tested the spatial autocorrelation in the abundance of insects among all fields using Moran's I statistic (Paradis, 2018) (Appendix A.5). We standardised (mean centred and scaled) landscape metrics for each model using the 'caret' package (Max et al., 2018). We applied a multi-model inference approach to obtain a robust parameter estimate using the 'MuMIn' package (Bartoń, 2018). The dredge function of the models was used to describe the effects of independent variables on each dependent variable. Models were selected by comparing the Akaike information criterion (AICc) with the values of the full model. Model averaging was performed on the model while set to ΔAICc < 2 (Burnham and Anderson, 2004). The model residuals were graphically inspected with qqplot and histogram graphics to ensure no violation of normality and homoscedasticity assumptions (Zuur et al., 2010). Finally, we used the 'effects' package (Fox et al., 2016) to represent the effects in partial residual plots.

3. Results

A total of 316,564 insects were trapped on 585 yellow sticky traps in 52 maize fields during the three years of the study: 39,539 in 2015 (*n* = 6 fields), 201,775 in 2016 (*n* = 23) and 75,250 in 2017 (*n* = 23). The identified taxa were: *Coccinella septempunctata* (L.), *Empoasca vitis* (Göethe), *Hippodamia variegata* (Goeze), *Frankliniella occidentalis* (Pergande), *Laodelphax striatellus* (Fallén), *Propylea quatuordecimpunctata* (L.) and *Zyginidia scutellaris* (Herrich-Schäffer), *Aeolothrips* spp., *Nabis* spp., *Orius* spp., and *Stethorus* spp. At the family level, Aphididae, Chrysopidae, Miridae, Staphylinidae, Syrphidae and other Thripidae species (other than *F. occidentalis*) were identified. The insect abundances varied between seasons and especially were higher for herbivores in spring (Fig. 2). The most abundant herbivore was *F. occidentalis*, followed by *Z. scutellaris,* other Thripidae and Aphididae (Fig. 2). In the case of predators, *Aeolothrips* spp. was the most abundant, followed by Syrphidae, *Stethorus* spp. and *Orius* spp. (Fig. 2). Models of Nabidae and *H. variegata* were not considered because of their low abundance. Miridae were also not considered because of their extremely diverse feeding regimes. Models of Nabidae, *H. variegata* and Miridae can be observed in Appendix B.

3.1. Flora abundance and composition survey in maize field edges

A total of 190 weed species were identified in the maize field edges. The most abundant monocotyledon species were: *Hordeum murinum* (L.), *Sorghum halepense* (L.), *Poa annua* (L.), *Cynodon dactylon* (L.), *Avena sterilis* (L.) and *Lolium rigidum* (Gaudin). In the case of dicotyledons, the most abundant species were: *Malva sylvestris* (L.), *Taraxacum officinale* (L.), *Capsella bursa-pastoris* (L.), *Sonchus oleraceus* (L.), *Chenopodium album* (L.) and *Veronica arvensis* (L.). The edges between

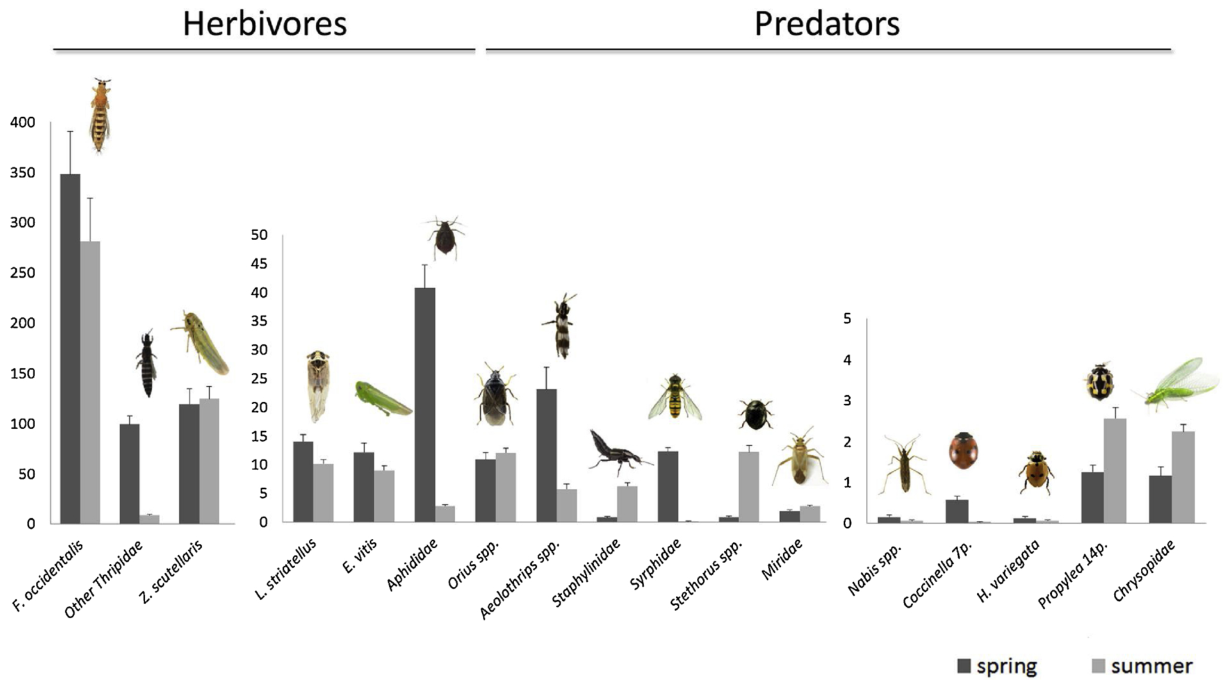

Fig. 2. Abundances of herbivores and predators trapped during the study in spring and summer.

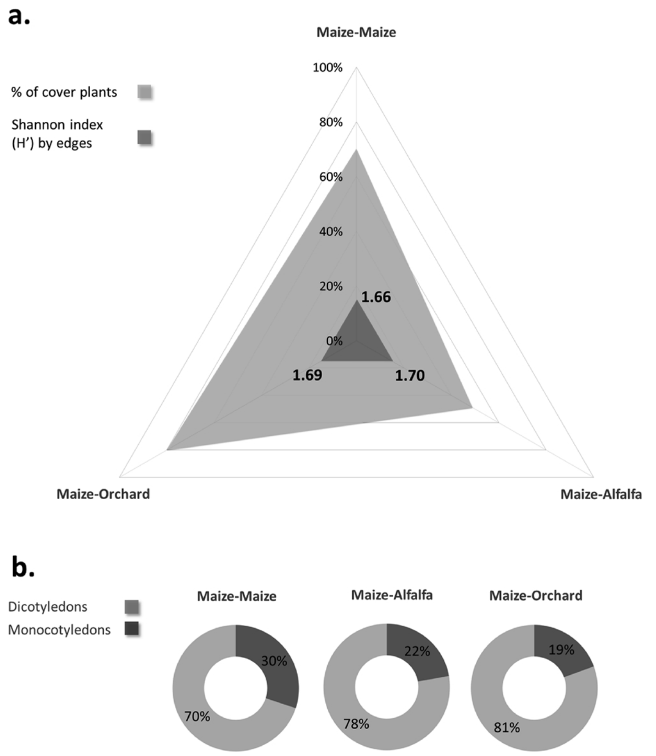

Fig. 3. Flora abundance and composition survey in maize field edges. A. Mean percentage of edge cover by flora in sampled maize fields and H' according to field neighbouring crop. B. Flora were grouped into dicotyledons and monocotyledons.

the maize and orchards showed the highest plant cover (80 %) (Fig. 3a) and a dominance of dicotyledons (80 %) (Fig. 3b). On the other hand, the edges between maize and alfalfa had low plant cover (48.97 %) but the highest H' (1.7) (Fig. 3a). Finally, the edges between maize fields had the lowest H' (1.66) (Fig. 3a) and the highest proportion of monocotyledons (30 %) (Fig. 3b).

3.2. *Responses of insects to landscape structure variables*

Most of the parsimonious models for predators and herbivores are shown in Appendix B (1 and 2, respectively). The results with only significant variables for predators are shown in Table 2 and for herbivores in Table 3. Overall, the abundance of insects was influenced by the landscape structure, with a characteristic seasonal pattern. The landscape variables with higher effects on the insect abundance were the proportion of alfalfa, orchard and edges. Alfalfa was the variable that was most positively related to insect abundances. Especially, in summer, the alfalfa had positive effects on the abundance of aphids and their predators and also on the herbivore thrips (*Frankliniella occidentalis* and other Thripidae) (Fig. 4). In addition, the proportion of orchards was the variable with more negative effects on insect abundances. In Fig.5 it can be seen that orchards was negatively related to two predators in spring, but in summer, they were positively related to two herbivores. In spring, the edges were positively related to *Orius spp*., the main generalist predator in this area, and to *Z. scutellaris,* this predator's main (Fig. 6). Overall, the proportion of cereals in the landscape was poorly related to insects. The winter cereal was positively related to two specialist predators in spring, and the maize was negatively related to *L. striatellus* in summer. In addition, some semi-natural habitats (forest and non-crop habitat) had a minor impact on the abundance of predators and herbivores.

3.3. *Responses of insects to local variables*

The local variables had important effects in both insect groups. Especially, the variables related to the maize phenology and the predator-prey relationship on maize had high effects on insect abundances, which are shown in Table 2 and 3 (see more parsimonious models for predators and herbivores in Appendix B 1 and 2, respectively). The results show that predators depended more on phenology in spring and herbivores in summer. In addition, the perimeter/area of maize fields was positively related to herbivores and especially SHDI-E (a descriptor of flora diversity in the maize edges) was negatively related to *Orius spp.* (Fig. 7) but positively related to its main preys in summer.

4. Discussion

As initially hypothesised, the proportions of orchards and alfalfa fields in the buffer were the most influential landscape variables for maize insect abundance (Fig. 8). We report for the first time results of the effects of orchard cultivation on herbivore and predator species in neighbouring Mediterranean maize crops. Specifically, the proportion of orchards in the landscape had a negative effect on the aphid predators, such as *P. quatuordecimpunctata* and Syrphidae, as well as on Staphylinidae, the second most abundant generalist predator in maize in both seasons. Some authors have seen similar negative relationships between the orchard surfaces and predator abundance (Samnegård et al., 2018; Yang et al., 2018, 2019). Aviron et al. (2016) concluded that intensively managed orchards had negative effects on the amount of natural colonisation of vegetable crops by predatory mirid bugs coming from surrounding plots. In addition, Markó et al. (2017) reported that the toxic effect of chemicals on predators in orchards was masked by the continuous immigration of predators from surrounding crops, mainly arable crops, which explains why the proximity of orchards is associated with a lower amount of aphid predators in arable crops. Indeed, the influence of orchard management practices on natural enemies has been supported by data showing that their abundance and diversity were higher in organic than in non-organic orchards (Happe et al., 2019).

In contrast to the observations for predators, the abundance of some herbivores on maize fields was positively related to the proportion of orchards, a feature especially relevant for two homopteran maize pests, *L. striatellus* (in summer) and *Z. scutellaris* (in both seasons). These two homopterans mainly feed on Poaceae, that is, on orchard ground cover (Wang et al., 2009), which provides greater coverage in comparison with the edges close to the maize fields. Orchard ground cover could act as an abundant source of the two species for surrounding crops, as Frei and Manhart, 1992 **found**. The close and positive relationship between the orchard proportion and *L. striatellus* abundance on maize is particularly relevant because that is the main vector of Maize Rough Dwarf Virus (MRDV), a common disease in the area (Achon et al., 2013). In the case of *Z. scutellaris*, its higher abundance on maize relative to the higher orchard proportion in the landscape could have positive consequences for maize, as *Z. scutellaris* has been identified as a key prey to facilitate the early establishment of *Orius spp.* on maize (Albajes et al., 2011).

The alfalfa surface was a source of predators for maize, mainly aphid predators in summer, confirming the results of previous studies conducted at the field level in the area (Madeira et al., 2014; Núñez, 2002; Pons et al., 2005). Continuous predator movement of Coccinellidae between alfalfa and maize has been shown in the area in summer and, facilitated by regular alfalfa cutting in the season, explains the positive relationship between the proportion of alfalfa in the landscape and the abundance of those predators on maize (di Lascio et al., 2016). The same explanation can be extended to the other aphid predators found on that crop (Madeira et al., 2014; Madeira and Pons, 2015). However, the abundance of maize aphids was found to be related to the proportion of alfalfa, although the two crops do not share

Table 2
Model results of the best models relating predator abundance with landscape and local variables. Significant variables in the best models (ΔAIC < 2) are presented. Variables are standardised (mean-centred and scaled). Relative importance is the sum of Akaike's weight associated with the variables in the best models.

	Spring season					Summer season				
Specie/Group	Variables	Est.	z value	Pr(> |z|)	Rel. imp.	Variables	Est.	z value	Pr(> |z|)	Rel. imp.
Orius spp.	(Intercept)	−2.78	3.34	< 0.001		(Intercept)	0.26	0.50	0.61	
	Edges	0.29	2.33	0.019	1	Prey	0.32	7.01	< 0.001	1
	Prey	0.77	5.56	< 0.001	1	SHDI-E	−0.30	4.62	< 0.001	1
	Maize phenology	0.88	7.30	< 0.001	1					
Stethorus spp.	(Intercept)	0.31	3.85	< 0.001		(Intercept)	1.60	5.95	< 0.001	
	Maize phenology	−0.12	2.10	0.036	1	Forest	−0.22	2.00	0.045	1
	Winter cereal	0.15	2.45	0.014	1	Non-crop habitat	0.31	2.19	0.028	1
						Maize phenology	0.33	3.31	< 0.001	1
						SHDI-L	−0.29	2.07	0.038	0.89
P. quatuordecimpunctata	(Intercept)	0.52	6.48	< 0.001		(Intercept)	0.86	5.72	< 0.001	
	Maize phenology	0.31	3.70	< 0.001	1	Alfalfa	−0.20	2.27	0.023	1
	Orchard	−0.19	1.93	0.05	0.66	Edges	−0.33	4.35	< 0.001	1
						Maize phenology	−0.24	3.59	< 0.001	1
						Orchard	−0.18	2.23	0.025	0.59
						Summer cereal	0.18	0.07	0.01	0.41
C. septempunctata	n.a.					(Intercept)	0.01	0.21	0.83	
						Alfalfa	0.02	2.30	0.021	1
Staphylinidae	(Intercept)	−0.54	0.90	0.36		(Intercept)	−0.37	0.96	0.33	
	Prey	0.70	5.03	< 0.001	1	Forest	0.18	2.16	0.031	1
	p/a	−0.26	2.71	0.006	1	Prey	0.35	4.58	< 0.001	1
	Maize phenology	−0.29	3.74	< 0.001	1	p/a	−0.22	2.56	0.011	1
						SHDI-E	−0.21	2.43	0.015	1
						Edges	0.19	2.01	0.044	0.85
						Orchard	−0.17	1.98	0.048	0.64
Aeolothrips spp.	(Intercept)	0.85	1.15	0.25		(Intercept)	−0.71	3.00	0.002	
	Forest	−0.34	2.42	0.015	1	Prey	0.37	7.96	< 0.001	1
	Prey	0.33	2.44	0.014	1	Maize phenology	−0.25	3.46	< 0.001	1
	p/a	0.39	2.59	0.009	1	Summer cereal	0.24	3.45	< 0.001	1
						Fallow-winter cereal	0.15	2.27	0.023	1
Chrysopidae	(Intercept)	0.40	1.99	0.046		(Intercept)	0.82	8.79	< 0.001	
	SHDI-L	−0.23	3.12	0.001	1	Edges	−0.16	2.34	0.019	1
	Winter cereal	0.18	2.58	0.009	1	Non-crop habitat	0.30	3.02	0.002	1
	Maize phenology	0.13	1.99	0.046	0.19	p/a	0.14	2.07	0.038	1
						Alfalfa	0.35	2.04	0.041	0.11
Syrphidae	(Intercept)	0.56	3.72	< 0.001		(Intercept)	0.03	1.00	0.31	
	Orchard	−0.33	2.08	0.038	0.76	Alfalfa	0.04	2.23	0.025	1
						Prey	0.09	3.62	< 0.001	1
						SHDI-L	−0.04	1.96	0.049	0.74

aphid species (Asín and Pons, 1998; Pons et al., 2005; Madeira et al., 2014). A possible reason could be the common presence of aphids on *S. halepense* (an invasive weed that is increasingly abundant in agricultural habitats (Juárez-Escario et al., 2018), which grows permanently around irrigation sprinklers in alfalfa fields, and it has been observed as a source of aphid migration from alfalfa to maize. In fact, it is a relevant feature for the epidemiology of *Maize Dwarf Mosaic Virus* (MDMV) and *Sugarcane Mosaic Virus* (SCMV), two important maize viruses vectored by Poaceae aphids (Achon et al., 1996; Peerzada et al., 2017) from the common virus reservoir. Additionally, the proportion of alfalfa is also related to the abundance in both seasons of *F. occidentalis* and other herbivores of the Thripidae family on maize. Although thrips rarely are damaging to these crops in this area (Meissle et al., 2010), they serve as prey for some predators such as *Orius spp.* The abundance of *Orius spp.* on maize was significantly related to the amount of potential prey on that crop but not on the alfalfa, according to a previous study in the area (Ardanuy et al., 2018). As reported by these authors, the role of alfalfa in relation to maize is to provide it with an abundant amount of prey to enhance *Orius* spp. establishment (Madeira et al., 2018). We need more studies to test if the positive effect of alfalfa on predator abundances can be hampered by the orchard surface.

Edges constitute a non-permanent habitat in the landscape of the study area, especially in annual crops. We did not find weed diversity differences between sampled edges but we found different weed covers that could be more important than the diversity in these habitats. The positive relationship between the edges and the abundance of *Z. scutellaris* and *Orius* spp. is similar to previous results describing the role of edges as a source for both species in the early season (Ardanuy et al., 2018). Thus, the presences of edges are a feature that allows the early establishment of the predator-prey system on the crop and prevents the later development of pest populations in this area, as Albajes et al. (2011) **found**. Later, the negative relationship of *Z. scutellaris* and the proportion of edges in summer is probably because **edges** become dry, and these species prefer the irrigated cover of orchards.

Summer and winter cereals are important components of the landscape in our study region. The proportions of cereals in the buffers studied varied from 0.4% to 50.6% in spring (winter cereal) and 11.2%–57.1% in summer (mostly maize). However, few relationships were found between insect abundance and the proportion of summer cereals, so that the phenomena of the concentration or dilution of resources do not seem to play an important role in the study area, at least for most of the insects studied, as found by other authors (Otway et al., 2005). Only in the case of *L. striatellus*, for which a negative relationship between its abundance and maize surface in the area was found in summer, can a resource dilution mechanism be postulated, perhaps due to the slow insect population increase during the later development stages of the crop. In contrast, the **increased** abundance of predators such as *Aeolothrips* spp. And *P. quatuordecimpunctata* may be the consequence of higher prey densities resulting from the concentration of developed maize in the landscape in summer. However, this potential

Table 3
Model results of the best models relating herbivore abundance with landscape and local variables. Significant variables in the best models (ΔAIC < 2) are presented. Variables are standardised (mean-centred and scaled). Relative importance is the sum of Akaike's weight associated with the variables in the best models.

	Spring season					Summer season				
Specie/Group	Variables	Est.	z value	Pr(> |z|)	Rel. imp.	Variables	Est.	z value	Pr(> |z|)	Rel. imp.
F. occidentalis	(Intercept)	2.59	2.05	0.04		(Intercept)	2.14	3.04	0.002	
	Predator	0.64	2.55	0.011	1	Alfalfa	0.24	2.66	0.007	1
						Edges	−0.24	2.19	0.028	1
						Predator	0.91	8.68	< 0.001	1
						Maize phenology	−0.51	4.92	< 0.001	1
						SHDI-E	0.41	4.11	< 0.001	1
						SHDI-L	−0.25	2.00	0.045	1
						Winter cereal-fallow	−0.18	2.01	0.044	1
Other Thripidae	(Intercept)	3.39	3.44	< 0.001		(Intercept)	0.12	0.32	0.74	
	Maize phenology	−0.67	3.95	< 0.001	1	Alfalfa	0.17	2.35	0.018	1
	Alfalfa	0.46	2.56	0.011	0.96	Predator	0.61	6.89	< 0.001	1
						Maize phenology	−0.36	4.24	< 0.001	1
						SHDI-E	0.17	2.10	0.035	0.84
						SHDI-L	−0.18	1.95	0.051	1
						Winter cereal-fallow	−0.21	2.73	0.006	1
Z. scutellaris	(Intercept)	2.27	2.63	0.008		(Intercept)	2.24	3.95	< 0.001	
	Edges	0.47	2.75	0.005	1	Edges	−0.32	2.21	0.02	1
	Predator	0.60	2.22	0.026	1	Predator	0.49	3.27	0.001	1
	Winter cereal	−0.41	2.30	0.021	0.64	Orchard	0.29	2.30	0.021	1
	Orchard	0.42	1.91	0.05	0.51	p/a	0.29	2.32	0.021	1
						Maize phenology	−0.57	4.11	< 0.001	1
						SHDI-E	0.26	2.00	0.045	0.77
E. vitis	(Intercept)	1.86	4.28	< 0.001		(Intercept)	0.86	2.51	0.012	
	Non-crop habitat	0.57	2.59	0.009	1	Predator	0.40	4.18	< 0.001	1
	Maize phenology	−0.35	2.16	0.031	1	p/a	0.20	2.31	0.021	1
	SHDI-L	−0.44	2.03	0.042	1					
L. striatellus	(Intercept)	0.62	0.72	0.47		(Intercept)	1.41	4.12	< 0.001	
	Predator	0.56	2.32	0.02	1	p/a	0.20	2.54	0.011	1
	Maize phenology	0.39	2.44	0.014	1	Maize phenology	−0.37	4.26	< 0.001	1
						Predator	0.25	2.73	0.006	0.92
						Non-crop habitat	−0.25	2.22	0.026	0.81
						Summer cereal	−0.30	2.51	0.012	0.67
						Orchard	0.28	2.06	0.039	0.61
Aphididae	(Intercept)	2.96	6.72	< 0.001		(Intercept)	1.02	7.63	< 0.001	
	Maize phenology	−0.97	5.70	< 0.001	1	Maize phenology	−0.14	2.33	0.02	1
						Alfalfa	0.13	1.96	0.05	0.83

mechanism would require further **studies**. The influence of the proportion of winter cereals on maize insects may occur in spring due to the role of these winter crops as overwintering sites or as a base for early population increase of some insects. In summer, these insects may come from fallows that remain in fields that are not sown again with a summer crop after winter cereal harvesting. *Zyginidia scutellaris* was the

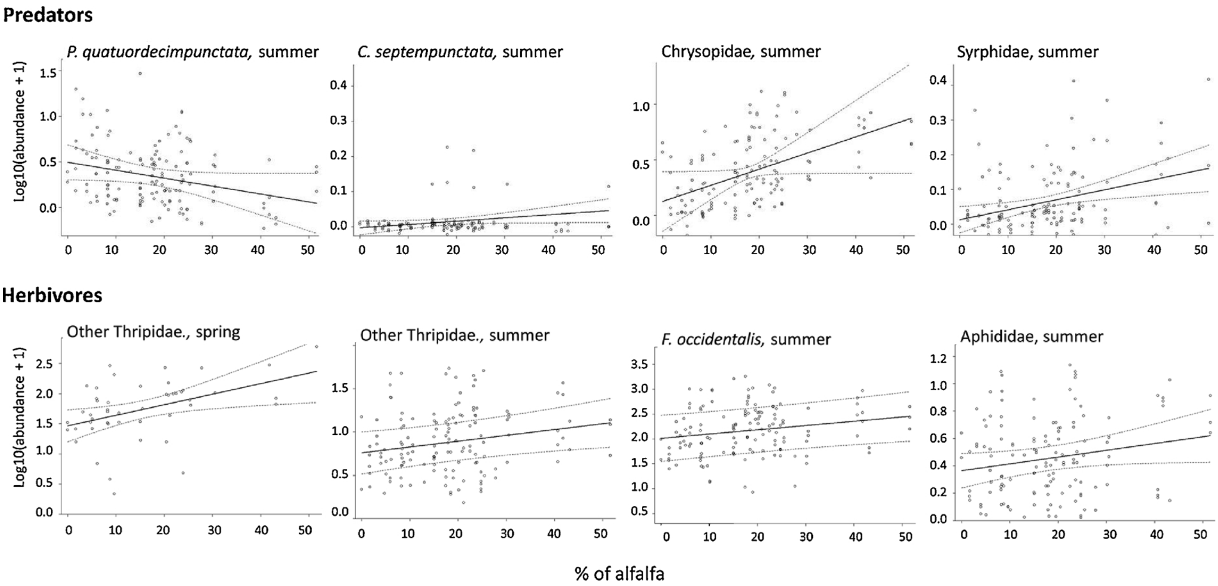

Fig. 4. Effects of the proportion of alfalfa (spring and summer) on the abundance of predators (*P. quatuordecimpunctata, C. septempunctata*, Chrysopidae, Syrphidae) and herbivores (other Thripidae, *F. occidentalis* and Aphididae).

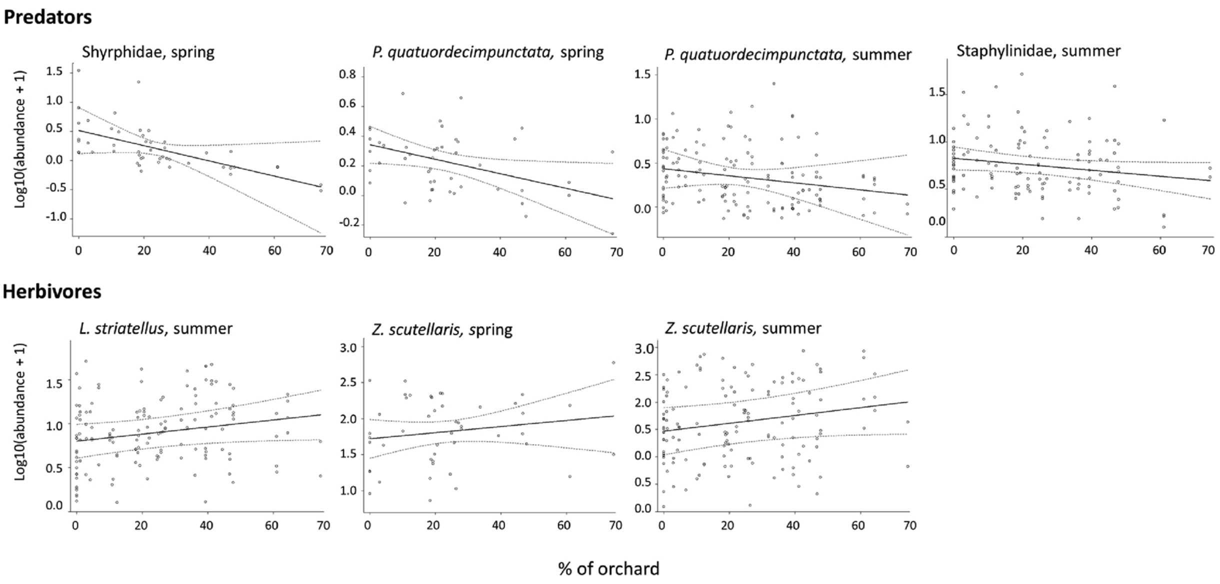

Fig. 5. Effects of the percentage of orchard (spring and summer) in the landscape on the abundance of predators (*P. quatuordecimpunctata*, Staphylinidae, Syrphidae) and herbivores (*Z. scutellaris* and *L. striatellus)*.

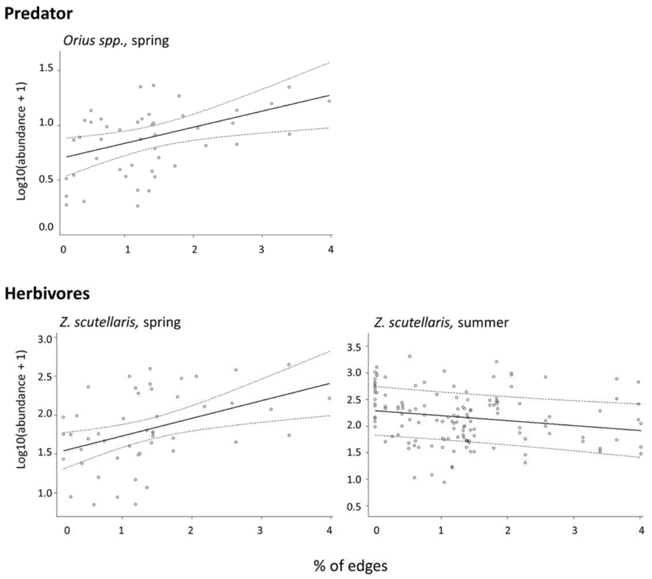

Fig. 6. Effects of the proportion of edges in the landscape on the abundance of the predator *Orius* spp. and its main prey, *Z. scutellaris*.

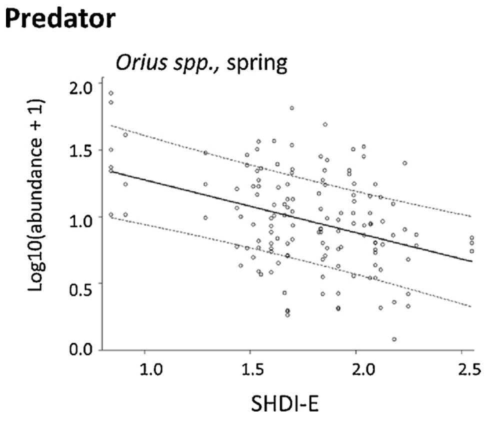

Fig. 7. Effect of SHDI-E on the abundance of the predator *Orius spp.*

only maize herbivore insect related to the amount of winter cereal, and that relationship was significantly negative in spring. This result contrasts with that reported by Ardanuy et al. (2018), who found a significantly positive relationship between the amount of winter cereals and abundance of *Z. scutellaris* on maize in spring. In this case, the authors included the field edges with the surface of winter cereals, which could be the source of the leafhopper for maize in spring. Instead, the greater presence of aphid predators on maize, such as Chrysopidae, in spring could be attributed to the greater abundance of winter cereals because aphids are abundant on winter cereals in spring in the area (Lumbierres et al., 2007). In addition, the greater amount of *Stethorus* spp. On maize in spring in areas with a higher proportion of winter cereals can be explained by the potential abundance of tetranychid mites (Burgio et al., 2004).

Non-crop habitats have classically been regarded to enhance the abundance and diversity of natural enemies in the landscape and therefore serve as pest population suppressors (Bianchi et al., 2006 and the review by Gurr et al. (2017)). In this study, the non-crop habitat proportion detected was between 0% min and 26%. However, few significant relationships between the abundance of insects on maize and the proportion of non-crop habitats in the landscape were found. In addition, the low diversity flora of herbaceous plants in non-crop habitats and in edges could have an effect on the maize insects that overwinter in trees or bushes, such as *E. vitis*, as shown by Decante and van Helden (2006). The significantly positive relationship found for the proportion of non-crop habitats and some predators could indicate the roles these non-crop habitats play as a source of predators in our latitudes, although only for a few predatory species. However, this limited role of non-crop habitats may complement the role played by the habitats categorised as edges that have been mentioned above. Forest habitats were a poor source of predators because the diversity of tree species (mostly *P. halepensis*) was low. The forest proportion detected in the buffers showed rather low variation, between 0 % and 11.2%. In fact, one of the reasons proposed to explain the limited contribution of non-agricultural habitats on pest suppression has been the relative low proportion of these habitats in the landscape as has been hypothesised by Tscharntke et al. (2016). On the other hand, we need more studies to test whether the low effect of semi-natural habitats and edges on predator abundances can be hampered by the orchard surface as found by Ricci et al. (2019).

The landscape diversity, as expressed by the Shannon diversity

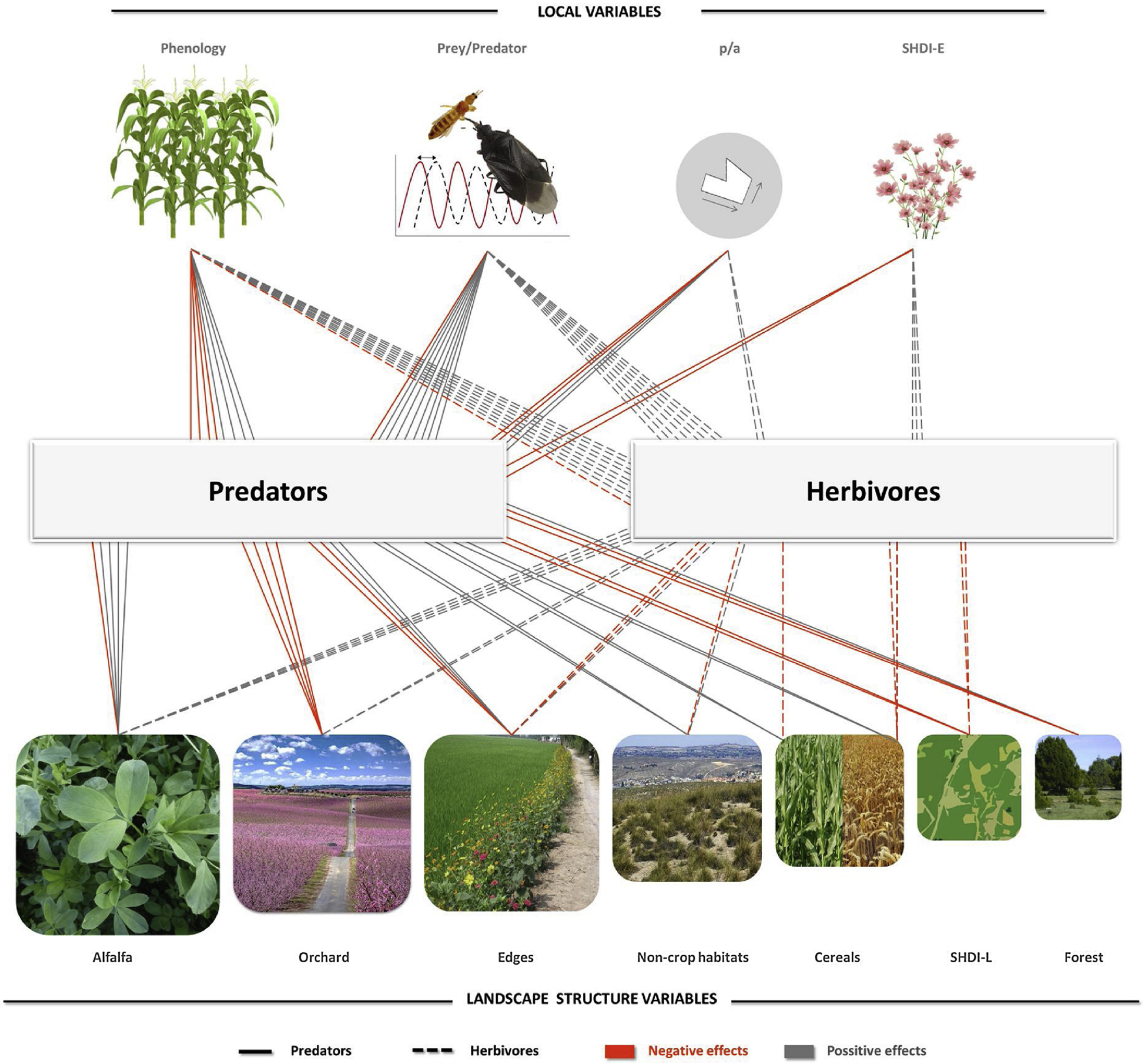

Fig. 8. Significant effects of local and landscape structure variables on each insect group detected. Size of squares indicates the number of relations of the variables with predators or herbivores group.

index in the landscape (SHDI-L), showed six significant relationships with maize insects (3 predators and 3 herbivores), all of which were negative. However, much literature on the relationships between landscape diversity and ecosystem services has reported positive values (see the review by Rusch et al., 2016). Some other authors, however, have **indicated** that landscape diversity itself is not a meaningful characteristic that affects biological control services and pest suppression (f.i. Martin et al., 2016; Rusch et al., 2016; Tscharntke et al., 2016; Landis, 2017; Karp et al., 2018). A deeper analysis is probably necessary to understand the relationships between landscape diversity and pest suppression (Médiène et al., 2011; Chisholm et al., 2014).

Local variables of sampled maize fields modulated the influence of the landscape on the abundance of the maize insects (Fig. 8). The maize growth stage was the most influential local variable. Most of the significant relationships for predators were positive in spring and negative in summer (abundance of predators increased or decreased, respectively, as the season progressed), whereas the relationships were mostly negative for herbivores (herbivore abundance mostly decreased along both seasons). These insect abundance-crop phenology relationships should prevent us from making definitive conclusions about how the surrounding landscape affects crop insect abundance because this landscape and insect abundance relationship may have temporal patterns rather than being permanent (Raymond et al., 2015) for aphids and their predators. Additionally, coupled predator-prey relationships on the crop were also the most significant variable. Predator-prey relationships may alter the influence of the landscape on crop insect abundance, as seen in this study and in which several of the predators and herbivores recorded were positively related with the abundance of their potential prey and predators, respectively, a feature reported by others (Ardanuy et al., 2018). Other local variables, such as the relation of the perimeter to the area and the diversity in maize field edges, play lesser roles than landscape variables on predators but are noticeable in herbivore insects in summer.

5. Conclusions

1. Landscapes dominated by orchards could highly negatively impact the abundance of predators on maize, likely as a result of the intensive management of orchards. In contrast, orchards are a relevant source of homopterans due to the presence of Poaceae in orchard ground cover, especially for vectors of maize virus species.
2. The presence of alfalfa in the agricultural landscape enhances the

abundance of aphids and their predators in maize crops. Alfalfa also enhances herbivore thrips but not their common predators, such as *Orius* spp. and *Aeolothrips* spp.

3. The presence of edges is a relevant feature, especially in the early establishment of prey-predator system of *Z. scutellaris* and *Orius* spp. in spring.

4. Semi-natural habitats (non-crop habitats and forest) and landscape diversity play minor role in determining the abundance of insects in Mediterranean maize crops.

5. Local variables contribute greatly to explaining insect abundance, especially maize growth stages and the abundance of prey or predators.

The results of the present study allow the improvement of maize management practices and the arrangement of landscape composition to enhance biological pest control by the conservation of naturally occurring predators. However, further tests of whether the low effects of semi-natural habitats on naturally occurring predators are due to the intensive orchard management are necessary.

Author contribution

G.C.O. collected the data, contributed data and analysis tools, performed the analysis and wrote the paper. F.M. contributed to study design, collected the data and revised the final version. I.B. and S.S collected the data. A.J.E collected the data and revised the final version. R.A. contributed to study design, collected the data, wrote the paper and revised the final version. All authors read and approved the final version of the manuscript.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106805.

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RESEARCH ARTICLE

Early planting, management of edges and non-crop habitats reduce potyvirus infection in maize

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Abstract

Viruses are a limiting factor in maize production areas around the world. The knowledge of the interactions between agroecosystems and the virus-vector-host system is limited, but a landscape-scale approach could help fill this gap. In this study, we show how the use of multiple spatial scales, i.e. 200, 500 and 1000 m, is a novel methodology for explaining the incidence of two closely related potyviruses: maize dwarf mosaic virus and sugarcane mosaic virus. To determine the factors involved in virus incidence, we recorded the proportion of surrounding crops and non-crop habitats at the landscape scale and, at the field scale, we recorded the planting date, the maize field area, the crop rotation and the weed diversity in the edges. In addition, we estimated the numbers of aphids with sticky yellow traps. Virus incidence in maize and in alternative grass hosts was determined by DAS-ELISA. Generalised linear mixed models were fitted using the multimodel inference method. The results showed that the most predictive model for the incidence of both potyviruses was at a scale of 200 m, but for the aphid abundance, it was at a scale of 500 m. Maize dwarf mosaic virus incidence was most affected by field management, and sugarcane mosaic virus by landscape variables. The planting date and the weed diversity in the edges were the field variables with the highest positive effects on both potyviruses. Moreover, both viruses were positively related to the abundance of aphids, and maize dwarf mosaic virus was only related to the cover of Johnson grass in the edges. Non-crop habitats had negative effects on potyvirus incidence at all spatial scales, showing that biodiversity in the landscape decreases the incidence of viruses. Here, we show that the early planting, the management of edges and the presence of non-crop habitats are key factors.

Keywords Maize virus · Aphids · Planting date · Alternative host · Non-crop habitats · Agricultural landscape · Sustainable crop protection

1 Introduction

Many factors have driven the emergence of diseases in plants: human demographics and behaviours, the global trade, the increase in the agricultural surface worldwide (i.e. ecological changes, economic development and land use), the introduction of invasive pathogens and climate change. Viruses account for 47% of emerging infectious diseases in plants and are the second most important group of plant pathogens that cause high losses, mainly in intensive agricultural crops (García-Arenal and McDonald 2003; Anderson et al. 2004). With technification in agriculture systems, insect pests, fungi or weeds can be controlled by management programs, but viral diseases are more difficult to control because there is no direct product against viruses. Moreover, the oversimplification of crop diversity, reduced genetic diversity, intensive farming systems and the increasing use of phytosanitary products have reduced the ecological functions of agroecosystems and could promote changes in the epidemiology of diseases (Stukenbrock and McDonald 2008).

The host plant, vector and virus are interdependent components of a complex pathosystem. The effect of biodiversity on the ability of viruses to infect their host plant and cause disease is a major question in plant pathology that is central to understanding the emergence of infectious diseases and developing strategies for their management (Pagán et al. 2012). Keesing et al. (2006) postulated that reduced biodiversity can increase disease incidence as a result of the increased abundance of susceptible major hosts, thus facilitating disease spread, which

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is known as the “dilution effect” hypothesis. The spread of infectious diseases is inherently a spatial process often embedded in physically complex landscapes (Biek and Real 2010). However, little is known about the linkage between spatial processes at the landscape scale, the ecology of vector colonisation and the virus transmission rate in the epidemiological disease process (Meentemeyer et al. 2012). In agroecosystems, crop viruses need to persist locally in a host plant with long life history stages or in an alternative weed host to ensure the temporal availability of inoculum in the landscape (Malmstrom et al. 2011). Thus, the local abundance of long-lived hosts, the host range and the movement of vectors are the key factors controlling infection risk (Borer et al. 2010; McLeish et al. 2017). Specifically, the behaviour and biology of vectors determine the incidence of viruses within geographical areas in the following manners: (1) the abundance of vectors coincides with virus-infected plants (crop or alternative weed hosts), (2) a moderate abundance of vectors coincides with a large number of virus-infected plants or (3) large numbers of both vectors and virus-infected plants coincide.

Since the 1980s, maize fields in Spain have been subject to severe losses, highlighting viruses as one of the main causes limiting their production. Maize dwarf mosaic virus (MDMV) is endemic in the Ebro Valley (Spain) (Achon et al. 1994), and the occurrence of sugarcane mosaic virus (SCMV) has increased since its detection in 2002 (Achon and Alonso-Dueñas 2009). MDMV and SCMV are included in the sugarcane mosaic virus subgroup (*Potyvirus* genus, Fam. Potyviridae) and the nucleotide sequences of isolates detected in Spain differed from each other by 31% (Achon et al. 2007). Both viruses are transmitted in a non-persistent manner by more than 15 species of aphids (Ford and Tosic 1989; Teakle et al. 1989) and by seeds at a low rate (< 0.5%). The host range of MDMV and SCMV is constrained to Poaceae, including maize and sorghum, the crops with the highest economic importance. Despite the large number of grasses reported as experimental hosts, alternative hosts in natural conditions are limited (Ford and Tosic 1989; Teakle et al. 1989; Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). *Sorghum halepense* (L.) Pers. (Johnsongrass) is the perennial reservoir for MDMV in Spain, and *Setaria verticillata* (L.) ands *Digitaria sanguinalis* (L.) Scop. are annual summer grasses infected with this virus in the field (Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). To date, *Setaria verticillata* has been the only alternative host detected for SCMV in Spain (Achon and Alonso-Dueñas 2009). No winter reservoirs have been found for SCMV, although the potential capacity of species of the genera *Bromus*, *Cynodon* and other winter annual grasses has been demonstrated under field conditions (Hohmann et al. 1998; Oertel et al. 1999).

In our study area, Ebro Valley, the number of aphids colonising maize is closely linked to migrations of these species from winter cereals (Pons et al. 1994). Thus, increasing the amount of winter cereal might directly increase aphid abundance due to the resource concentration effect (Root 1973), especially in landscapes dominated by cereals. The amount of virus host habitats and their connectivity may influence the global infection pressure in certain areas. However, knowledge of larger-scale interactions among host spatiotemporal heterogeneity, environmental conditions, and the rates at which pathogens disperse through and among fragmented host populations is limited until now (Meentemeyer et al. 2012). We take into account this perspective and conducted our study under a landscape perspective in combination with field variables of crop management. During two consecutive years, we selected 46 commercial maize fields located in areas with different proportions of cereals in the landscape each year. We quantified the landscape composition at three spatial scales (i.e. 200 m, 500 m and 1000 m) within concentric cycle buffers. To further extend the knowledge of infection risk drivers in northeast Spain, we asked the following questions: (1) what are the main drivers of maize infection risk by MDMV and SCMV under different landscape and field variables? (2) Does the main driver of infection risk vary over different landscape scales? (3) What is the best explanatory spatial scale to elucidate the infection risk of two closely related potyviruses?

2 Materials and methods

2.1 Study area

This study was carried out during 2016 and 2017 in the Ebro Basin in NE Spain (41° 48′ 12.20″ N, 0° 32′ 45.77″ E; 120–346 m altitude; 200–400 mm rainfall, Tmin 8–24 °C and Tmax 18–38 °C) (Fig. 1a). The agroecosystem has been classically dominated by field crops; alfalfa rotates with winter (from December to June) and summer cereals (from April to November) mainly maize. Recently, commercial demand has led to an increase in the stone fruit orchard surface in some areas, leading to an intensive-production agroecosystem in this region. Crops are interspersed with scattered patches of non-crop habitats (non-productive areas, long fallows, semi-natural habitats and repopulated forest). Common pest management practices in cereals include pre- and post-emergence herbicide applications and cereal seed treatment with both insecticides and fungicides. The management of alfalfa consists of 5/6 cuttings during the productive period (March–October), and the crop is in the field for 4–5 years.

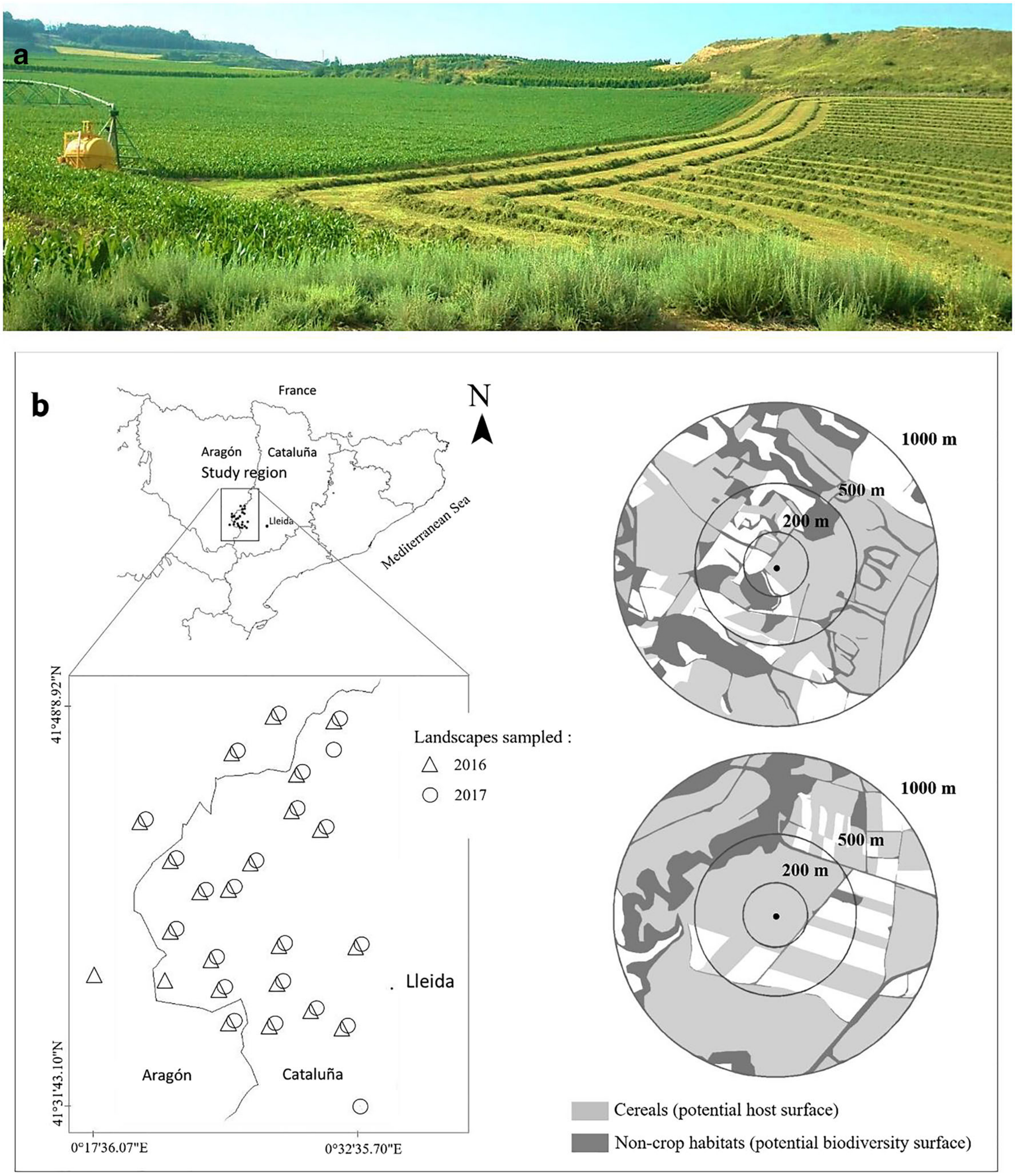

Fig. 1 **a** Agricultural landscape in northeastern Spain. **b** Landscape sampled in 2016 and 2017. The proportion of cereals (grey) and non-crop habitats (black) vary among the scale chose in the study (radii of 200 m, 500 m and 1000 m)

2.2 Factors measured at the field level

2.2.1 Maize field variables

During the 2 years of the study, we selected 46 maize fields with a gradient of winter and summer cereal proportions in the surrounding landscapes. Some of the selected maize fields were not the same each year due to crop rotations. The size of the maize fields where virus incidence was measured varied between 0.9 and 13.68 ha, and they were separated from each other by at least 2 km. The agricultural landscape covered by the selected fields was 700 km^2 (Fig. 1b). The following explanatory maize field variables were included in the analysis: maize field surface (ha), planting date (number of weeks from January) and rotation/not rotation (with winter cereal).

2.2.2 Maize surveyed

The survey for virus incidence was conducted at maize anthesis following the scheme described in Achon and Sobrepere (2001).

In each field, we systematically collected 30 maize plants following a W-shaped pattern. The distance between plants varied according to maize field size. In addition, we collected at least two grass plants reported in the literature as potential virus hosts that were located inside of the maize field. Maize samples consisted of the two youngest leaves of the plant, and grass samples consisted of the leaves or the entire plant. In each field, each sample was placed in a separate plastic bag, grasses were identified at the species level, and maize and grasses were examined for virus-like symptoms or no symptoms. All samples were stored at − 80 °C until virus identification.

2.2.3 Edge surveys for weeds and grass collection

Floristic surveys were conducted in the edges of the 46 maize fields surrounded by crops or non-crops areas during May–June in the 2 years. To determine the abundance and composition of plant species in the edges, especially the species of grasses, we carried out surveys in edge areas when the maize was at an early growth stage or recently sown. For each sampling point, the cover-abundance of weed species was recorded using the Braun-Blanquet scale (1979) in three rectangular plots (2×5 m^2) along the edges. The number of edges surveyed in each landscape was between 2 and 6 but depended on the number of different crops and non-crop habitats close to the sampled maize field. For instance, in very diverse landscapes, we sampled six edges: maize-orchard, maize-alfalfa, orchard-alfalfa, maize-maize, orchard ground cover and non-crop habitats. Then, the cover-abundance values were transformed into the mean value of the percent cover of each field, and the Shannon index (H) was calculated:

$$H = -\sum_{i=1}^{46} \pi_i \times ln\pi_i$$

where ‘π’ is the proportional abundance of species, and ‘i’ is the number of observations. Johnson grass plant cover and H were the explanatory field variables in the models.

In addition, for information about the cover plants and diversity groups of the edges, we used floristic surveys to transform the cover-abundance of species into the mean value of the percent cover according to six types of edges sampled to calculate the Shannon index and grouped the recorded plant species as dicotyledons or monocotyledons (Fig. 2a). These variables were only descriptive and are not included in the analysis.

Furthermore, to detect edge grasses as an alternative host of virus inoculum, we collected samples in the surveyed edge plots mentioned above according to the following criteria: (1) two samples of the most abundant grass, (2) one sample of the second most abundant grass, (3) two samples of the least frequent grass species and (4) if present, one Johnson grass plant exhibiting virus-like symptoms (leaf mosaic). In each field, each sample was placed in a separate plastic bag, identified at the species level and examined for virus-like symptoms or no symptoms. All samples were stored at − 80 °C until virus identification.

2.2.4 Virus detection

Virus identification of maize and grass leaf samples were performed by the double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (Adams and Clark 1977) using polyclonal antisera against MDMV and SCMV (Loewe GmbH). Commercial antisera were used at the dilution and in the buffers recommended by the manufacturer. Samples were extracted (1:20 g/ml of fresh tissue and 1:100 of died tissue) by grinding with a mortar and pestle. Extracts from healthy maize and Johnson grass plants were used as negative controls, and extracts of MDMV-Sp and SCMV-Sp were used as positive controls. Samples were considered positive when the A_{405nm} values were three-fold higher than the negative controls on the same plate.

2.2.5 Aphid sampling

Aphids were collected in the field between the maize phenological stages V3 (vegetative growth) to VT (reproductive development-anthesis) using yellow sticky traps (30 × 25 cm, Serbios, Badia Polesine, Italy). In each field, we placed 3 traps on stakes at the crop canopy height along a transect perpendicular to the nearest edge (approx. 30 m). The traps were separated from each other by 15 m and left for 7 days. Then, the traps were collected and stored at 6–8 °C until insect identification and recording. The number of aphids caught on each trap was counted under binocular conditions in the lab.

2.3 Factors measured at landscape scales

Data on the landscape composition were obtained for both years from Instituto Geográfico Nacional (IGN) and Declaració única agrària (DUN) of Generalitat de Catalunya, Spain. ArcGIS software was used to identify four types of land use: orchard, cereals, alfalfa and non-crop habitats. Then, the proportions of each type of land in the landscape surrounding the central point of each maize field within radii of 200 m, 500 m and 1000 m were calculated (Fig. 1b). Autocorrelation can be a problem for classical statistical tests, which rely on independently distributed errors, as it may lead to erroneous conclusions on the significance of covariates in studies of species-environment relationships. Thus, the correlations among the four land use variables in all the fields were assessed using Spearman rank correlation coefficients. These analyses showed that the proportions of cereals and orchards in the landscape were negatively correlated in the three spatial scales (Spearman’s rho ≥ 0.71); therefore, the proportion of orchards was excluded to build the models according to the criteria of Campbell and Swinscow (2009).

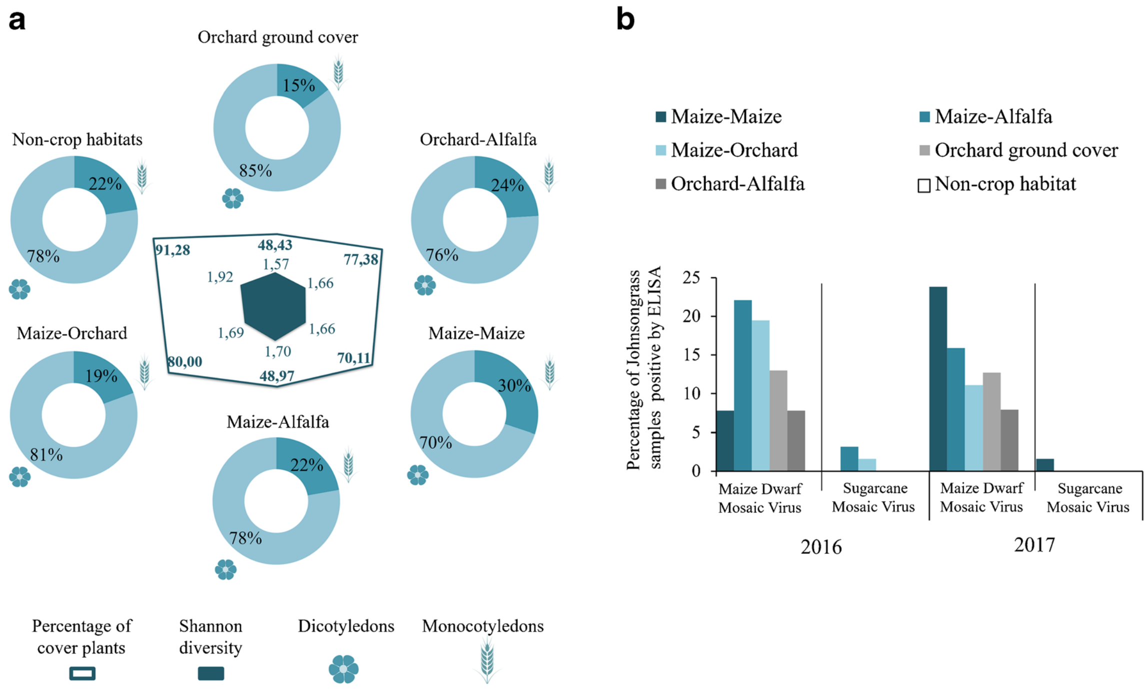

Fig. 2 **a** The composition of plant species in edges was estimated by the Braun-Blanquet scale. The cover-abundance values were transformed into the mean value of the percent cover according to the six types of edges sampled. The radar graph represents the mean percentage of the plant edge cover in sampled maize fields and H according to the field edge of the neighbouring crop. Circles represent the flora grouped into dicotyledons and monocotyledons. **b** Percentage of Johnson grass samples positive with maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV) antisera by DAS-ELISA in maize field edges and surrounding habitats.

2.4 Data analysis

We used multimodel inference (MuMIn package, Bartoń 2018), a procedure that fits models using all possible combinations of predictors and weights them using the Akaike information criterion (AIC) (dredge function). This method allows the data-based selection of a "best" model and the ranking and weighting of the remaining models in a pre-defined set. This procedure generated AIC values and Akaike weights for each candidate model. Model averaging was performed on the set of ΔAICc < 2 criteria. The selection of a best approximating model represents an inference from the data and tells us what "effects" (represented by parameters) can be supported by our data.

First, we used Moran's I statistic for the spatial autocorrelation (measure of the correlation of a variable with itself through space) of the incidence of MDMV, SCMV and aphid abundance. The results indicated that there was no significant spatial autocorrelation (MDMV Moran's $I = -0.015$, $p = 0.92$; SCMV Moran's $I = -0.007$, $p = 0.83$; aphid Moran's $I = -0.014$, $p = 0.89$). Second, the landscape and field metrics for each model were standardised (mean centred and scaled). Third, to analyse the relationships between the incidence of MDMV, SCMV, and aphid abundance with the field and landscape variables, we used a generalised linear mixed model (GLMM) in R within the lme4 package. After that, models were fitted following the different spatial scales mentioned above: 200, 500 and 1000 m from the selected maize fields. We used the percentage of viral incidence in each field, including the weight of the variable (number of maize samples per field), to analyse the effects. In the virus (percentage of vital incidence) and aphid (vector abundance) models, the planting date, maize field area, crop rotation, H in the edges, percentage of Johnsongrass plants in the edges and proportions of alfalfa, cereals and non-crop habitats were included as fixed factors, and in the virus models, the sum of aphids was also included. The year was included as a random factor in all models. The models of viruses were fitted using glmer (for the binomial distribution), and the abundance of aphids was fitted using glm.nb (for the negative binomial distribution) using the R package MASS (Ripley 2019). Then, models of virus incidences residuals were graphically inspected with qqplot and histogram graphics to ensure there was no violation of normality and homoscedasticity assumptions. Finally, in the virus models, the relative importance of each predictor variable was plotted to check the weight of the variables included in the best model.

3 Results and discussion

3.1 Incidence of MDMV and SCMV in maize fields

Virus incidence in the maize fields was determined using serological analyses of 1324 maize plants collected in the systematic surveys. Virus incidence varied significantly between the two years for both viruses, that is, MDMV ($F_{1,45} = 5.09$, p

= 0.03) and SCMV ($F_{1,45} = 7.10$ $p = 0.01$). The highest incidence of MDMV and SCMV was observed in 2016 (24% and 28%, respectively). In 2017, the incidence decreased notably, with values of 7% for MDMV and 6% for SCMV. Moreover, the highest incidences were detected in fields sown later in the year (from May to end of June) with values of 22% of MDMV and 23% of SCMV compared with early sown (from March to end of April) 10% of MDMV and 12% of SCMV. In the study period compared with previous years, the overall incidence of SCMV in the Ebro Valley increased by 13.8%, and the MDMV remained at a similar level (Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). The increasing incidence of SCMV in the last years is in concordance with the predictions of Achon and Alonso-Dueñas 2009 from the first increasing detection during 1997-1999 (Achon and Sobrepere 2001). Albeit other factors could not discard, the increased incidence of SCMV may be the result of the greater susceptibility of the current maize varieties grown in the study area (Achon and Alonso-Dueñas, unpublished results). In addition, we found a high correlation between the incidence of both viruses within the same year (R^2 0.94, $p \leq 0.001$; df = 45).

The grass species found and collected within the maize field were Johnson grass, *Setaria* spp., *Cynodon dactylon* (L.) Pers. and *Echinochloa crus-galli* (L.) P.B. Although these samples were not considered in the virus incidence models, a total of 66 grass samples were analysed using DAS-ELISA. Only Johnson grass was infected with MDMV (39.29% of samples in 2016 and 57.14% of samples in 2017), and unexpectedly, one sample was infected with both SCMV and MDMV in 2016. These results confirm that Johnson grass continues to be the main perennial reservoir of MDMV, as Achon and Sobrepere (2001) reported, but may also be an inoculum source of SCMV, a role that has not been reported before in our area. Thus, the perennial character of Johnson grass is important to the role of this weed as a virus host as virus infection risk increases with increasing local abundance of the perennial grass (Borer et al. 2010).

3.2 Plant diversity and alternative hosts of MDMV and SCMV in maize edges and surrounding habitats

A total of 203 plant species were identified in the 504 sampling points in the edge surveys. The maximum plant cover and *H* were detected in the edges of non-crop habitats (Fig. 2a), but none plant collected in this habitat resulted infected with the two viruses. On the other hand, the proportion of monocotyledons, the only potential virus reservoirs, was highest in edges between maize-maize fields (Fig. 2a). Of the 203 plants sampled, 12% of the species identified were grasses, among which the most abundant species were *Hordeum murinum* L., *Cynodon dactylon*, *Bromus diandrus* (L.), *Poa annua* L., Johnsongrass, *Avena sterilis* L., *Bromus catharticus* Vahl. and *Lolium rigidum* Gaudin.

During the edge survey, we collected a total of 641 grasses belonging to 25 species reported as a host, possible host or potential anecdotic host that were analysed by DAS-ELISA for MDMV and SCMV (Table 1). Specifically, high abundances of Johnson grass were found in all surveyed edges, in alfalfa fields around sprinklers and in the ground cover of orchards. Although the management of edges includes herbicide treatments and/or mechanical labour, during samplings in the study, we observed that Johnson grass was particularly present and frequently exhibited mosaic virus symptoms in the edges and the base of sprinklers. A total of 110 samples of Johnson grass were positive with MDMV (approximately 75% of the samples), although there were variations among edges and years (Fig. 2b). Although Johnson grass was abundant around alfalfa sprinklers and hosted abundant aphids, only 1 of the 9 Johnson grass samples collected in this situation was infected with MDMV. In addition, 1 of the 69 samples of *C. dactylon* and 1 of the 37 samples of *B. catharticus* were positive for MDMV (Table 1); these species have not been reported as MDMV hosts until now (Achon and Sobrepere 2001; Achon and Alonso-Dueñas 2009). This is a remarkable result for the virus epidemiology given that both species are particularly abundant and multiannual, increasing the host range in our agroecosystem (McLeish et al. 2017).

Concerning SCMV, we found 4 positive samples of Johnson grass, representing 0.8% and 2% of the samples in 2016 and 2017, respectively; these percentages were much lower than those observed for MDMV. Moreover, three samples with mixed MDMV and SCMV infections were detected (4% of Johnson grass samples in 2016) (Table 1, Fig. 2b). No previous Johnson grass samples positive for SCMV had been detected in our area, but this species is among the most persistent weeds (Peerzada et al. 2017), and it has been positively detected as an SCMV host in another Mediterranean country (Moradi et al. 2017). Although Achon and Alonso-Dueñas (2009) reported positive samples of *Setaria verticillata* with SCMV, no evidence of grass hosts for SCMV other than Johnson grass was found in this study when we analysed 641 grass samples belonging to 25 species. This could be because the edge areas we sampled in spring, *Setaria* spp. showed a low cover because it is a summer grass. However, the results of our random edge survey to find Johnson grass plants positive with SCMV and the high incidences observed on maize in our study suggest that the long duration of the life history stages of this specie make it a potential alternative host that ensures the temporal availability of inoculum in the landscape. Although it has been reported in other countries that species of the genera *Bromus*, *Cynodon* and other winter annual grasses could act as hosts in the absence of maize, many samples of these genera in this study were negative for SCMV. Thus, the low occurrence of the winter host of SCMV continues to be the bottleneck in the epidemiological knowledge of this potyvirus. These results suggest more

Table 1 Relation of grasses collected in edge surveys and analysed by DAS-ELISA. Data in the 'host' column were taken from the literature. ***host, **possible host, *anecdotic species; A: annual species, P: perennial species. The three right columns show the number of plants that reacted with antisera of the plants collected for analysis. The numbers in parentheses represent the percentages of ELISA-positive samples for MDMV and SCMV

Year	Grass species collected	Host	Growth habitat	Reacted with antisera		
				MDMV	SCMV	Double infection
2016	*Avena sativa* L.	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Avena sterilis L.	**	A	0/58 (0)	0/58 (0)	0/58 (0)
	Brachypodium phoenicoides (L.)	**	P	0/27 (0)	0/27 (0)	0/27 (0)
	Bromus catharticus Vahl.	**	P	0/17 (0)	0/17 (0)	0/17 (0)
	Bromus spp.	**	A	0/32 (0)	0/32 (0)	0/32 (0)
	Cynodon dactylon (L.) Pers.	**	P	1/45 (2.22)	0/45 (0)	0/45 (0)
	Dactylis glomerata L.	*	P	0/5 (0)	0/5 (0)	0/5 (0)
	Hordeum murinum L.	**	A	0/58 (0)	0/58 (0)	0/58 (0)
	Koeleria phleoides (Vill.)	*	A	0/2 (0)	0/2 (0)	0/2 (0)
	Lepturus repens (G.Forst.)	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Ligeum spartum (L.) Kunth	*	P	0/1 (0)	0/1 (0)	0/1 (0)
	Lolium rigidum Gaudin	**	P	0/14 (0)	0/14 (0)	0/14 (0)
	Mellica celiata L.	*	P	0/3 (0)	0/3 (0)	0/3 (0)
	Oryzopsis miliacea (L.)	*	P	0/9 (0)	0/9 (0)	0/9 (0)
	Phalaris arundinacea L.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Phalaris minor Retz.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Poa annua L.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Poa pratensis L.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Polygonon sp.	*	P	0/2 (0)	0/2 (0)	0/2 (0)
	Setaria pumila (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria verticillata (L.)	**	A	0/2 (0)	0/2 (0)	0/2 (0)
	Setaria viridis (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Sorghum halepense (L.)	***	P	54/77 (70.13)	3/77 (3.9)	3/77 (3.9)
2017	*Avena barbata* Pott	**	A	0/3 (0)	0/3 (0)	0/3 (0)
	Avena sterilis L.	**	A	0/33 (0)	0/33 (0)	0/33 (0)
	Brachypodium phoenicoides (L.)	**	P	0/10 (0)	0/10 (0)	0/10 (0)
	Bromus catharticus Vahl.	**	P	1/20 (5)	0/20 (0)	0/20 (0)
	Bromus diandrus Roth	*	A	0/16 (0)	0/16 (0)	0/16 (0)
	Bromus madritensis L.	*	A	0/4 (0)	0/4 (0)	0/4 (0)
	Bromus spp.	**	A	0/7 (0)	0/7 (0)	0/7 (0)
	Cynodon dactylon (L.) Pers.	**	P	0/24 (0)	0/24 (0)	0/24 (0)
	Echinochloa crus-galli (L.) P.B.	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Eragrostis spp.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Hordeum murinum L.	**	A	1/44 (0)	0/44 (0)	0/44 (0)
	Lolium rigidum Gaudin	**	P	0/18 (0)	0/18 (0)	0/18 (0)
	Oryzopsis miliacea (L.)	*	P	0/6 (0)	0/6 (0)	0/6 (0)
	Phalaris minor Retz.	*	P	0/3 (0)	0/3 (0)	0/3 (0)
	Phleum paniculatum Huds.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Poa annua L.	*	A	0/6 (0)	0/6 (0)	0/6 (0)
	Poa pratensis L.	*	P	0/10 (0)	0/10 (0)	0/10 (0)
	Polygonon sp.	*	P	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria pumila (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Setaria verticillata (L.)	**	A	0/4 (0)	0/4 (0)	0/4 (0)
	Setaria viridis (L.)	**	A	0/1 (0)	0/1 (0)	0/1 (0)
	Triticum spp.	*	A	0/1 (0)	0/1 (0)	0/1 (0)
	Sorghum halepense (L.)	**	P	51/63 (81)	1/63 (1.6)	0/63 (0)
	Total samples			105/641 (16.4)	4/641 (0.62)	3/641 (0.46)

powerful detection methods, such as next-generation sequencing (NGS) tools, should be used in future research.

3.3 Effects of landscape and field variables on the vectors of MDMV and SCMV

Aphids are one of the primary pests in the cultivation of maize in Spain, with variable abundances seasonally and spatially (Pons et al. 1994; Asín and Pons 1999). During the 2-year study, a total of 240 traps were placed in 46 maize fields where 2684 aphids were recorded. The abundance of aphids varied significantly between years ($F_{1,45} = 15.23$, $p \leq 0.001$). Aphids were notably more abundant in 2016 than in 2017 (2390 and 294 aphids, respectively). Moreover, the highest densities of aphids in June coincidence with the highest incidence of MDMV and SCMV in maize fields sown later (since the week number 25) (Fig. 3b, graph aphid abundance).

The most parsimonious model relating the aphid abundance with the landscape and field variables is shown in Table 2. Only significant variables of the best model are shown. Although the model at 500 m was slightly more predictive than the model at 200 m, the two scales can be considered valid because the differences between their AIC values were less than 2. At the scale of 500 m, the aphid abundance on maize was also found to relate to some landscape variables in a study carried out recently in the area (Clemente-Orta et al. 2020). Moreover, in the model with a 200 m scale, an important relationship was found between the proportion of cereals in the landscape and the maize aphid abundance, although this effect was not detected at the two higher scales (i.e. 500 and 1000 m). These results obtained at the landscape scale confirm that the colonisation of maize is closely linked to migrations of these species from nearby winter cereals, as Pons et al. (1994) reported. Thus, the presence of winter cereal surfaces could lead to increased aphid abundances on maize because of a possible concentration effect (Root 1973) in early seasons at small landscape scales. This trend was also reported by Gilabert et al. (2017), who showed that aphid populations increase in homogeneous landscapes dominated by cereals. Although the effect of non-crop habitats on the abundance of herbivorous insects has been found to be inconsistent (Chaplin-Kramer et al. 2011), the proportion of non-crop habitats had a positive effect in this study on the early-season aphid abundance at the three scales. The lack of infected grasses, as found in this study, as well as the higher species diversity in non-crop habitats than in other habitats, suggest that these are a source of aphids in the early season, although likely not viruliferous.

3.4 Effects of landscape and field variables on maize potyvirus incidence

It has been suggested that common single-scale analyses can underestimate the impact of humans on biodiversity, diseases and the environment (Cohen et al. 2016). In fact, we used an approach based on the proportion of cereals, alfalfa and non-crop habitats surrounding the sampled fields at three spatial scales to determine whether a high proportion of cereals in the landscape contribute to the risk of viral diseases. The most parsimonious models relating MDMV and SCMV incidences with the landscape and field variables are shown in Table 2. Only significant variables of the best model are shown. The most predictive model according to the AIC value for both viruses was at the 200 m scale. This small spatial scale mostly involves close field edges. These results are in concordance with those reported by Borer et al. (2010), who showed that local context provides the strongest explanation of disease risk variation in generalist viruses. Overall, the incidence of MDMV was most influenced by field effects, whereas the SCMV incidence was most affected by landscape factors.

Field variables related to field management had strong effects on both viruses as Fig. 3a shows. All field variables used in the analysis had strong positive effects on MDMV, but only the planting date, the aphid abundance and the weed diversity of edges had positive effects on SCMV. Concretely, the planting date was the first and the weightiest field variable linked positively to the virus incidence in both virus models especially, in later planting dates (since week number 25) (Fig. 3b). The strong effect of late sowing maize resulted from spatial-temporal encounters of high aphid populations and high inoculum pressure. By contrast to the early planting where the only source of viruses is grass reservoirs, in late showing, source of viruses included also infected-maize planting earlier. This result is particularly relevant in our area and in other areas where maize is sown late after winter cereals have been harvested. We therefore note the necessity to review the adequacy of maize planting dates, especially for late sown maize. In addition, the important relationship between the plant species composition of edges and the potyvirus incidence indicates that edges are an important driver of infection at 200 m (Fig. 3b, graph of diversity of edges). Furthermore, when we grouped the information relating flora surveys by the type of edges, we found that the species diversity value was not different between edges, but plant cover was especially high in the edges of multiannual crops (for example, in the edges of alfalfa or in orchard ground covers) (Fig. 2a). This feature confirms that the importance of virus dispersal to maize fields could depend more on the cover and multiannual character of edge plant species cover than their diversity, especially in spring. Therefore, analyses of infection risk by potyviruses in the future must include the cover of non-abundant grass.

On the other hand, the percentage of non-crop habitats was a landscape variable that was very negatively related to the incidence of both viruses in all models, especially at 200 m (Fig. 3b, graph of non-crop habitat and Table 2). Thus, increased levels of human management that is associated with decreased habitat species diversity result in increased virus infection risk, as stated by Pagán et al. (2012) for virus epidemics. However, although biodiversity in non-crop habitats has been reported as a factor determining disease risk (Keesing et al. 2006; Pagán et al. 2012), few studies have focused on host plant-virus systems. Our results seem to follow the “dilution effect” hypothesis (Keesing et al. 2006), which means that an increase in plant species diversity in the landscape could decrease the overall disease risk by increasing the possibility that vectors will feed on noninfected plants.

The study area was a landscape dominated by winter and summer cereals, mainly maize (the maximum proportions for all sites were 87.05 at 200 m, 86.26 at 500 m and 73.60 at

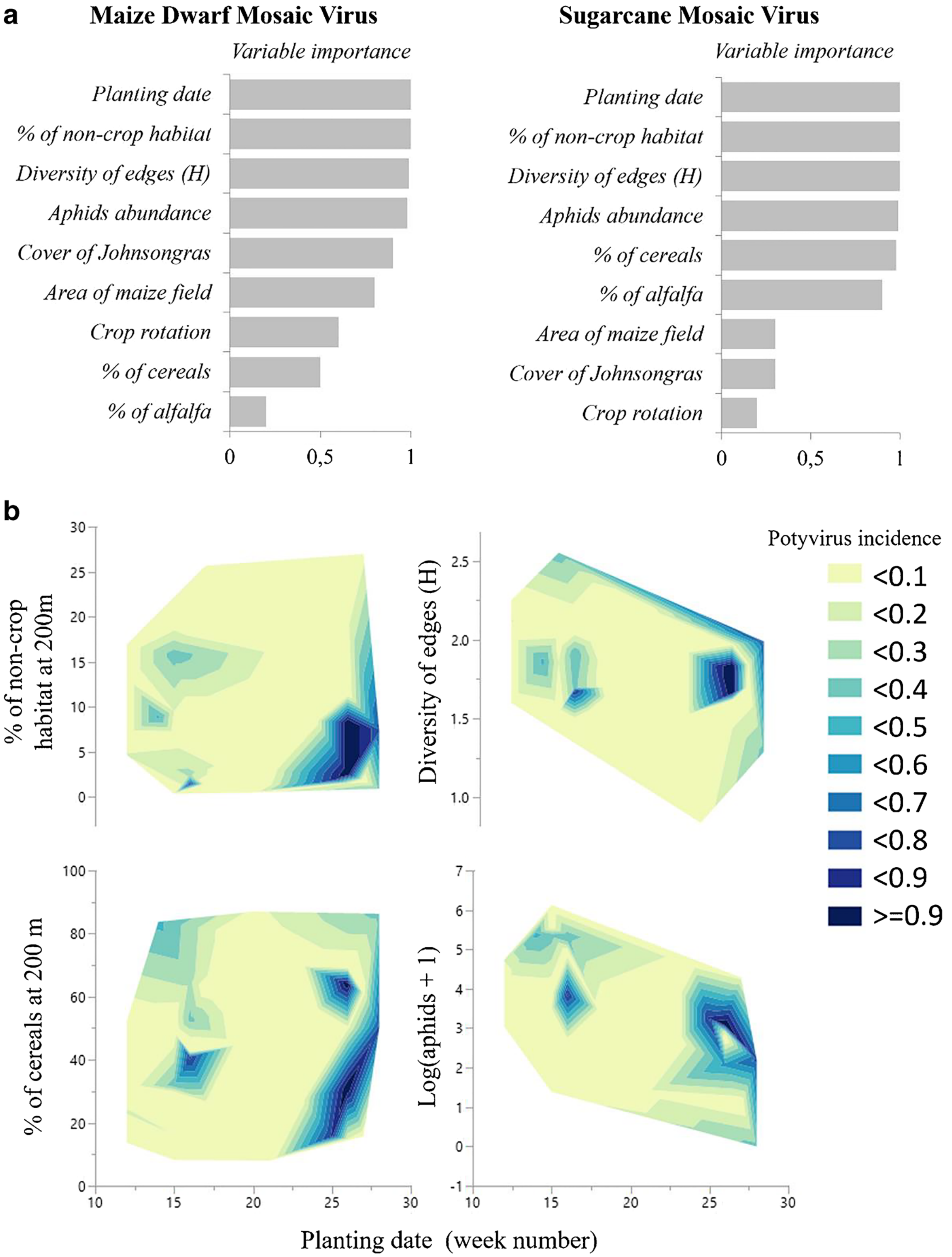

Fig. 3 **a** Graphs of relative importance of each predictor variable (sum of Akaike weights of the best models in which each variable appears) on virus incidence models at 200 m. In the best models at 200 m for both viruses, the percentage of non-crop habitats, the maize planting date and the diversity of edges were strong predictors. **b** Contour plots show the response values and desirable operating conditions. The contour plot contains the following elements: predictors on the X (planting date) and Y (% of non-crop habitats and % of cereals at 200 m, aphid abundance and *H* of edges) axes. Contour lines connect points that have the same adjusted response value

Table 2 Generalised linear mixed models used in multimodel inference to select the best effects model on aphid abundance, MDMV and SCMV incidence relating the influence of landscape and field variables. Models were fitted at three spatial scales from 200 to 1000 m around the sampled fields. Only significant variables in the best models (ΔAIC < 2) are presented. AIC values indicate little differences in support from data model

		200 m			500 m			1000 m		
Scale	Variables	Estimate	*z* value	*p* value	Estimate	*z* value	*p* value	Estimate	*z* value	*p* value
Aphid abundance										
Field	(Intercept)	3.46	5.45	< 0.001	3.45	5.15	< 0.001	3.45	5.15	< 0.001
	Planting date (weeks)	− 0.56	3.16	0.002	− 0.48	3.42	0.001	− 0.48	3.42	< 0.001
	Area maize field (ha)									
	Rotation (winter/summer cereal)									
	H in the edges									
	Johnson grass plant cover									
Landscape	Percentage of cereals	0.24	1.73	0.058						
	Percentage of alfalfa									
	Percentage of non-crop habitats	0.30	2.13	0.033	0.49	2.87	0.004	0.37	2.86	0.004
	Akaike information value (AIC)	436.33			*434.21*			441.64		
MDMV incidence										
Field	(Intercept)	− 2.47	2.89	0.004	− 2.30	3.77	< 0.001	− 2.24	4.34	< 0.001
	Planting date (weeks)	0.97	8.93	< 0.001	0.97	8.84	< 0.001	0.97	8.25	< 0.001
	Area maize field (ha)	0.39	2.90	0.004	0.20	2.17	0.030	0.29	2.90	0.004
	Rotation (winter/summer cereal)	0.27	2.02	0.044				0.44	3.10	0.002
	H in the edges	0.79	6.83	< 0.001	0.51	4.99	< 0.001	0.61	5.44	< 0.001
	Johnson grass plant cover	0.37	2.84	0.005				0.29	2.36	0.018
	Aphid (sum)	0.44	3.22	< 0.001	0.34	3.02	0.003			
Landscape	Percentage of cereals				− 0.38	3.76	< 0.001	− 0.27	2.67	0.008
	Percentage of alfalfa							0.55	6.26	< 0.001
	Percentage of non-crop habitats	− 0.98	8.47	< 0.001	− 0.90	6.23	< 0.001	− 0.32	3.67	< 0.001
	Akaike information value (AIC)	*485.41*			538.71			537.15		
SCMV incidence										
Field	(Intercept)	− 2.54	2.35	0.019	− 2.35	3.00	0.003	− 2.15	2.87	0.004
	Planting date (weeks)	0.97	10.33	< 0.001	0.97	10.29	< 0.001	0.97	10.40	< 0.001
	Area maize field (ha)									
	Rotation (winter/summer cereal)									
	H in the edges	0.96	8.30	< 0.001	0.80	7.03	< 0.001	0.70	6.29	< 0.001
	Johnson grass plant cover									
	Aphid (sum)	0.39	3.43	< 0.001	0.39	3.74	< 0.001			
Landscape	Percentage of cereals	0.36	3.43	< 0.001	− 0.50	5.04	< 0.001	− 0.20	2.10	0.036
	Percentage of alfalfa	0.30	2.71	< 0.001				0.52	6.17	< 0.001
	Percentage of non-crop habitats	− 0.98	8.52	< 0.001	− 0.87	7.56	< 0.001	− 0.27	3.42	< 0.001
	Akaike information value (AIC)	*523.98*			561.16			584.29		

1000 m), with the relevant presence of non-crop habitats in some areas. Although at 200 m the percentage of cereals had positive effects on SCMV, in contrast to our expectations and as suggested by Rodríguez-Nevado et al. (2017), the high proportion of cereals did not amplify the virus incidence of MDMV and SCMV at large spatial scales (Fig. 3b, graph of % of cereals). The positive relationship between the percentage of alfalfa in the landscape with both viruses at 1000 m and with SCMV at 200 m suggests that the durability and presence of grasses in the edges and within this crop result in a broad source of host plants of multiannual species, particularly Johnson grass, as mentioned above.

4 Conclusions

Our results show for the first time the main drivers of potyvirus infection in maize crops by using a novel analysis methodology considering landscape and field variables at different spatial scales. We show that infections by the two potyviruses follow different patterns that are more predictive at a small spatial scale (200 m). The fact that the best spatial scale for both viruses is 200 m means that maize fields itself and close edges, that is, the local context is the strongest predictor of the risk of infection. While MDMV infection risk is more linked to field management than SCMV, infection risk of SCMV is more dependent than MDMV on the close field edges measured in this study as landscape variables. In addition, infection risk demonstrates a strong dependency on the proportion of non-crop habitats, the maize planting date, and the diversity of weeds in the edges. Moreover, Johnson grass is the main driver of infection by the two viruses, especially in maize fields shown late in coincidence with the more abundant flights of vectors. On the other hand, the use of more powerful tools to detect infected samples by SCMV could improve our understanding of the role of minor multiannual grasses in the epidemiology of the virus, especially in grasses growing in edges between alfalfa and cereal fields.

Overall, we report that in areas where generalist viruses are transmitted in a non-persistent manner, the local context is the most appropriate context to prevent virus infection. Thus, we recommend the following measures: (1) avoid late maize planting dates as much as possible to minimise infection risk, (2) integrate or keep non-crop habitats in the landscape in order to increase plant biodiversity and (3) confirm the convenience of the eradication of grass weeds, particularly Johnson grass, within the field and in maize edges.

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Contributions G.C.O. contributed to collect the landscape information, the insect abundance, grass and maize samples, analysed of the data, interpreted the results, and drafted the article. R.A. contributed to the design of the work, the collect insect data and drafted the article. M.A. contributed to the design of the collect maize and grass samples, and revised the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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