PhD Thesis
Biological Control and Pollination in Cider Apple Orchards: a Socio-ecological Approach

Control Biológico y Polinización en Plantaciones de Manzana de Sidra: una Aproximación Socio-ecológica

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Biological Control and Pollination in Cider Apple Orchards: a Socio-ecological Approach

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RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

1.- Título de la Tesis	
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RESUMEN (en español)

La expansión agrícola y su intensificación son unas de las principales causas del deterioro medio ambiental y de la pérdida de biodiversidad en todo el mundo. Aunque suene contradictorio, esta tendencia actual pone en peligro el suministro futuro de alimentos a escala global. Sin embargo, una agricultura rentable que haga compatible la seguridad alimentaria con la conservación de la naturaleza es posible. En los últimos años, muchos esfuerzos se han destinado a detener los daños generados por la agricultura y hacerla más sostenible. Lamentablemente, queda mucho camino por recorrer. La biodiversidad, asociada al suministro de servicios ecosistémicos, puede aportar diversos beneficios al rendimiento de los cultivos. Sin embargo, para asentar dicha biodiversidad es necesario cumplir ciertas condiciones favorables dentro y cerca del cultivo. Por lo tanto, debemos ampliar nuestros conocimientos acerca de cómo el paisaje y las características de los agrosistemas pueden fomentar la biodiversidad para maximizar el suministro de servicios ecosistémicos. De la misma manera, necesitamos comprender la compleja relación entre la biodiversidad y los servicios ecosistémicos. Finalmente, debemos acotar las diferencias que existen entre los objetivos de las estrategias de manejo y los resultados reales obtenidos en los paisajes agrícolas.

El objetivo de esta tesis doctoral es proporcionar conocimientos acerca del suministro simultáneo de los servicios de control biológico de plagas y polinización en la zona por excelencia del cultivo de manzana de sidra (Malus x domestica Borkh) en Asturias (España). Para ello, en primer lugar, la tesis se centra en los impulsores de la biodiversidad que operan en los paisajes agrícolas. En segundo lugar, trata de revelar las relaciones entre la biodiversidad y los dos servicios ecosistémicos. Y, en tercer lugar, evalúa las percepciones y el conocimiento de los agricultores sobre el control biológico y los enemigos naturales. En concreto abarca tres estudios:

El primero evalúa en profundidad los principales efectos ambientales (i.e. paisaje y características a escala local) que impulsan simultáneamente la avifauna insectívora y los insectos polinizadores en las plantaciones de manzana. Asimismo, demuestra la relación positiva entre esta biodiversidad y el suministro de los servicios de control biológico y polinización.

El segundo estudio también aborda los principales efectos medio ambientales que impulsan a las poblaciones de carpocapsa y a sus parasitoides. Sin embargo, en este caso, las interacciones tróficas (i.e. “bottom-up” y “top-down”) dentro del sistema manzana - carpocapsa - parasitoides parecen gobernar el parasitismo y el daño en la producción de manzana generado por la carpocapsa.

Finalmente, el tercer estudio, a través de 90 encuestas “face-to-face”, intenta comprender los conocimientos y percepciones sobre el control biológico y los enemigos naturales que poseen los agricultores de manzana de sidra. En colaboración con ellos tratamos de proporcionar conocimientos para una gestión exitosa de los huertos de manzanas de sidra basada en el control biológico.

Mediante un enfoque integrador, combinando aproximaciones empíricas y participativas basadas en la teoría que vincula biodiversidad con el funcionamiento ecosistémico (BEF) y el marco de los servicios de los ecosistemas; los resultados de esta tesis sugieren que las aves insectívoras y los insectos polinizadores pueden promoverse simultáneamente aumentando los hábitats leñosos semi-naturales alrededor de las plantaciones y un dosel continuo y extenso dentro de ellas. Asimismo, el control biológico y la polinización responden positivamente a la biodiversidad de aves insectívoras, insectos polinizadores y parasitoides de carpocapsa. En el caso del control biológico de la carpocapsa, la disponibilidad de recursos alimentarios, tanto para ella como para sus parasitoides, es esencial para comprender la dinámica de ambas poblaciones y controlar eficazmente esta plaga. Por último, el estudio participativo revela que los agricultores conocían mejor a los enemigos naturales vertebrados que a los invertebrados. Además, demostraron que la capacidad para reconocer a un enemigo natural está asociada a conocimientos previos sobre el organismo (i.e. conocimientos ecológicos locales y formales). En cuanto a las percepciones sobre las interacciones enemigos natural - plaga, revelaron importantes lagunas de conocimiento. Por consiguiente, la combinación de estudios empíricos y participativos en marcos integradores es esencial para lograr políticas agrícolas y prácticas de gestión exitosas en relación con el suministro de servicios ecosistémicos en los paisajes agrícolas.

Esta tesis ofrece una perspectiva integradora sobre el suministro de los servicios de control biológico de plagas y polinización en cultivos de manzana por diferentes grupos de biodiversidad (i.e. aves insectívoras, parasitoides de carpocapsa e insectos polinizadores). A su vez, esta biodiversidad está condicionada por el paisaje y factores a escala local. Por último, esta tesis demuestra que los estudios participativos son esenciales para diseñar estrategias de gestión exitosas. Una nueva agricultura basada en prácticas agrícolas sostenibles y en la biodiversidad puede satisfacer la demanda futura de alimentos y otros productos, reduciendo al mismo tiempo los daños en el medio ambiente y la pérdida de biodiversidad.

RESUMEN (en Inglés)

The increasing land use conversion to agriculture and intensification are damaging the environment and threatening biodiversity worldwide. Although it may seem contradictory, this current trend in agriculture is jeopardizing the future world´s food supply. However, an economically profitable agriculture that makes compatible food security with biodiversity conservation is feasible. In recent years, an increasing effort has been oriented to halt the damage generated by agriculture and make it more sustainable. Unfortunately, much work remains to be done. Biodiversity can render benefits to crop yield through the provision of ecosystem services. But, these biodiversity needs some habitat conditions to stay close to or within the crop. Thus, we need more research on how landscape and local-scale features foster biodiversity to maximize the provision of ecosystem services in agroecosystems. At the same time, we are still far from understanding the complex relationship between biodiversity and ecosystem services. Finally, we should bridge the gap between the management strategies promoted and their true implementation in agricultural landscapes.

The present PhD thesis aims to gaining insights into the simultaneous provision of biological control and pollination in the main cider apple (*Malus x domestica* Borkh) crop area of Spain (Asturias). For this purpose, first, the thesis focuses on the drivers of animal biodiversity that operate in agricultural landscapes. Second, it tries to reveal the relationships between biodiversity and the two ecosystem services. Third, it assesses farmers' perceptions and knowledge of the concept of biological control and natural enemies underpinning its provision. Specifically, it comprises three studies:

In the first one, we deal in depth with the main environmental effects (landscape and local-scale features) that drive simultaneously insectivorous birds and pollinator insects communities. For it, censuses and captures where performed to evaluate both biodiversity groups. This study also aims to prove the positive effects of both groups in the provisioning of pest control and pollination. Insectivory was estimated from sentinel model and exclusion experiments. The contribution of pollinator insects to crop yield and fruit quality were measured as fruit set and seed set.

In the second study, we also try to dissect the main environment effects that drive codling moth populations and their parasitoids. Codling moth was sampled from overwintering larvae in cardboard traps wrapped around the trunk and the parasitism was estimated from the parasitoids emerging from the collected codling moth. However, in this case, the strong trophic interactions (i.e. top-down and bottom-up) within the apple-codling moth-parasitoid system seem to drive the ecosystem service supply of biological control by parasitoids and the crop damage generated by the codling moth.

Finally, in the third one, we conducted 90 face-to-face surveys with cider-apple farmers to better understand their knowledge and perceptions on biological control and natural enemies. Co-working with farmers we try to provide insights for a successful management of cider apple orchards based on biological control.

By means of empirical and participatory approaches based on the biodiversity-ecosystem functioning (BEF) theory and the ecosystem services framework, the results of this thesis suggest that insectivorous birds and wild pollinators can be simultaneously promoted by the cover of semi-natural

woody habitats around the orchards and a continuous well developed apple canopy cover. Biological control and pollination respond positively to insectivorous bird, pollinator insect and codling moth parasitoid biodiversity. In the case of codling moth control, the availability of food resources for codling moth and their parasitoids is essential to understanding the dynamics of both populations and effectively controlling this pest. To conclude, the participatory study reveals that farmers knew vertebrates natural enemies better than invertebrates. Besides, they proved that the ability to recognize a natural enemy is associated with previous knowledge about the organism (i.e. local ecological and formal knowledge). Regarding farmers' perceptions about prey-pest interactions, they revealed important knowledge gaps. Therefore, combining empirical and participatory studies within integrative frameworks is essential to achieve successful agricultural policies and management practices in relation with the supply of ecosystem services in agricultural landscapes.

Overall, this thesis provides an integrative overview of how the supply of important ecosystem services in apple orchards is defined by different biodiversity groups (i.e. insectivorous birds, codling moth parasitoids and wild pollinators), which, in turn, are conditioned by landscape and local-scale features. Besides, this thesis proves that participative researches are essential to design successful management strategies. A new agriculture based on sustainable agricultural practices and biodiversity can meet future demand for food and other products while reducing environment externalities and biodiversity loss.

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Los estudios presentados en esta Tesis doctoral se han desarrollado en el Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA) del Principado de Asturias, el departamento de Biología de Organismos y Sistemas de la Universidad de Oviedo y el Instituto para la Investigación Transdisciplinaria de la Sostenibilidad en la Universidad de Leuphana en Lüneburg.

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A todos los que piensan que la ciencia tiene una gran belleza.

A todos los que realmente comparten y transmiten esa belleza.

Si quieres llegar rápido camina solo,

si quieres llegar lejos ve acompañado.

Proverbio africano

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Summary

SUMMARY

The increasing land use conversion to agriculture and intensification are damaging the environment and threatening biodiversity worldwide. Although it may seem contradictory, this current trend in agriculture is jeopardizing the future world´s food supply. However, an economically profitable agriculture that makes compatible food security with biodiversity conservation is feasible. In recent years, an increasing effort has been oriented to halt the damage generated by agriculture and make it more sustainable. Unfortunately, much work remains to be done. Biodiversity can render benefits to crop yield through the provision of ecosystem services. But, these biodiversity needs some habitat conditions to stay close to or within the crop. Thus, we need more research on how landscape and local-scale features foster biodiversity to maximize the provision of ecosystem services in agroecosystems. At the same time, we are still far from understanding the complex relationship between biodiversity and ecosystem services. Finally, we should bridge the gap between the management strategies promoted and their true implementation in agricultural landscapes.

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in turn, are conditioned by landscape and local-scale features. Besides, this thesis proves that participative researches are essential to design successful management strategies. A new agriculture based on sustainable agricultural practices and biodiversity can meet future demand for food and other products while reducing environment externalities and biodiversity loss.

General Introduction

Agriculture is a dominant form of land use, accounting for almost 40% of the world's terrestrial surface (MA, 2005; Power, 2010). During the last 50 years, the unacceptable food shortages in many parts of the world and the exponential population growth, underpinned the continuous worldwide expansion of agricultural production (Evenson and Gollin, 2003; Cohen and Garrett, 2009; FAO, 2017). It is our responsibility to choose the way in which we want to increase the production of our crops to face future challenges. Expanding food production come at a heavy cost to the natural environment: eutrophication of ecosystems, depletion of groundwater sources, increase of air and land pollution, loss of soil fertility, habitat destruction, unprecedented ecosystem simplification and fragmentation of natural and semi-natural habitats (Lambin and Meyfroidt, 2011; Kissinger et al., 2012; FAO, 2017). As an unavoidable result, biodiversity has been deeply eroded (Newbold et al., 2016; FAO, 2017; IPBES, 2019).

Although the damages arising from the agriculture are clear and there are numerous studies advocating for an agriculture more committed to the environment (Edwards-Jones et al., 2008; Cunningham et al., 2013; Garibaldi et al., 2017). The trend seems to still choose high-input, resource-intensive systems that are accompanied by high environmental costs (Pe'er et al., 2014). These farming systems try to maintain high yields at the expense of the utilization of increasingly large quantities of fossil fuel, agrochemical and other industrial inputs (Foley et al., 2011). High-input, resource-intensive systems are controlled by global markets and involving large corporations such as Monsanto and Nestlé that encourage monoculture cropping and the use of chemical and mechanical inputs (Nyström et al., 2019). The combination of this intensive agriculture on a global scale and the influence of these corporations, as well as industry, markets and indifferent consumption of food by society reinforce the negative effects of agriculture (van Vliet et al., 2015; O'Neill et al., 2017). The uncontrolled agriculture intensification not only increases on the already intensive land, it also causes the abandonment of less productive and extensively managed land (Plieninger et al., 2012).

The need to guide agriculture into the adoption of sustainable production systems and practices to ensure a natural resource base has become in an extremely urgent goal (Kneafsey et al., 2013; UN, 2015; Rockström et al., 2017). Produce more with less in a sustainable way requires as a first step to know and understand the mechanisms that explain the potential of agriculture to improve crop productivity while that halt and reverse environmental degradation (UN, 2015; FAO, 2017). Low-input farming systems can help to address both challenges. Low-input farming systems seek to optimise the management and to minimise the use of off-farm resources, such as chemical fertilisers and pesticides. Thereby, low-input farming systems reduce production costs, pollution of surface and groundwater, pesticides residues in food and farmers' overall risk (Garibaldi et al., 2017; Lechenet et al., 2017). Also, contrary to the general thought, low-input farming systems can increase both short- and long-term agroecosystem profitability (Garibaldi et al., 2017; Lechenet et al., 2017).

Agroecosystems are any type of modified or managed ecosystem by human beings with the objective of optimizing the provisioning ecosystem services of food, fibres, fuel or other materials of biotic origin (Zhang et al., 2007). Ecosystem services have been defined as the direct and indirect contributions of ecosystems to human well-being (de Groot et al., 2010), or as any activity or ecosystem function that supply benefits to people (Mace et al., 2012). Ecosystem services can be classified in four main categories: (1) provisioning services, which are products or goods we obtain from ecosystems such as food and timber; (2) regulating services, which are benefits from regulating of ecosystem processes such water and air purification, pollination and pest control; (3) cultural services, which are non-material benefits to people obtain from ecosystems such as recreation, educational and spiritual values; and finally (4) supporting services such as nutrient cycling and primary production whit underpin all other services (MA, 2005). Depending on the intensification degree of the agroecosystems, the dependence and demand of ecosystem services from neighboring natural ecosystems and external biodiversity can be very high (Zhang et al., 2007; Gabriel et al., 2013; Ekroos et al., 2014). In many cases, in an effort to maximize crop production, agroecosystems are mainly supported by human inputs (e.g. fertilizers, pesticides, herbicides, water supply) that decouple them form the ecosystem services provided by biodiversity (Potts et al., 2010). However, some agroecosystems less intensively managed (e.g. low-input agroecosystems) can provide services by their self or by near surrounding habitats (Bommarco et al., 2013; Torralba et al., 2016). For instance, crop production in low-input agroecosystems relies no only on human inputs such us fertilizers or chemicals products to control pests and weeds, but also on the biodiversity present in the agroecosystem. Going one step further, agroecosystems also can provide a range of cultural services to human communities, including scenic beauty, education, recreation, tourism and traditional use (MA, 2005).

Using the ecosystem services framework, we can classify the different functions provided by agroecosystems and the functions needed for a sustainable production (MA, 2005). This framework can highlight how functionally important biodiversity (of the agroecosystem itself and the surrounding landscape) leads to a range of services that benefit human well-being, including provisioning and regulating services (Power, 2010) (**Fig. 1**). However, the embedment of the ecosystem service framework into the wider concept of sustainability and conservation is problematic (de Groot et al., 2010). The predominance of only considering nature as a provider of flows of services is blinding us from the complexity of the agroecosystems: ecological, economic, political and social interconnected challenges (Norgaad, 2010). The bad use of the ecosystem services framework as a management tool, for instance, focused only in some ecosystem services (e.g. provisioning services) and benefits (e.g. production) may lead ecosystems to undesirable final points (Martínez-Sastre et al., 2017). In addition, the relationship between biodiversity and ecosystem services can become entangle until the meaning of both concepts is lost. Mace et al. (2012) defines biodiversity as an underlying ecosystem process, a final ecosystem service or a good in its own right. Consequently, recent efforts are being made to rebrand ecosystem services as “Nature´s Contributions to People” (Pascual et al., 2017; IPBES, 2019) trying to find the best term to describe the new anthropocentric forms of conservation and sustainability. It is essential to stablish proper frameworks and approaches to consider all values of nature (e.g. intrinsic, instrumental and relational) important for decision making, even relational values that emanate from our relationship with nature and our responsibility toward it (Pascual et al., 2017).

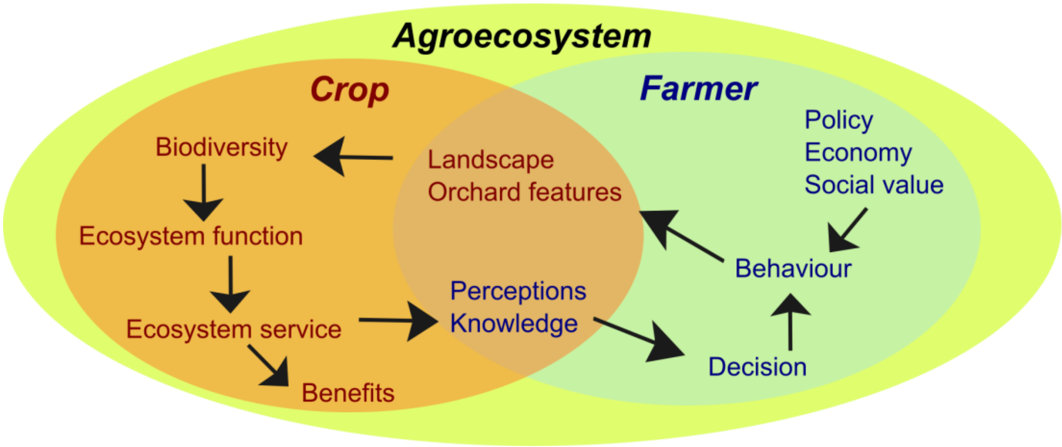

Fig. 1 Outline of the conceptual framework of an agroecosystem. The different components of biodiversity play a key role in the development of essential ecosystem services for the crop and for human well-being (orange ellipse). In turn, this ecosystem services are perceived by farmers who make management decision about the landscape and orchard features (blue ellipse).

Once the importance of ecosystem service framework and its current transformation toward "Nature´s Contributions to People" are recognized, a transparent participatory process is required to study, inform and guide agroecosystems. Agroecosystems are socio-ecological systems defined as dynamic adaptive complex ecosystems composed of human and ecological entities that interact (Maes et al., 2013). Due to the fact that people play a significant role, particularly, farmers are no longer seemed as external managers of agricultural systems, they become part of them. Scientist community and farmers should work together to reach common goals across agriculture, such as environmental sustainability and food security. Interdisciplinary studies are essential to achieve permanent conservation and sustainable changes (de Groot, 2006; Díaz et al., 2011). The integration of biological and social knowledge, combined with the ecosystem services framework, can bridge the gap between scientist and farmers in agriculture (Collins et al., 2011) (**Fig. 1**). Engaging farmers in knowledge co-production, trying to study variables that link natural and human components (e.g. behavioural components, farmers' perceptions and knowledge) can provide very valuable information. The ecological benefit of a particular ecosystem service depends on how different actors in society perceive it (Lamarque et al., 2014).

The value of nonmarket functions, such as biodiversity conservation, pollination or pest control, depends on societal perception that is contextual and diverse (Randall, 2002). These perceptions can be the difference between success and failure in final agricultural policies (van Oudenhoven et al., 2012, Martín-López et al., 2012).

In a European context, where agriculture is ruled by Common Agriculture Policy (CAP), agrienvironmental schemes and concrete policies are designed to offset and/or reverse the negative effects of agricultural intensification on biodiversity (EEA, 2009; Riffell et al., 2009). Specific measures have been designed to improve ecosystem services delivery by functionally important biodiversity in agroecosystems, for instance protecting and enhancing the environment, including habitat management to accommodate target biodiversity groups (EC, 2020). There are mutual and complex interactions between agriculture and biodiversity. Agriculture is based in biodiversity and it influences biodiversity (Thrupp, 1997; Riffell et al., 2009). Interactions between biodiversity and agricultural production can be translated into sustainable management practices. These practices can help to ensure the delivery of safe and sufficient food, as well as environmental, biodiversity and human well-being benefits.

A much explored research question has been to examine how biodiversity relates to ecosystem functioning can delivery ecosystem services. Over the last decades, this functional perspective of biodiversity on ecosystems has been growing interest in agriculture (Laureto et al., 2015). There is often a positive but saturating effect of species richness and the level of ecosystem function provision (Hooper et al., 2005; Duncan et al., 2015). Diversity also often promotes stability in the provision of an ecosystem function; normally more species will be needed to maintain several ecosystem functions (Cardinale et al., 2012). Several mechanisms are responsible for these positive relationships including: (1) species complementarity, many different species can extract more resources in space and time than a species-poor community can (Hoehn et al., 2008); (2) facilitation, through individual interactions emerge positive community-level effects (Greenleaf and Kremen, 2006); (3) "sampling effects", species-rich communities are more likely to include better providers of ecosystem services (Loreau et al., 2001); and (4) response diversity, changes in the environment affect species differently (Elmqvist et al., 2003). Therefore, understanding how to enhance biodiversity can improve ecosystem functions that deliver ecosystem services in agroecosystems, which can ultimately improve crop production.

Alternatively, in order to manage the effect of biodiversity on agroecosystem functioning, we also need to understand factors that modulate biodiversity. In this sense, the structure of the landscape surrounding farmlands, as well as in situ agricultural practices (local-scale managements) can be approached as environmental drivers of biodiversity at different spatial scales (Shackelford et al., 2013) (**Fig. 1**). Functional importance of landscape in community composition and food-web structure has been proved to be essential for developing management solutions to sustain key ecosystem processes and services such as biological control or pollination (Tscharntke et al., 2012). According to several studies, natural or semi-natural habitats supply different key resources for settle biodiversity in agroecosystems such as, alternative food resources, shelters, hibernation sites or nesting places (Otieno et al., 2011; Tscharntke et al., 2012; Escobar-Ramírez et al., 2019). Simultaneously, different local-scale managements can be also a good strategy for promoting those resources in agroecosystems (Otieno et al., 2011; Ekroos et al., 2014). Different alternative farming systems can be designed to harness biodiversity and optimize the ecosystem services that underpin agricultural production (Garibaldi et al., 2017).

The whole picture is difficult to find in agroecosystem research. Usually the information is broken down into pieces. For example, we can find information about the relationship between biodiversity and multiple ecosystem services or functions (Hooper et al., 2005; Cardinale et al., 2012), or the effects of landscape composition and configuration on biodiversity (Blitzer et al., 2012; Tscharntke et al., 2012). Alternatively, the consequences of different agricultural managements or intensification in biodiversity have also been studied (Tscharntke et al., 2005; Bailey et al., 2010). But, there is a serious lack of knowledge about all these links together in a same agroecosystem (Biggs et al., 2012). Moreover, multiple ecosystem services at the same time and in the same agroecosystem remains poorly studied. Understanding these links in real agroecosystem has become a priority due to the current expansion of agriculture, its associated damage to the environment and the demand of different ecosystem services by society.

CROP POLLINATION AND PEST CONTROL

A major agricultural goal is support pollination and biological control whilst we get the right balance between food production and the responsibility we have in conserving biodiversity and sustainable agroecosystems (Bommarco et al., 2013; IPBES, 2019). Pollination and biological control constitute ecosystem services of global importance, providing economics and aesthetic benefits as well as socio-cultural value to human society, alongside vital ecological processes in terrestrial ecosystems. In agroecosystems they are critical ecosystem services. Over 75% of agricultural crop species are reliant on animal pollination (Klein et al., 2007; Garibaldi et al., 2013), with the suggestion that a loss of this service could reduce yields by 40% and 16% for fruit and vegetables respectable (Klein et al., 2007). In the EU, the annual economic value of insect pollinated crops is about €15 billion (Gallai et al., 2009). Likewise, biological control of pests, are central to the sound functioning of the world's ecosystems and to a sustained production of food and agricultural produce. In the US, biological control have been valued at €4-13 billion annually (Losey and Vaughan, 2006).

In agricultural landscape, huge resources have been invested in crop protection during the 20th century, mainly as chemical control (Oerke and Dehne, 2004). Despite this, crop yield losses to pest, the creation of new agrochemical products and their number of treatments have increased (Popp et al., 2013). In the current agriculture, to remediate farmers' dependency upon chemical products is a priority. Alternative solutions are required to prevent an increasing pest population from reaching a high economic injury level using chemicals only as a backup option. However, not only direct economic benefits are generated, other benefits such as the reduction of pesticides use, increase human health, conserve biodiversity and protect surrounding natural habitats emerge (Pimentel and Burgess, 2014). The role of biodiversity in the function of pest suppression in agroecosystems was already highlighted by Altieri in 1994. More recently Crowder and Jabbour (2014) review the relationships between biodiversity and biological control of pests in agroecosystems, showing that pest suppression is generally positively associated with biodiversity of natural enemy guilds. The relative abundance of natural enemies also positively affects the provision of proper pest suppression (Crowder et al., 2010). Besides, depending on the pest, the occurrence of specialist or generalist natural enemies also influences pest suppression (Jacobsen et al., 2016). In order to increase biological control in agroecosystems we must be clear about our objectives. Depending on whether we want to control a single pest or, for example, control general populations of arthropods, different natural enemies will be chosen and different management strategies implemented. Agricultural food webs that involve crop plants, pests and natural enemies guilds are very complex and with diverse mechanism underlying effects of biodiversity (Crowder and Jabbour, 2014). The range of natural enemies in agroecosystems include predators (e.g. insects, birds, mammals), parasitoids (e.g. wasp, flies), and pathogens (e.g. viruses, bacteria, fungi).

Plant-pollinator interactions have held the attention of researchers since the eighteen century (Wasser, 2006). However, the relationship between pollinators and pollination process in agroecosystems around the world has been studied more recently (Klein et al., 2007; Garibaldi et al., 2013). The decline of wild pollinators (Potts et al., 2019) and the honey bee health problems (van Engelsdorp et al., 2010) have set off alarms for ecologist and society. The agricultural demand for pollination has already for several decades been outgrowing the global supply of honey bee colonies (Aizen and Harder, 2009). Current trends are focused on how unmanaged pollinators can provide crop pollination for a number of agroecosystems (Klein et al., 2007; Garibaldi et al., 2013). There are examples of wild bee populations in agroecosystems that can fully pollinate crops (Rader et al., 2012). Promoting abundance and richness of wild pollinators can improve crop pollination (Garibaldi et al., 2013, Hoehn et al., 2008). Among the most widely recognized pollinators are honey bees, wild bees and bumblebees, but other insects such as flies, beetles, butterflies and wasps have also been reported (Rader et al., 2016).

Therefore, we should recognise our capability to maintain sustainable and healthy populations of insect pollinator and natural enemies in agroecosystems. We should take full advantage of these “free” ecosystem services effectively. In many agroecosystem we can find that native pollinators and natural enemies are unable to provide the level of pollination and pest control services required for a successful production (Rader et al., 2012, Escobar-Ramírez et al., 2019). By this way, through interdisciplinary studies that involve farmers’ knowledge and perceptions, we can conserve and promote biodiversity, as well as assure key flows of ecosystem services to make agriculture more sustainable. In an extreme example, apple and pear orchards of

Suchuan (province of China) suffered a huge decline of wild pollinator populations resulting in a loss of the ecosystem service and in a full pollination by hand (Partap and Ya, 2012). This situation that we could describe as the most undesirable point of an agroecosystem should be only found in fiction movies.

OVERVIEW OF STUDY SYSTEM

The richness and the abundance of natural enemies and pollinators are tightly linked to the agroecosystem management and surrounding landscape. To understand the provision of biological control and pollination in agroecosystems we need to think in local and regional scales. What are the local and landscape variables that create the most suitable conditions for stablishing natural enemies and pollinators in agroecosystems? Answer this question is a priority for current sustainability challenges in agricultural landscapes. Therefore, in our studies we focus at two levels: (1) the study systems comprised by cider apple orchards located in Asturias (N Spain) (**Fig. 2**), and (2) the landscape in which they are embedded (hereafter Asturian cider apple landscape) (**Fig. 3A**).

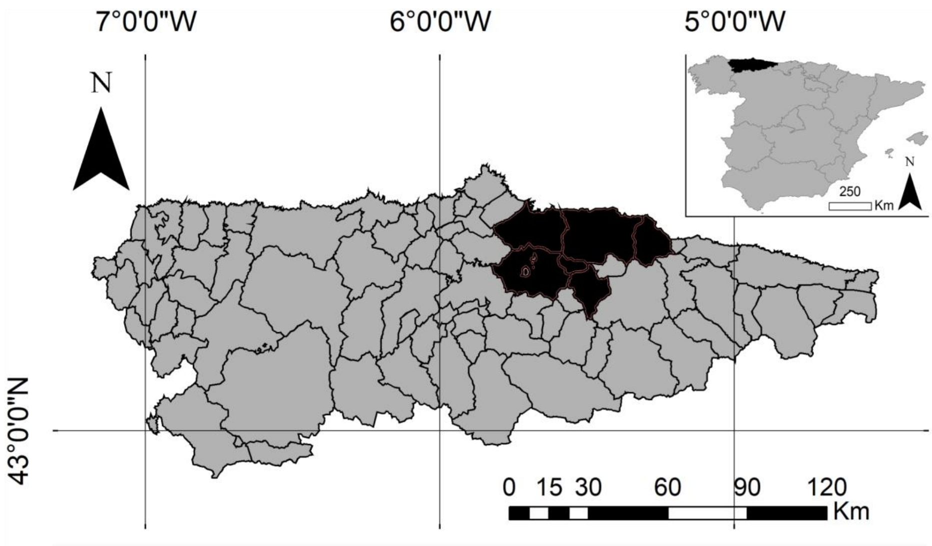

Fig. 2 Study area. Inset shows location within Spain of Asturias region. Larger image shows the municipalities of Asturias, with those selected for this thesis depicted in dark.

Asturian cider apple orchards are devoted to cider production, a drink with economic importance at regional scale and strong cultural roots. In fact, many families carry out the agricultural management by their self in a traditional way, even making their own cider. Due to the long tradition of cider and orchards, Asturian cider has qualities, reputation and characteristics unique to this region, being a valuable product with Protected Denomination of Origin status.

Asturian cider apple orchards can be considered low-input agroecosystems. As agroecosystems with a low degree of agricultural intensification, they are managed with a minimum use of mechanical and external inputs, such as purchased fertilizers and pesticides, usually applied at low quantity and intensity. Besides, to reduce competition with trees, weeds in the tree-row are managed by mowing, shallow tillage or herbicide application, depending on the orchard. In all orchards, alleys are periodically cleaned using a shredder, but still maintain a natural ground cover, rich in wild plants that flower throughout the year. Furthermore at the immediate neighbourhoods, cider apple orchards are typically surrounded by natural woody vegetation in the form of hedgerows and patches of unmanaged forest (**Fig. 3B-C**). In addition, they usually cover an area ranging from 0.4 to 4 ha. In total they occupy more than 10,000 ha in Asturias (INDUROT 2010). The majority of the cider apple orchards are traditional, with large trees grown on seedling rootstocks. These traditional orchards typically have a density of between 250 to 500 trees/ha. Their trees have good anchorage and high branches, however, they are not precocious and their management involves some disadvantages. In order to improve productivity and facilitate management, they have been progressively substituted by semi-intensive ones (Dapena et al., 2005). Semi-intensive orchards have trees growing on semi-dwarfing rootstocks and have a density of between 500 to 650 trees/ha.

Fig. 3 Photographs of the study system: (A) Asturian cider apple landscape, smooth hills and valleys covered by different land uses (e.g. pastures, semi-natural forests, cider apple orchards); (B) an example of semi-natural vegetation at the end of a cider apple orchard; (C) an example of common hedgerow surrounding cider apple orchards.

Both types of cider apple orchards are based on local cultivars that are tolerant to common apple diseases such as scab (*Venturia inaequalis*), European canker (*Nectria galligena*), brown rot (*Monilia fructigena*) and powdery mildew (*Podosphaera leucotricha*). In addition, there is a cultural tolerance of growers to pests and diseases, because aesthetical damage is not relevant to make cider and thus, pest are not perceived as severe threats to productivity. The most relevant pest is the codling moth (*Cydia pomonella*), which damages the fruit. The rosy apple aphid (*Dysaphis plantaginea*) and the green apple aphids (*Aphis* spp.), which harm young shoots, being important pests for young trees. The apple blossom weevil (*Anthonomus pomorum*), which damages blossoms and affects productivity. Finally, although it does not directly damage the apple, the fossorial water vole (*Arvicola scherman*), which attacks the roots and may cause tree death, can be also one of the main current cause of economic loss for farmers. In Asturian cider apple orchards we can also find a high biodiversity of natural enemies that prey on these various pests. These include arachnids, a wide variety of insects (e.g. ladybug, earwig, hoverflies, parasitoids), insectivorous birds with frequent tree-dwelling behavior (e.g. tits, thrushes, robin, woodpeckers), birds of prey (e.g. buzzard, owls), and carnivorous mammals (e.g. mustelids) (Miñarro et al., 2011).

Cider apple orchards are highly dependent on insects for success full pollination and fruit production. Insects pollinators are indispensables for pollen movement between cultivars that grow self-incompatible ones (Jahed and Hirst, 2017). Pollination is provided by both wild and managed bees. Although honeybees are effective apple pollinators (Park et al., 2016), they are less effective pollinators than wild bees (Martins et al., 2015). Asturian cider apple orchards sustain a large number of pollinator species (Miñarro and García, 2018), until now 82 species have been recorded. Among the different groups, wild bees (e.g. *Bombus* spp., *Andrena* Spp, *Halictus* spp., *Lasioglossum* spp.) is the richest one with 39 species, hoverflies are characterized by 21 species (e.g. *Syrphus* spp., *Melanostoma* spp.) and beetles by 8 species (e.g. *Oxythyrea funesta, Rhagonycha fulva*).

This high diversity of natural enemies and pollinators can be understood due to Asturian cider apple orchards are not only low-input agroecosystems but also they are embedded in a mosaic landscape. Among all the land uses that we can find in Asturian cider apple landscape (**Fig. A1A**) we highlight grasslands, green the whole year, and with blooms depending of the season. Most of these grasslands are periodically mowed or grazed by cattle certain periods of the year. We can also find riverine forests, semi-natural temperate broad-leaved forests of native species and some shrublands that are growing up in abandonment areas. Exotic tree plantations, mostly eucalyptus for timber, are easily found in slopes throughout the landscape. Cider apple orchards are not the only crop in the region. Blueberries, kiwis, corn and different vegetables can be found around. Asturian cider apple landscape can be considered as a traditional agricultural landscape comprise by a mosaic of land uses that provided a balance of provisioning, regulating and cultural ecosystem services. By trading heterogeneity for intensification, landscape simplification adversely impacts biodiversity. However, Asturian cider apple landscape can habor high number of pollinator and natural enemy species, as well as habitat diversity for achieves a proper biological control and pollination (García et al., 2018; Miñarro and García, 2018).

Therefore, cider apple orchards can benefit from this landscape. A better understanding of how this landscape and low-input cider apple orchards themselves can sustain pollinator and natural enemy populations will be important for success agricultural policies at local and landscape levels. They can combine sustainable management, biodiversity conservation and production, being an example for other low-input farming systems spread worldwide (Pywell et al., 2015). Although traditional agricultural systems, part of the European landscapes, have been proved to enhance environmental conditions to the benefit of society and nature (Plieninger and Beileng, 2013); they are in danger due to the expansion of intensive agricultural production and its associated damages. It is in our hands try to understand part of the system and promote its conservation, in any case, find a transition towards sustainable models that cover the needs of its citizen.

OBJECTIVES AND GENERAL OUTLINE

The main purpose of this thesis is to gain further insight into the ecosystem services of biological control and pollination in cider apple orchards from Asturias. We try to understand the mechanisms that allow us to enhance the biodiversity related to these two ecosystem services. Specifically, on one hand, we focus on the positive ecological effects of natural enemies as suppliers of pest control and, on the other hand, in the ecological effects of pollinator insects as suppliers of pollination. Simultaneously, we assess the environmental drivers of this biodiversity, trying to find local and landscape features that drive pollinator and natural enemy biodiversity. Among all natural enemies found it in the orchards, we focus on birds as generalist suppliers of pest control and, parasitoids as specialist natural enemies of codling moth, the most important apple pest worldwide. Among all pollinators found in the orchards, we focus on wild bees and wild pollinators.

In addition, to complement this more ecological aspect of the thesis we introduce a participative study with farmers. For that purpose, in this study we performed face to face interviews with cider apple orchards farmers to analyse their perception and knowledge of natural enemies. We highlight the importance of integrate biological and social knowledge to encourage a transformative change towards a sustainable agroecosystem able to protect biodiversity and provide ecosystem services.

This thesis is organised in three chapters. The specific objectives of each one are outlined below:

Chapter 1 "*Animal biodiversity in cider apple orchards: Simultaneous environmental drivers and effects on insectivory and pollination*"

In this chapter, for two years, we assess the environmental drivers of biodiversity, and the effects of animal biodiversity on the provision of multiple ecosystem services, for different animal groups in a given agroecosystem. In particular, this study aims to achieve the following goals:

1.1 To evaluate the ecological function of insectivorous birds as pest enemies, and that of wild insects as pollinators.

1.2 To find local and landscape features driving biodiversity of insectivorous birds and pollinator insects.

Chapter 2 "*Apple production and parasitoids mediate codling moth abundance and damage in cider apple orchards*"

This chapter consists on an assessment of the trophic interactions driving codling moth and parasitoid populations over two consecutive years, taking into account possible landscape and local-scale effects. This study seeks the following objectives:

1.1 To evaluate codling moth populations and their associated damage to apple production.

1.2 To evaluate the parasitism rate carried out by codling moth parasitoids.

1.3 To find local and landscape features driven parasitoid biodiversity and codling moth abundance.

Chapter 3 "*Farmers' perceptions and knowledge of natural enemies as providers of biological control in cider apple orchards*"

In contrast to the two previous chapters, in this one we examine cider apple farmers' perceptions and knowledge of the concept of biological control and the specific organisms underpinning its provision (i.e. natural enemies). Particularly, this study addresses the following goals:

1.1 To evaluate farmers' perception regarding biological control and the different natural enemies that provide it.

1.2 To assess farmers' knowledge of the specific interactions between natural enemies and pests.

1.3 To find farming and socio-economic characteristics that influence farmers' perception and knowledge of natural enemies.

Chapter 1

Animal biodiversity in cider apple orchards: simultaneous environmental drivers and effects on insectivory and pollination

Agriculture, Ecosystems and Environment 295 (2020), 106918

ABSTRACT

Making agriculture more sustainable requires a greater understanding of animal-mediated ecosystem services. The beneficial effects of pest-control and pollination provided by, respectively, insectivorous birds and pollinator insects are essential for many crops. Improving these ecosystem services simultaneously in the same crop system means, first, identifying the drivers of animal biodiversity that operate in agricultural landscapes, and second, revealing the relationships between biodiversity and the two services. Here, for two years, we addressed how landscape and small-scale orchard features affected bird and insect biodiversity (abundance and species richness) in cider apple orchards in northern Spain. We examined the effects of bird and insect biodiversity on the magnitude of, respectively, insectivory and pollination. Bird biodiversity was positively affected by the cover of apple canopy within orchards, whereas that of pollinators responded positively to the cover of semi-natural woody habitats and eucalyptus plantations in the surrounding landscape, and also on the level of bloom at the orchard scale. Insectivory, estimated from sentinel model and exclusion experiments, was positively affected by increased abundance and richness of birds across orchards. Similarly, fruit set responded positively to higher abundance and richness of wild bees, whereas seed set mostly depended on the abundance of wild pollinators. Our findings suggest simultaneous positive effects of animal biodiversity on pest-control and pollination in apple orchards, with no sign of trade-offs between biodiversity groups or between ecosystem functions. A multi-scaled management of orchard-level features (apple canopies and surrounding hedgerows for birds, and apple bloom and ground cover for pollinators) and landscape-level ones (surrounding cover of semi-natural woody habitats, moderate for birds, high for pollinators) is encouraged for the simultaneous enhancement of pest-control and pollination. Biodiversity-farming win-win scenarios are possible in cider apple orchards by simultaneously promoting multiple animal-mediated ecosystem services.

INTRODUCTION

Sustainable agriculture faces the challenge of ensuring food production while reducing environmental impact and biodiversity loss (Foley et al., 2011; Bommarco et al., 2013). The ecosystems within which farming is integrated (i.e. agroecosystems) can harbor variable levels of biodiversity which, in turn, may provide crop-beneficial ecosystem services (Kremen and Miles, 2012; Tscharntke et al., 2012a). In fact, different groups of animals, plants or microorganisms are involved in a wide array of services, such as biological control of crop pests (Maas et al., 2013; Cross et al., 2015), pollination (Kleijn et al., 2015; Rader et al., 2016), maintenance of soil fertility (Edwards, 2004) and water purification (Gharabaghi et al., 2006). Understanding how to simultaneously foster different biodiversity groups to maximize multiple ecosystem services related to the same crop is, therefore, a pivotal question in sustainable agriculture (Shennan, 2008; Tscharntke et al., 2012a).

Birds and insects are two animal groups targeted as being highly relevant in sustainable agriculture (Power, 2010; Shackelford et al., 2013). On the one hand, insectivorous birds provide generalist biological control by preying upon different types of arthropod pests across annual and perennial crops, in both temperate and tropical regions (Karp and Daily, 2014; Rey Benayas et al., 2017). On the other hand, flower visiting insects are the necessary pollinators of many crops, from annual crops to tree-fruit productions, where they increase crop yield, fruit quality and harvest stability (Klein et al., 2007; Garibaldi et al., 2013). Despite these findings, most studies provide segregated information for insectivorous birds and for pollinator insects with respect to various crops. The few studies that do target both biodiversity groups simultaneously have successfully shown the occurrence of combined ecological effects (e.g. Classen et al., 2014), although they have followed small-scale approaches, insufficient to predict the combined role of the two biodiversity groups across the environmental gradients of real agroecosystems. In this context, the importance of insectivorous birds and pollinator insects can be only truly understood through the positive effects animal biodiversity has on ecosystem functions (hereafter B-EF link) (Kremen, 2005; Duncan et al., 2015). Namely, higher bird abundance has been associated with stronger pest control (Jedlicka et al., 2011), as has higher bird richness (Bael Van et al., 2008) and functional diversity (Philpott et al., 2009). In the case of flower visiting insects, richer assemblages, especially of wild bees, are known to increase pollination services (Mallinger and Gratton, 2015). Nevertheless, in order to manage the B-EF link in agroecosystems, we need first to understand the factors that modulate the biodiversity of pest predators and pollinators. In this sense, both the structure of the landscape surrounding a farming site, as well as the in situ agricultural practices, can be approached as environmental drivers of biodiversity at different spatial scales (Shackelford et al., 2013).

Landscape structure may affect bird and pollinator biodiversity in agroecosystems by containing semi-natural habitats that support animals with external resources (i.e. beyond those provided by the crop itself) such as shelter, food, breeding areas, and nesting places (Tscharntke et al., 2012b; Heath et al., 2017; Alomar et al., 2018). This leads to positive relationships between the amount and spatial configuration of semi-natural habitats around agroecosystems and the abundance and richness of different animal groups (Tscharntke et al., 2012b; Kennedy et al., 2013). The small-scale features of farming sites and their immediate surroundings (e.g. hedgerows and farm fringes), which frequently depend on farming management, may also be seen as modulators of resource availability for animals (Kennedy et al., 2013; Rey Benayas et al., 2017). For instance, vegetated margins (Quinn et al., 2014) or dense ground cover (Rey et al., 2019) both increase bird and insect biodiversity, whereas frequent tillage impacts negatively on the persistence of bee populations (Ullmann et al., 2016). In sum, identifying common or differential responses of pest-predators and pollinators to landscape or within-farm features is essential for targeting the management practices that foster multiple ecosystem services in agroecosystems (Manning et al., 2019).

In this study, we assess the environmental drivers of biodiversity, and the effects of biodiversity on the provision of multiple ecosystem services, for different animal groups in a given agroecosystem. We evaluate the ecological function of insectivorous birds as pest enemies, and that of wild insects as pollinators, in cider apple orchards of Asturias (N Spain), along a gradient of environmental variability at local (i.e. within orchards) and landscape (i.e. around orchards) scale. Cider apple crop is a key agroecosystem across the whole Cantabrian region in Spain (Pereira-Lorenzo et al., 2007), and is highly variable in terms of management regimens and landscape contexts, and may harbor rich assemblages of insectivorous birds (García et al., 2018) and pollinator insects (Miñarro and García, 2018). Specifically, we aim here to answer the following questions: (1) What are the local and landscape features driving the biodiversity (abundance and richness) of insectivorous birds and pollinator insects? (2) Does the biodiversity of birds and pollinator insects affect, respectively, pest control and crop pollination services? Based on our results we propose agricultural and Landscape management actions for promoting multi-functional animal biodiversity and its derived ecosystem services.

MATERIAL AND METHODS

Study system

The study was conducted in the cider apple (*Malus x domestica* Borkh.) crop area of central Asturias (N Spain) (**Fig. 1A**). In this region cider is a valuable traditional product, strongly ingrained in society, and linked to tourism, gastronomy and leisure. Cider apple annual yield reaches 50,000 tons. The majority of cider apple orchards are comprised of local cultivars that are grown on seedling rootstocks, but new orchards are also being grown on semi-dwarfing rootstock. Both systems typically have a density of between 250 and 500 trees/ha. Orchards are embedded in a highly variegated traditional landscape (**Fig. 1D**), containing a fine-grained mosaic of orchards, livestock pastures, annual crops (e.g. corn), other fruit (e.g. blueberry, kiwi) and timber (mainly eucalyptus) plantations, human infrastructures, and semi-natural woody vegetation patches (temperate broad-leaved forest, riparian forest and heathland patches). At the small scale of their immediate neighborhoods, apple orchards are typically surrounded, either totally or partially, by natural woody vegetation in the form of hedgerows and/or small forest patches which are mostly unmanaged by farmers (**Fig. 1C**; for a comprehensive description of hedgerows and small forest patches see García et al., 2018).

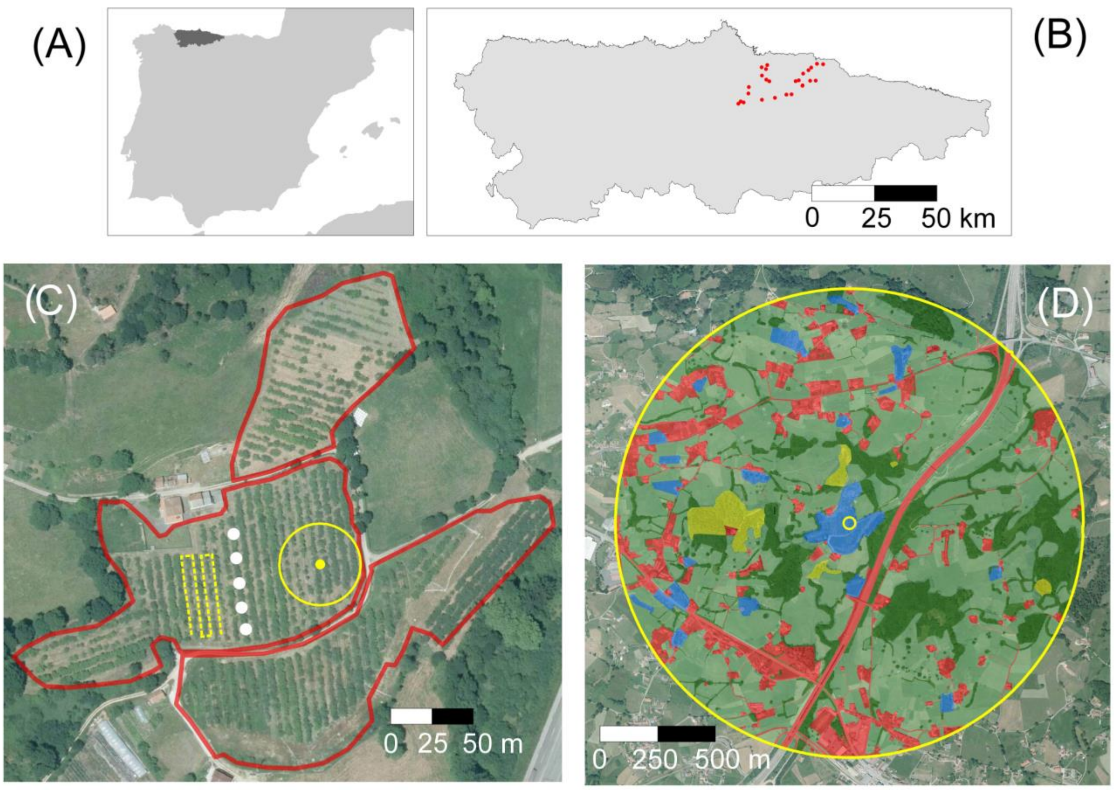

Figure 1. Schematic representation of study sites and spatial design, showing: A) the region of study (Asturias province in dark gray within the Iberian Peninsula); B) the twenty-six study sites; C) an example of a study orchard, detailing a pollinator sampling station with 5 focal trees in a row of "Regona" apple trees (white points), two additional "Regona" rows selected for transects (yellow dashed line), and the 25-m radius plot around one bird sampling station (yellow circle); D) an example of land uses in the 1000-m radius plot around a sampling station: semi-natural cover vegetation (dark green patches), timber (mainly eucalyptus) plantation (yellow patches), fruit tree plantation (blue patches), pastures (pale green patches) and urbanized ground (red patches).

Orchards are relatively small (most cover between 0.5 and 4 ha). To reduce competition with trees, weeds in the tree-row are managed by mowing, shallow tillage or herbicide application, depending on the orchard. In all orchards, alleys are periodically cleaned using a shredder, but still maintain a natural ground cover, rich in wild plants that flower throughout the year.

Among the arthropod pests present in Asturian cider apple orchards (Miñarro et al., 2011), the most prevalent are the codling moth (*Cydia pomonella* L.), the rosy apple aphid (*Dysaphis plantaginea* Passerini), green aphids (*Aphis* spp.) and the apple blossom weevil (*Anthonomus pomorum* L.). Growers frequently tolerate moderate levels of pests and diseases, as aesthetic damage is not relevant for cider apples and, thus, pests are not perceived as severe threats to productivity. Furthermore, orchards are based on local cultivars tolerant to common apple diseases (scab, canker and powdery mildew). Consequently, the use of pesticides is not generalized and, when used, they are applied at low intensity. The low degree of agricultural intensification in some orchards and in the surrounding landscape allows for a high diversity of arthropods within orchards, including crop pests as well as their natural enemies (e.g. spiders, earwigs, hoverfly larvae, predatory beetles) or mutualists (e.g. aphid-tending ants) (Miñarro et al., 2011; García et al., 2018).

Previous studies in these orchards have registered a rich (53 species) assemblage of wild birds, from which 54.7 % of species were classified as having a predominantly insectivorous diet and a tree-dwelling habit (García et al., 2018). The most common insectivorous birds are robin (*Erithacus rubecula*), tits (Paridae), thrushes (Turdidae), warblers (Sylviidae and Phylloscopidae), wren (Troglodytes troglodytes), and woodpeckers (Picidae). The low use of pesticides, as well as the permanence of flowering ground-cover most of the year, facilitates a high diversity of pollinators in Asturian apple orchards (Miñarro and García, 2018): 82 species of floral visitors being recorded, of which honeybee (61 %) was the dominant flower visitor, followed by hoverflies (21 %, 21 species), wild bees (7%, 39 species), flies (6%, 8 species) bumblebees (3%, 4 species), beetles (1.3 %, 8 species) and butterflies (0.4 %). Pollinators determine cider apple production quantitatively, as fruit set requires cross pollination and hence relies almost completely on insect vectors (Miñarro and García, 2018).

Spatial design of sampling

Between 2015 and 2017, sampling was conducted in 26 cider apple orchards distributed over 600 km2 in the central part of the cider apple area in Asturias (N Spain) (**Fig. 1B**). Minimum distance between orchards was 1.3 km (average distance in km: 8.02 ± 0.94). Orchards were chosen to represent a gradient of variability in the environmental conditions within apple orchards and in the surrounding landscape (i.e. presence of semi-natural habitats; García et al., 2018). For the monitoring of insectivorous birds and insectivory, in each orchard, we established a sampling station within the plantation, 25 m away from the orchard edge, which was the center of a 25-m radius sampling plot (R25 plot, hereafter; **Fig. 1C**). This guaranteed that sampling corresponded exclusively to apple plantation habitat, and excluded different surrounding habitats (e.g. hedgerows) even in the smallest orchard. To monitor flower visiting insects and measure pollination, in each orchard we selected five focal trees of the local cultivar "Regona" (target trees, hereafter) within a given row (as rows contain a single cultivar and each orchard has several cultivars) (**Fig. 1C**), at least 15 m away from the edge (to avoid potential edge effects; Campbell et al., 2017), and in front of a row of a different cultivar (to enhance cross pollination; Ramirez and Davenport, 2013). In order to conduct additional surveys in relation to pollinators, two 150–200 m transects were set up along two additional "Regona" rows (**Fig. 1C**).

Landscape structure and orchard features

Landscape structure was quantified by means of a Geographic Information System of the study area (GIS, ArcGIS9.3) based on 1:5000- scale orthophotographs (2014). We delimited a circular plot of 1000-m radius (R1000 plot, hereafter), centered on the R25 plot of each orchard, within which we distinguished, by carefully digitizing landscape patches, six general types of cover: 1) semi-natural woody habitats (including forest, heathland, hedgerows, isolated trees within pastures or plantations); 2) timber (mainly eucalyptus) plantations; 3) fruit tree plantations (apple, kiwi and blueberry); 4) pastures (meadows), 5) other habitats (mainly water courses) and 6) urbanized ground (roads, buildings, gardens around houses) (**Fig. 1D**). We estimated the availability of each cover type around each orchard from the percentage of cover in each R1000 plot.

As orchard features have the potential to affect bird biodiversity, we measured, based on the GIS mentioned above, orchard size and the amount of cover provided by apple tree canopy in each R25 plot (apple canopy cover; from a layer of apple canopy projection). In order to describe the vertical complexity of apple canopy, we randomly selected 25 trees within the R25 plots. We held a 5-m long, scaled pole vertically 50 cm from the trunk of each of these trees, and counted the number of contacts of apple branches or leaves with the pole. We also measured canopy height from the lowest to the tallest branch. We calculated apple canopy thickness by multiplying the number of pole-canopy contacts by canopy height, and averaged this estimate across all 25 trees per orchard. Orchard features can also affect pollinator biodiversity, and so, in addition to orchard size and apple tree canopy cover, we included bloom level as an indicator of the number of apple flowers in the orchard. We recorded bloom level when the target cultivar ("Regona") was in full bloom, by walking perpendicular to tree rows (in order to avoid a cultivar effect) and covering the full extent of the orchard. For 30 randomly chosen trees per orchard and year, we scored the number of flowers per tree by using a semi-quantitative scale: 0 (0 flowers); 1 (1–10 flowers); 2 (11–50 flowers); 2.5 (51–100 flowers); 3 (101–500 flowers); 3.5 (501–1000 flowers); 4 (1001–5000 flowers); 4.5 (5001–10,000 flowers); 5 (more than 10,000 flowers). We calculated bloom level per orchard and year by averaging this estimate across trees. Finally, during apple bloom we also measured the density and the richness of flowers on the ground cover (variables ground cover density and ground cover richness respectively), as these flowers may attract pollinators (Rosa García and Miñarro, 2014). This was visually assessed over 150–200 m transects, in 50 × 50 cm ground quadrants placed at 10 m intervals (14 intervals per transect in 2015 and 20 in 2016). Half of the quadrats were placed in tree rows and half between rows (as ground cover is differently managed in the two areas). Ground cover density was estimated as the number of flowers per square meter by averaging the density of flowers across quadrats.

Animal assemblages in cider apple orchards

Insectivorous birds

Bird biodiversity was evaluated by censuses in the R25 plot of each orchard. During 30 min, all individual birds heard or seen were counted and identified at the species level. Due to the small size and the homogeneous habitat structure of the plots (with regularly distributed trees and continuous herbaceous cover) we did not expect any differences in detectability among bird species. When possible, we discarded repeated observations attributable to the same individual birds which had remained in the plot during a given slot (e.g. individuals that appear intermittently at the same perching site within short time periods; see also García et al., 2018). Censuses were performed every two weeks during Autumn-Winter (September to December) and Spring-Summer (April to July) for two consecutive annual periods (2015–2016 and 2016–2017, years hereafter), resulting in 36 censuses per orchard (9 censuses per season and year). From all species detected, we selected for analysis only the forest insectivorous birds (insectivorous birds henceforth), i.e. those with a frequent tree-dwelling behaviour and an insect-based diet (**Table A1**; for details about species classification see García et al., 2018). We estimated the abundance and richness of insectivorous birds (bird abundance and bird richness henceforth) per orchard, season and year, as the cumulative number of, respectively, bird individuals and bird species recorded in the R25 plots. We assume that bird abundance metric might, despite our efforts, include some repeated counting of individual birds, and thus it must be considered as an estimate of bird activity in functional terms, rather than a measure of bird population sizes.

Pollinators

The biodiversity of apple flower visitors was surveyed during bloom in the spring of 2015 and 2016. Each orchard was surveyed at three different times (between 11 and 13 h, 13 and 15 h, and 15 and 17 h) by different observers under standard climatic conditions (i.e. total of 75 min per orchard per year). In each orchard, in one 0.5-m radius area of the canopy of each target tree, and for a period of 5 min, we visually recorded each insect visiting a flower, estimating the number of visits and the total number of flowers in the selected area. We were only able to reliably identify the most easily recognized species (e.g. *Apis mellifera*, *Bombus species*, *Andrena pilipes*, *Episyrphus balteatus*, *Oxythyrea funesta*, etc.). Most pollinators were, thus, assigned to one of the following groups: bumblebees, wild bees (categorized according to body size as either large, medium or small, when, respectively, bigger than, similar to or smaller than honeybees), hoverflies (predatory hoverflies with aphidophagous larvae, *Eristalis* hoverflies), flies (Diptera other than hoverflies), beetles and butterflies. In order to better assess species richness, we also made a separate assessment of apple pollinators by capturing all pollinators we observed along “Regona” tree transects in an additional 10-min period during each survey event (i.e. a sum of 30 min per orchard per year). Captures were made by sweep netting complemented by a slow approach to the insect which was captured in a vial. All captured specimens were identified at the species level in the laboratory (**Table A2**).

We estimated two variables of abundance and richness for apple pollinators per orchard and year: 1) abundance and richness of wild pollinators, i.e. the cumulative number of, respectively, pollinator individuals and pollinator species excluding honeybee; and 2) abundance and richness of wild bees (i.e. solitary bees and bumblebees). Although honeybee *Apis mellifera* is a dominant floral visitor in cider apple in Asturias (Miñarro and García, 2018), its occurrence and abundance are highly variable across orchards and highly dependent on the local management of hives, making it somewhat independent of environmental gradients. Therefore, we excluded this species from our analysis, focusing exclusively on wild pollinators. These have been recognized globally as crucial crop pollinators (Garibaldi et al., 2013; Rader et al., 2016), frequently more efficient, at least in qualitative terms, than honeybee (Thomson and Goodell, 2001; Garibaldi et al., 2013). Wild bees have, in fact, been found to have an important role in apple pollination (Mallinger and Gratton, 2015; Martins et al., 2015) and to respond differentially to landscape and local features (Martins et al., 2015; Joshi et al., 2016).

Estimates of ecological function

Bird insectivory

We estimated bird insectivory in apple trees through two complementary methods: 1) observations of bird attack on a sentinel pest, mimicked by plasticine caterpillar models (sentinel model experiment, hereafter); and 2) measurements of the removal of arthropods from apple trees through the comparison of branches which were manipulated to exclude birds with unmanipulated branches (exclusion experiment, hereafter).

As a sentinel pest, we recreated the caterpillar of codling moth (**Fig. B1A-B**; see also Peisley et al., 2016, for a similar procedure). In Asturias, the codling moth is bivoltine and, from July to the harvest time in October-November, the larvae seek shelter, usually bark crevices in the trunk and main branches, for pupating and/or overwintering (Minarro, 2006). During this period, both by day and at night, larvae move along upward and downward routes, avoiding smaller branches and leaves, from a hatched egg to apple or from apples to shelters (MacLellan, 1960; Geier, 1963; Welter, 2009). During these displacements codling moth larvae may suffer predation by birds (Solomon and Glen, 1979; Wearing and McCarthy, 1992; Welter, 2009). The caterpillar models used in the experiment were 15-mm long and 3-mm diameter size, and were molded with creamy pink (body) and brown (head) plasticine (**Fig. B1C**). Each model was presented to birds, in a posture imitating natural movement on a branch bearing apples, pierced through its longitudinal axis with a green wire to attach it to the branch. Sentinel model experiment was set up simultaneously in all orchards, and replicated in mid-October 2015 and 2016, and mid July 2016. For each experiment, we deployed 10 caterpillar models on branches of similar diameter and height, across 10 trees of similar size and apple crop within the R25 plot of each orchard (i.e. 100 caterpillar models per plot; **Fig. 1C**). These numbers of caterpillar models per tree and per plot was lower than the average number of codling moth larvae found in the same trees in the study plots (mean number of larvae per tree: 2015: 31.52 ± 2.20, min-max: 0–189; 2016: 38.38 ± 2.32, min-max: 0–206, authors' unpublished data). Caterpillar models were examined 7 days after set up, recording whether they showed signs of bird attack (beak marks) on their surface or had been partially removed (Peisley et al., 2016) (**Fig. B1D-E**). The ground under the branches where models were attached was also inspected for models which might have fallen 'naturally'. The negligible number of models fallen under branches, the type of damage (no signs of rodent teeth marks were detected), and the detection of bird attack on the models through camera trapping (authors' unpublished data), make model removal almost completely attributable to birds (see also Geier, 1963; Garfinkel and Johnson, 2015; Peisley et al., 2016). For each tree in each orchard, we estimated the number of attacked caterpillar models as those showing signs of attack or having been removed.

The bird exclusion experiment was performed in April-June of 2017 in all study orchards. Two large branches of similar length and diameter, but located on opposite sides of a tree, at approximately 1.5-m height, were selected in 5 trees within the R25 plot of each orchard. In April, access to one branch by birds was excluded (excluded treatment) by means of cylindrical (80-cm long and 16-cm radius) cage of wire mesh (12 mm pore), held parallel to the main branch with tensors and covered at both ends by 3-mm pore plastic mesh. The other branch (open treatment) was left unaltered except for being labeled. In June, we sampled the whole arthropod assemblage on exclusion and open branches using a beating method. Three taps per branch were given with a stick, and all the arthropods which fell from the branch were collected in a plastic tray (80 × 50 × 8 cm) held below the branch. Beating samples were inspected in the laboratory for arthropod collection, and arthropod samples were kept frozen at -18 °C. The total biomass of arthropods per branch and tree was estimated from the wet weight of frozen samples, applying the same time frame after collection to all samples, and using a precision balance with 0.1 mg accuracy.

Pollination

We estimated the contribution of pollinator insects to yield and fruit quality by measuring fruit set (number of flowers to set) and seed set (number of seeds) on three trees per orchard. At the beginning of the flowering period (end of April), 3 similar "Regona" target trees per orchard were selected, and 40 recently opened flowers per tree were marked with colored wire. Twenty randomly selected flowers were kept unmanipulated, potentially allowing for self-pollination and cross-pollination through insect and wind vectors (open-pollination treatment). The other 20 flowers were supplemented with pollen collected previously from different cultivars (hand-pollination treatment). These flowers were saturated with pollen, meaning that fruit set and seed set in the hand-pollination treatment would be the maximum possible for the corresponding tree. In July, when fruits were large enough to distinguish seeds, we counted the number of fruits that had developed from all marked flowers in each treatment. These fruits were harvested and taken to the laboratory to count the number of well-developed seeds per fruit. To estimate fruit set we related the number of developed fruits in the open-pollination treatment of each tree with that in the hand-pollination treatment. In this way, we explored the effect of pollinators relative to the maximum number of fruits potentially set under no pollen-limitation. We followed a similar rationale with seed set, relating the number of well-developed seeds per fruit in the open-pollination treatment of each tree with that in the hand-pollination treatment (maximum 10 seed capsules per fruit). The proportion of fruit set per tree was estimated as the ratio of open-pollinated fruits relative to the hand-pollinated fruits. A similar approach was used for calculating the proportion of seed set per tree.

Statistical analysis

We sought to represent the general trends of variability in landscape structure around apple orchards across the study site. To do this, we applied a Principal Component Analysis (PCA, performed with the PCA function in the *FactorMineR* R package; Husson et al., 2008) to the six general cover types in R1000 plot across orchards (**Table C1**). The first three principal components accounted for more than 82.2 % of the variation in our landscape data: PC1 (42.4 % of variance explained) described a gradient covering from pasture-dominated landscapes to landscapes dominated by timber (mainly eucalyptus) plantations; PC2 (25.4 %) gradient extended from urbanized landscapes to landscapes dominated by semi-natural woody habitat; and PC3 (14.4 %) represented a gradient of increased proportions of other habitat types (mainly water courses) and fruit plantations around the orchards. These three principal components were used in the subsequent analyses as independent measures of landscape structure.

In order to evaluate the effects of landscape and orchard features on bird biodiversity, we used Generalized Linear Mixed Models (GLMM; Bolker et al., 2009), considering bird abundance and bird richness per orchard as two different response variables (both response variables were checked for normality, and thus models considered Gaussian distribution and identity link). In each model, we considered as main predictors the three principal components of landscape structure, apple canopy cover, apple canopy thickness and orchard size. Apple canopy cover and apple canopy thickness were positively correlated (Pearson's correlation: $r = 0.46$, $P = 0.02$, $N = 26$), although we considered this correlation level weak to lead to collinearity constraints. Consequently, all the main predictors were initially included in full models, together with season (Autumn-Winter, Spring-Summer) and year (2015–2016, 2016–2017), which were considered as categorical fixed factors (Bolker et al., 2009). In order to avoid over-parameterization and over-fitting in these models, we pursued a step-wise deletion of non-significant ($p>0.05$) fixed factors from full models, using likelihood ratio tests. A similar GLMM step-wise procedure was applied to evaluate the effects of landscape and orchard features on pollinator biodiversity. In this case, response variables (abundance and richness of wild pollinators and wild bees) were transformed (log10) to meet normality requirements. All bird and insect models included orchard identity as a random factor given that all orchards were replicated across seasons and/or years (Bolker et al., 2009).

We evaluated the effects of bird biodiversity on insectivory rate, first, by means of GLMMs using, as a response variable, the proportion of attacked caterpillar models per tree (sentinel model experiment), considering a binomial error distribution and a logit-link function. As fixed-effect main predictor, we considered, in separate models, bird abundance and bird richness per orchard. Each model also incorporated season and year as categorical fixed factors, as well as tree identity (nested within orchard, dataset considered different measurements made on the same tree in different seasons and years) and orchard identity as random factors. Second, based on the data of the exclusion experiment, we developed GLMMs considering arthropod biomass (log_{10}) per branch as response variable (Gaussian distribution, identity link), and, in separate models, bird abundance and bird richness as fixed-effect main predictor. All models also included as predictor the experimental treatment (excluded vs. open; fixed factor) as well as tree identity (nested within orchard) and orchard identity as random factors. The main-effect and treatment interaction was removed from models after they have proven to be non-significant.

Similar GLMMs were used to analyze the effects of pollinator biodiversity on pollination rates. Namely, we considered, fruit set and seed set per tree as response variables with a binomial error distribution and a logit link function. These binomial variables considered the number of fruits or seeds in the open-pollination treatment as success, and the difference in the numbers in hand-pollination and open-pollination treatments as failures. As fixed-effect main predictors, we considered, in separate models, the abundance and the richness of wild bees and wild pollinators. All models also included year as categorical fixed factor, as well as tree identity (nested within orchard) and orchard identity as random factors. All GLMMs analyses were performed with *lme* function in the *nlme* R package (Pinheiro et al., 2014). Variance explained by the final complete models and by fixed effects was estimated from conditional and marginal R2 values, respectively (Nakagawa and Schielzeth, 2013). Means are shown ± Standard Error (SE) throughout the text.

RESULTS

Effect of landscape and local-scale orchard features on insectivorous bird and pollinator biodiversity

The orchards studied showed wide variability in the structure of their surrounding landscape, as judged by the three main vectors obtained from the PCA (**Fig. C1, Table C1**). Orchards also differed greatly in terms of local-scale features, as indicated by the variability in ground cover richness (mean = 7.16 ± 0.59, min-max = 0–19), ground cover density (mean = 29.65 ± 3.82, min-max = 0–125.7), bloom (mean = 2.14 ± 0.12, min-max = 0.38–3.38), apple canopy cover (mean = 0.43 ± 0.03, min-max=0.18-0.73), and apple canopy thickness (mean = 17.4 ± 1.3, min-max = 6.5–29.0).

The step-wise approach applied led to a model of abundance of insectivorous birds that included significant effects of apple canopy cover within apple orchards, season and year, but no effect of PCA vectors representing landscape features (**Table 1, Table D1**). Namely, bird abundance increased in those orchards with higher apple canopy cover, and it was higher in Autumn-Winter and 2016‐2017 (**Table 1, Fig. 2**). The bird richness model included the same set of significant predictors and trends as that of bird abundance, and, in addition, a positive significant effect of orchard size, indicating the occurrence of more bird species in bigger orchards (**Table 1, Table D1**).

Table 1. Results of Generalized Linear Mixed Models evaluating the effects of landscape structure and orchard features on abundance and richness of birds. Presented models are those selected by a step-wise deletion of non-significant fixed predictors (Table D1). Values of marginal and conditional (between parentheses) R2, as well as variance (±SD) estimate for orchard identity, considered as a random factor, are also shown.

Bird abundance	$\mathbf{R^2m}$ 0.380; $\mathbf{R^2c}$ 0.589		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	11.366 ± 4.319		
Apple canopy cover	45.516 ± 9.042	5.034	<0.001
Season (Spring-Summer)	-7.167 ± 1.645	-4.358	<0.001
Year (2016)	4.513 ± 1.645	2.744	0.007
Orchard (random factor)	6.056 ± 8.198		
Bird richness	$\mathbf{R^2m}$ 0.291; $\mathbf{R^2c}$ 0.421		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	4.138 ± 0.829		
Apple canopy cover	7.122 ± 1.540	4.626	<0.001
Orchard size	0.133 ± 0.062	2.137	0.044
Season (Spring-Summer)	-1.065 ± 0.327	-3.261	0.002
Year (2016)	0.815 ± 0.327	2.496	0.015
Orchard (random factor)	0.809 ± 1.630		

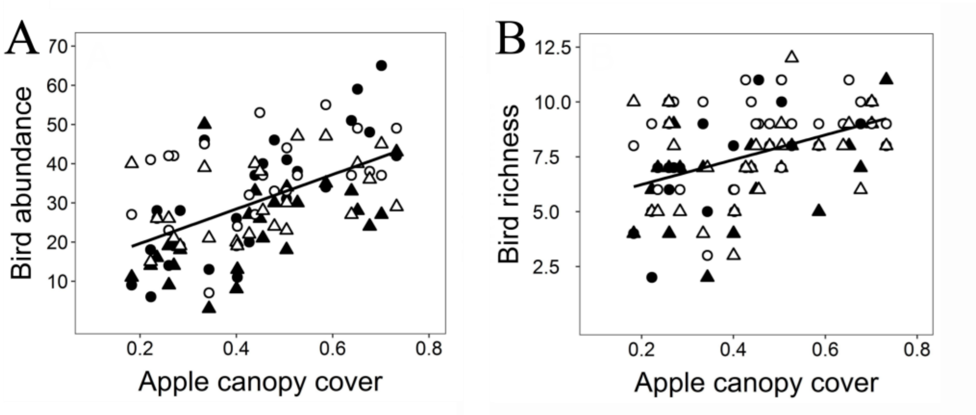

Fig. 2. Examples of significant effects of orchard features on the abundance and richness of insectivorous birds. Colors indicate different years, 2015-2016 (black) and 2016- 2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

In terms of all wild pollinators, we found significant biodiversity responses to landscape structure (**Table D1**). Namely, wild pollinator abundance was positively and significantly affected by both PC1 (**Table 2**) and PC2 (**Table 2, Fig. 3A**) (which represented, respectively, eucalyptus cover and semi-natural woody habitat cover), but negatively affected by PC3 (representing the cover of water courses and fruit plantations). Wild pollinator abundance was also significantly higher in 2016–2017 (**Table 2**). Wild pollinator richness was positively affected by PC1 (**Table 2**) and orchard-scale bloom level (**Table 2, Fig. 3B**). In the case of wild bees, abundance was negative and significantly affected by PC3 (representing the cover by water courses and fruit plantations (**Table 2, Fig. 3C**). It also responded positively to PC2 (semi-natural woody habitat cover), a predictor approaching significance, and whose inclusion in the step-wise reduced model led to a negligible difference in likelihood ratio with an increasingly purged model (**Table D1**). Wild bee richness was also positive and significantly related to bloom magnitude within orchards (**Table 2, Fig. 3D**). No effects of abundance and richness of flowers in the ground cover were detected (**Table D1**).

Table 2. Results of Generalized Linear Mixed evaluating the effects of landscape structure and orchard features on pollinator biodiversity. Presented models are those selected by a step-wise deletion of non-significant fixed predictors (Table D1). Values of marginal and conditional (between parentheses) R2, as well as variance (±SD) estimate for orchard identity, considered as a random factor, are also shown.

Wild pollinators abundance	**R^2m** 0.344; **R^2c** 0.344		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.102 ± 0.039		
PC 1	0.074 ± 0.029	2.565	0.017
PC 2	0.073 ± 0.029	2.495	0.021
PC 3	-0.081 ± 0.032	-2.555	0.018
Year (2016)	0.130 ± 0.059	2.217	0.039
Orchard (random factor)	7.515 ± 0.197		
Wild pollinators richness	**R^2m** 0.284; **R^2c** 0.540		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.872 ± 0.046		
PC 1	0.061 ± 0.020	3.031	0.006
Bloom	0.060 ± 0.460	3.121	0.006
Orchard (random factor)	0.071 ± 0.095		
Wild bees abundance	**R^2m** 0.189; **R^2c** 0.327		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	-0.514 ± 0.051		
PC 2	0.104 ± 0.051	2.033	0.054
PC 3	-0.144 ± 0.056	-2.580	0.017
Orchard (random factor)	2.696 ± 0.347		
Wild bees richness	**R^2m** 0.113; **R^2c** 0.184		
Predictors	**Estimate ± SE**	**t**	**p**
Intercept	0.372 ± 0.089		
Bloom	0.095 ± 0.039	2.443	0.024
Orchard (random factor)	0.060 ± 0.203		

Effects of bird biodiversity on insectivory

The sentinel model experiment suggested the high, but variable across orchards, potential for avian predation on codling moth (mean attack rate on caterpillar models per tree per orchard: 64.2 % ± 4.7; min-max: 24.3–94.3 %). The proportion of attacked caterpillar models per tree increased significantly in those orchards harboring a higher abundance (**Table 3**, **Fig. 4A**) as well as a greater richness (**Table 3**, **Fig. 4B**) of insectivorous birds.

Table 3. Generalized Linear Mixed Models evaluating the effects of bird abundance and richness on the attack of caterpillar models (sentinel model experiment) and on arthropod biomass (exclusion experiment). For sentinel model experiment response variable was fitted by considering a binomial error distribution (logit link). Exclusion experiment models included treatment (excluded vs. open) as a main predictor (fixed factor). Values of marginal and conditional (between parentheses) R^2 are shown, as well as the variance (± SD) estimate for tree identity (nested within orchard) and orchard identity, considered as random factors.

Sentinel model experiment - Prop. attacked caterpillar models				
	Predictors	**Estimate ± SE**	**z**	**p**
Abundance model	Intercept	-2.978 ± 0.343		
R^2m 0.224**; R^2c** 0.471	Bird abundance	0.015 ± 0.006	2.736	0.006
	Season (Spring-Summer)	0.886± 0.092	9.655	<0.001
	Year (2016)	2.688 ± 0.092	29.011	<0.001
	Tree [Orchard] (random factor)	0.27 ± 0.519		
	Orchard (random factor)	2.992 ± 1.412		
Richness model	Intercept	-5.047± 0.368		
R^2m 0.231**; R^2c** 0.487	Bird richness	0.331± 0.030	11.190	<0.001
	Season (Spring-Summer)	1.125± 0.083	13.530	<0.001
	Year (2016)	2.572 ± 0.092	27.850	<0.001
	Tree [Orchard] (random factor)	0.288 ± 0.537		
	Orchard (random factor)	1.926 ± 1.388		
Exclusion experiment - Biomass (mg) of arthropods (log)				
	Predictors	**Estimate ± SE**	**t**	**p**
Abundance model	Intercept	4.556 ± 0.296		
R^2m 0.332**; R^2c** 0.503	Bird abundance	-0.031 ± 0.009	-3.28	0.003
	Treatment (Open)	-1.398 ± 0.118	-11.839	<0.001
	Tree [Orchard] (random factor)	0.486 ± 0.929		
	Orchard (random factor)	0.251± 0.181		
Richness model	Intercept	4.546 ± 0.335		
R^2m 0.324**; R^2c** 0.503	Bird richness	-0.123 ± 0.043	-2.828	0.009
	Treatment (Open)	-1.398 ± 0.118	-11.839	<0.001
	Tree [Orchard] (random factor)	0.485 ± 0.929		
	Orchard (random factor)	0.284 ± 0.123		

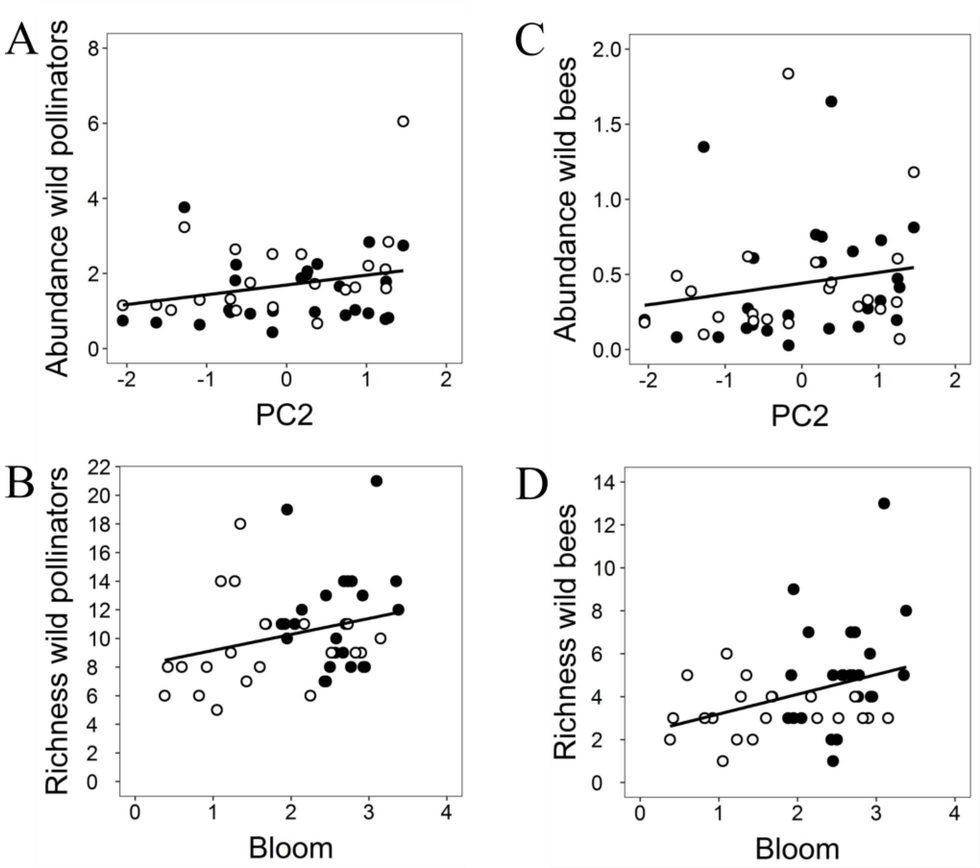

Fig. 3. Examples of significant effects of landscape and orchard features on the abundance and richness of pollinators. Dots indicate different orchards, with different colors for years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variables.

The exclusion experiment demonstrated significant effects of insectivorous birds on the abundance of arthropods in the cider appleorchards. The presence of insectivorous birds significantly decreased the total biomass of arthropods on apple branches, with excluded branches harboring 3.72 times more biomass than open branches (**Table 3**, **Fig. 4C–D**). Interestingly, arthropod biomass was negatively affected by bird abundance and richness irrespective of the experimental treatment (**Table 3**, **Fig. 4C–D**). That is to say, a lower abundance of arthropods was found on the open branches of apple trees in those orchards with higher abundance and richness of insectivorous birds.

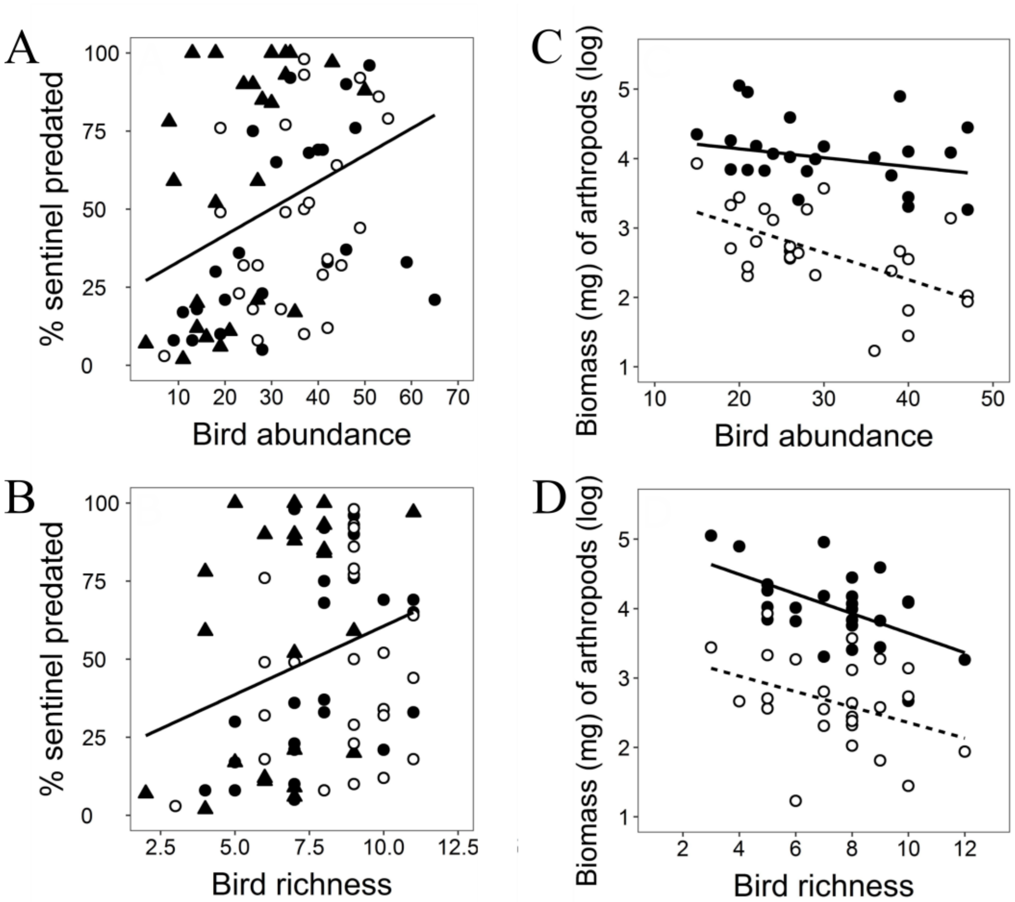

Fig. 4. Significant effects predicted by Generalized Linear Mixed Models of birds biodiversity on insectivory, estimated as the percentage of attacked caterpillar models (AB), and the biomass (log) of arthropods in beating samples (C-D). In A-B, colors indicate different years, 2015-2016 (black) and 2016-2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles). In C-D, dots indicate different orchards, with different colors for exclusion (black) and open (white) treatments. Linear fits are shown for each combination of predictor and response variables.

Effects of pollinator biodiversity on pollination

The proportion of developed fruits per tree in the open-pollination treatment averaged 0.312 (± 0.017) whereas in the hand-pollination treatment reached 0.503 (± 0.017; **Table E1**). The proportion of developed seeds per tree was also lower in the open-pollination treatment (0.630 ± 0.019) than in the hand-pollination treatment (0.808 ± 0.011; **Table E1**). Fruit set per tree, estimated as the quotient between the value of fruit set in open-pollination treatment and that of the hand-pollination treatment, presented a positive relationship with the abundance and richness of wild pollinators (**Table 4**). The response of fruit set to pollinator biodiversity was much stronger in the case of wild bees, with positive significant effects related to their abundance and richness, and fitted by non-linear, saturating trends (**Table 4**; **Fig. 5A–B**). Apple seed set per tree, estimated as the quotient between the value of seed set in the open-pollination treatment and that of the hand-pollination treatment, was also significantly higher in those orchards harboring higher abundances of all wild pollinators as well as wild bees (**Table 4**; **Fig. 5C–D**). However, the richness of wild pollinators had a negative and significant effect on seed set (**Table 4**).

Table 4 Generalized Linear Mixed Models evaluating the effects of the abundance and richness of wild pollinators and wild bees on fruit set and seed set. Models included the variance (± SD) estimate for tree identity (nested within orchard) and orchard identity, considered as random factors. Response variables were fitted by considering a binomial error distribution (logit link).

		Fruit set			**Seed set**		
	Predictors	**Estimate ± SE**	**z**	**P**	**Estimate ± SE**	**z**	**p**
Wild pollinators abundance model	Intercept	0.178±0.230			1.178 ± 0.162		
Fruit set	Abundance wild pollinators	0.110 ± 0.060	1.850	0.064	0.354 ± 0.043	8.265	<0.001
R^2m 0.022**; R^2c** 0.101	Year (2016)	0.296 ± 0.077	3.865	0.001	-0.022 ± 0.052	-0.429	0.668
Seed set	Tree [Orchard] (random factor)	1.482 ± 1.217			0.964 ± 0.982		
R^2m 0.034**; R^2c** 0.058	Orchard (random factor)	0.657 ± 0.811			0.239 ± 0.489		
Wild pollinators richness model	Intercept	0.051 ±0.302			2.995 ± 0.223		
Fruit set	Richness wild pollinators	0.024 ± 0.019	1.272	0.203	-0.118 ± 0.014	-8.667	<0.001
R^2m 0.022**; R^2c** 0.096	Year (2016)	0.420 ± 0.067	6.281	<0.001	0.077 ± 0.045	1.706	0.088
Seed set	Tree [Orchard] (random factor)	1.467 ± 1.211			0.087 ± 0.295		
R^2m 0.021**; R^2c** 0.057	Orchard (random factor)	0.604 ± 0.777			0.094 ± 0.306		
Wild bees abundance model	Intercept	-0.338 ± 0.264			1.340 ± 0.155		
Fruit set	Abundance wild bees	1.629 ± 0.135	12.063	<0.001	0.845 ± 0.084	10.063	<0.001
R^2m 0.038**; R^2c** 0.175	Year (2016)	0.276 ± 0.063	4.401	<0.001	0.097 ± 0.044	2.198	0.028
Seed set	Tree [Orchard] (random factor)	1.530 ± 1.237			0.984 ± 0.992		
R^2m 0.019**; R^2c** 0.053	Orchard (random factor)	1.159 ± 1.077			0.231 ± 0.481		
Wild bees richness model	Intercept	0.001 ± 0.235			-0.909 ± 0.255		
Fruit set	Richness wild bees	0.066 ± 0.022	2.990	0.003	-2.4e-5 ± 0.015	0.790	0.999
R^2m 0.028**; R^2c** 0.092	Year (2016)	0.475 ± 0.068	6.997	<0.001	0.227 ± 0.047	1.911	<0.001
Seed set	Tree [Orchard] (random factor)	1.462 ± 1.209			0.937 ± 0.968		
R^2m 0.014**; R^2c** 0.047	Orchard (random factor)	0.580 ± 0.762			0.187 ± 0.433		

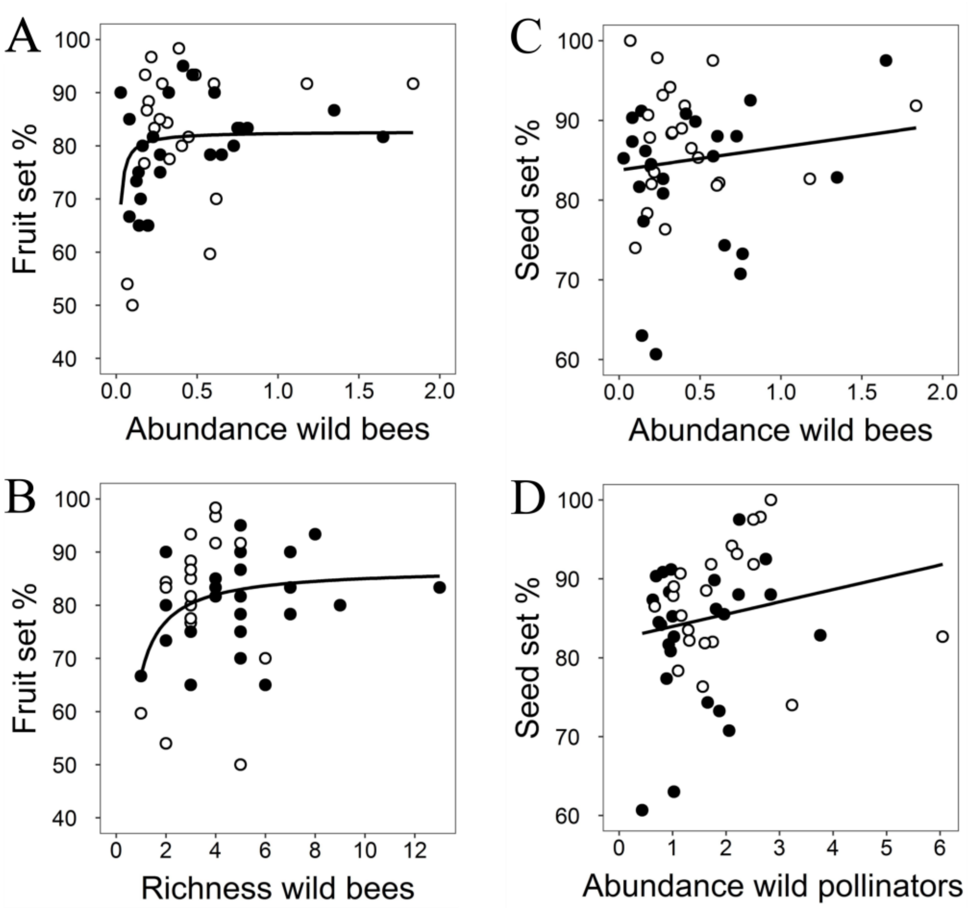

Fig. 5. Examples of significant effects predicted by Generalized Linear Mixed Models of pollinator insect biodiversity on pollination in terms of: (A) abundance and (B) richness of wild bees on fruit set; (C) abundance of wild bees and (D) abundance of wild pollinators on seed set. Fruit/seed set (represented in percentages) were estimated as the quotient between the value of fruit/seed set in open-pollination treatment and those in the hand-pollination treatment. Dots indicate different orchards, with different colors for years, 2015 (black) and 2016 (white). Non-linear trends are fitted for fruit set combinations and linear trends for seed set combinations are shown.

DISCUSSION

In this work, we disentangle both the environmental drivers and the functional effects of biodiversity in agroecosystems, focusing on different groups of wild animals (forest insectivorous birds, and pollinator insects) responsible for distinct ecosystem services (pest control and pollination) in the same crop, the cider apple in Asturias (N Spain). We followed a two-step approach in which, first, we found that landscape structure and local-scale orchard features influenced the biodiversity of pest predator birds and pollinator insects within cider apple orchards. Specifically, bird biodiversity was affected by within-orchard apple canopy cover, whereas pollinator biodiversity depended on landscape structure and apple bloom within orchards. Second, our study evidences positive effects of both bird and pollinator biodiversity on the magnitude of the respective ecological functions (insectivory and pollination) supplied by each animal group. Indeed, insectivory rates in orchards increased with both the abundance and richness of birds, as did fruit set and seed set with those of pollinators, especially wild bees. We thus found a consistent positive B-EF link across animal groups and functions performing simultaneously in a given crop type. Although our methodological approach to the complex inter-relationships among habitat structure, biodiversity and ecosystem functions was not strictly integrative (e.g. Heath and Park, 2019), we discuss below the determinants of animal biodiversity and its consequences, in relation to the preservation of ecosystem services with potential benefits for cider apple production.

Effects of landscape and local-scale orchard features on bird and pollinator biodiversity

Against expectations, our analysis did not detect any effect of landscape cover types on the biodiversity of birds within apple orchards. Several studies have shown that surrounding semi-natural woody vegetation promotes bird abundance and richness within woody crops (Karp and Daily, 2014; Heath and Long, 2019; Rey et al., 2019). In fact, our previous study in these cider apple orchards also evidenced positive effects of semi-natural woody cover at the large scale (García et al., 2018). This discrepancy between our previous and present results may be related to two analytical facts. First, the response of within-orchard bird biodiversity to the availability of surrounding semi-natural woody habitat may show non-linear trends, scarcely detected by the linear model incorporating integrative landscape predictors here applied. In fact, a positive response of bird biodiversity to semi-natural woody habitat availability emerges at low-to-medium values of the habitat gradient, becoming null or even negative beyond a threshold of 25–30 % habitat availability (**Fig. F1**; **Table F1**; see also García et al., 2018). Second, we also estimated bird biodiversity at a smaller extent (a 25-m radius plot in each apple orchard) than in our previous analysis (50-m radius plot which incorporated apple orchard and nearby habitats; García et al., 2018). The narrower analytical grain used here for response variables probably weakened our ability to detect clear landscape effects on local bird biodiversity (García et al., 2011).

In contrast, we found clear effects of orchard-scale features on bird abundance and richness. Namely, apple canopy cover strongly affected bird biodiversity, with more continuous and wider tree covers, rather than denser canopy volumes (no effect of canopy thickness was found) benefiting bird abundance and richness within orchards. Covering a longer period of time, these findings corroborate our previous results (García et al., 2018) and suggest the importance of apple canopy cover for ensuring safe foraging conditions for birds, as well as small-scale connectivity for them when moving within orchards (Henry et al., 2007), or when using orchards as stepping stones between habitat patches (Blitzer et al., 2012). Moreover, our results also evidenced that bigger orchards also harbored richer assemblages of insectivorous birds, suggesting that they operate as a suitable habitat that brings together species from large-scale, landscape bird assemblages (Tscharntke et al., 2012b).

In the case of pollinators, we found that landscape structure did influence biodiversity in cider apple orchards. The insects studied here responded to large-scale environmental gradients, probably as a result of wide foraging ranges and their capability for long-distance flights (Walther-Hellwig and Frankl, 2000; Gathmann and Tscharntke, 2002). As judged by the effects of PC2 vector, the cover of surrounding seminatural woody habitats increased the abundance of wild pollinators, including wild bees, in cider apple flowers (see similar patterns in Martins et al., 2015; Joshi et al., 2016). These habitats often increase pollinator resource availability in the agricultural landscape, in the form of flowers (Kennedy et al., 2013), refuges (Motzke et al., 2016), or nesting sites (Kremen et al., 2007). Our analysis also suggests the positive effect of timber plantations (which increase across the landscape at the expense of pastures) on wild pollinator abundance and richness. Eucalyptus, the dominant timber in the region, is a mast-flowering species that may represent a complementary food resource for pollinators (Horskins and Turner, 1999; Fontúrbel et al., 2015), contributing to some spillover of pollinators to apple orchards. However, contrary to what has been found in other studies (Öckinger and Smith, 2007; Venturini et al., 2017), the availability of surrounding pastures did not increase pollinator biodiversity in cider apple orchards.

Finally, the extension of other habitat types such as water courses (a supposedly suboptimal habitat for pollinators) as well as that of fruit plantations (probably representing habitat homogenization and a saturation effect; Samnegard et al., 2019), negatively affected wild bee abundance.

We also found clear effects of local-scale orchard features on pollinator biodiversity. Specifically, greater magnitudes of bloom in apple trees attracted more wild pollinator and wild bee species (see also Westphal et al., 2003; Holzschuh et al., 2013). However, in terms of the flower availability in the ground cover, our results contrast with studies suggesting positive effects of this feature on crop pollinators (e.g. Alomar et al., 2018; for other apple orchards see also Campbell et al., 2017; Samnegard et al., 2019). The lack of ground cover effect shown here may be due to the high contrast represented by the mass flowering of apple and the disperse flowering of ground cover in Asturian orchards, with apple monopolizing generalist pollinators and making them indifferent to other floral resources (Holzschuh et al., 2011; Joshi et al., 2016).

Effects of animal biodiversity on insectivory and pollination

Our study shows birds and insects to be effective providers of respectively, insectivory and pollination in cider apple orchards. More importantly, by addressing these ecological functions across orchards, we evidence positive effects of abundance and species richness of both animal groups on the magnitude of their respective functions. We found, therefore, functional consequences of biodiversity across groups of organisms co-occurring in a given agroecosystem.

Our results suggest the strong ability of insectivorous birds to reduce arthropod load on cider apple trees. Namely, excluding birds from branches led to an almost four-fold increase in arthropod biomass, a considerably higher figure than applying this condition to other woody crops such as coffee (Karp and Daily, 2014) or cacao (Maas et al., 2013). The positive effects of bird biodiversity on insectivory may emerge from sampling (or dominance) effects, with richer orchards incorporating abundant and highly effective insectivores (e.g. tits; Mols and Visser, 2002), and from functional complementarity, with richer orchards including a birds with a greater variety of traits and behaviours (i.e. flycatchers, foliage gleaners, bark gleaners; García et al., 2018) which would lead to additive predatory effects across bird species.

As in the case of insectivorous birds, we found evidence of a positive eB-EF link between wild insects and pollination in cider apple orchards, especially when focusing on wild bees. Namely, abundance and richness of wild bees impacted positively on fruit set (see also Mallinger and Gratton, 2015; Martins et al., 2015). The relationship between fruit set and wild bee abundance and richnes showed a nonlinear, saturating pattern, suggesting a dominant effect of abundant species at low richness levels but redundancy at higher richness levels, when maximum fruit set levels are attained (Winfree, 2013). These positive patterns on fruit set were, however, somehow diluted when all wild pollinators were considered. This may be due to the greater pollination effectiveness of wild bees compared to other groups (Martins et al., 2015), facilitating that they would better reflect dominance or complementarity effects across their biodiversity gradients (Fontaine et al., 2005; Foldesi et al., 2016). In other words, some inefficient non-bee pollinators could have almost null effects on fruit set: having these species or individuals in the pollinator assemblage would not necessarily mean significant improvement in pollination function, even at low richness levels (Schwartz et al., 2000). Concerning seed set, although wild pollinator abundance positively affected this pollination parameter, our study shows a surprisingly negative effect of wild pollinator richness (but see, for example, Martins et al., 2015; Campbell et al., 2017). Such negative effects of richness could emerge from interspecific competition, as the incorporation of some species may trigger negative interactions that reduce the global effectiveness of the pollinator set (Valido et al., 2014; Agüero et al., 2018).

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Our results evidence strong potential, on the basis of animal biodiversity, for the compatible provision of two important ecosystem services, pest control and pollination, in cider apple crops. We must acknowledge that the insectivorous birds studied here may also provoke ecosystem disservices, by consuming beneficial insects (pollinators and other natural enemies such as spiders) or even damaging fruit (e.g. Pejchar et al., 2018; Gonthier et al., 2019). However, in this sense, we did not find signs of negative trade-offs either between biodiversity groups (**Table G1**) or between insectivory and pollination (**Table G1**), suggesting no strong effects of predatory birds on pollinator assemblages and pollination. Moreover, our previous studies evidence the strong capacity of birds to control cider apple pests even when intraguild predation occurs (i.e. towards arthropods acting as natural enemies; García et al., 2018; Miñarro and García, 2018). And finally, although birds occasionally damage apples (by picking at the pulp) crop losses are usually negligible in Asturian orchards, probably due to the early harvest and the high availability of wild fleshy-fruits in surrounding hedgerows for frugivorous birds (authors unpublished data). We thus suggest that the combined activity of insectivorous bird and pollinator insects will have positive net effects on apple crops (see also Peisley et al., 2016). In this sense, it is likely that lower pest damage and enhanced pollination will benefit apple farmers in the form of higher yield (Mols and Visser, 2002; Mallinger and Gratton, 2015), increased harvest quality (Garratt et al., 2014; Peisley et al., 2016), and increased profitability (due to decreased expenditure on insecticides; Cross et al., 2015). Future studies should include the relationship between the ecological variables measured here and explicit yield parameters in order to properly assess the ultimate agronomic role of biodiversity on cider apple farming. These should also include assessments of negative effects, both direct and indirect, of birds on fruit production, in order to explicitly quantify animal services in terms of the balance between costs and benefits (Peisley et al., 2015). Nevertheless, our results suggest that win-win solutions for biodiversity conservation and sustainable agricultural production are possible in cider apple crop.

The present results suggest co-occurring agricultural benefits of two different biodiversity groups, opening the door to simultaneous management. This is a challenging task, as even single biodiversity groups, such as vertebrate pest enemies, require integrative and multi-scaled management plans to be implemented (Lindell et al., 2018). Nevertheless, here we have identified several, albeit none of which were clearly common, environmental drivers of bird and insect assemblages. This hinders the identification of simple strategies for the simultaneous improvement of pest predation and pollination. In other words, different measures at landscape and orchard scales are needed in order to enhance simultaneously the biodiversity of birds and that of insects. At the landscape scale, maintaining semi-natural woody habitats (i.e. shrubs, hedgerows, mixed forests), by conserving extant patches (i.e. avoiding losses due to land consolidation programs) or even allowing rewilding (i.e. ecological succession in abandoned fields towards shrubland and secondary forest), but also allowing some eucalyptus plantations, would enhance wild pollinators. At least moderate levels of landscape-scale forest cover also seem to be beneficial to bird biodiversity, which also benefits from woody hedgerows and small forest patches in orchard boundaries (García et al., 2018). These large-scale and out-of-orchard features may not be open to management by apple farmers, and thus should be considered in land management plans that also involve municipal and regional public administrations. At the orchard scale, maintaining wide apple canopy cover would promote insectivorous birds. This measure may indirectly ensure wider flowering canopies and therefore the bloom that fosters the biodiversity of pollinators. However, bloom promotion may be in conflict with the interest of stabilizing yield across years (Asturian apple varieties show bi-annual masting, a production problem generally treated with chemicals and pruning). The trade-off between bloom and masting control, mediated by apple canopy cover, needs further study to assess management thresholds. Finally, even with no evidence of any direct effect on apple pollination, we would still encourage farmers to maintain well-developed and diverse ground covers in order to promote indirect benefits, such as the provision of habitat for other natural enemies of apple pests (e.g. hoverflies or parasitoid wasps; Rosa García and Miñarro, 2014), as well food and shelter resources outside of the apple blossom season for apple pollinators.

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Chapter 2

Top-down and bottom-up regulation of codling moth populations in cider apple orchards

ABSTRACT

The success of biological control by natural enemies in agricultural crops relies on a clear understanding of trophic interactions between natural enemies, pests and host plants. Top-down and bottom-up trophic effects, in combination with potential landscape and local-scale factors, may determine pest populations. For two years, we analyzed codling moth populations (*Cydia pomonella*, Lepidoptera, Tortricidae), their crop damage and their parasitoid communities in 26 low-input cider apple orchards in northern Spain (Asturias). Codling moth abundance was estimated from overwintering larvae sampled in cardboard traps on apple trees, parasitism was estimated from parasitoids emerged from lab-reared codling moth larvae, and pest damage was assessed from apples before ripening. Codling moth abundance differed between orchards across years, and was positively related to apple production and the cover of apple plantations in the immediate surrounding landscape. The effects of the availability of plant resources (apple) on pest abundance suggest bottom-up regulation of codling moth populations. Apple damage per orchard reached a maximum of 71%, but decreased with apple production, indicating satiation by codling moth. Seven parasitoid species were recorded on codling moth larvae. Parasitism rate per orchard reached 42.5% of codling moth larvae. The number of parasitized larvae per orchard was positively related to parasitoid richness, but also to codling moth abundance, suggesting simultaneous top-down and bottom-up effects between parasitoids and pests. This study highlights the need of tackling the whole parasitoid-pest-plant system for managing codling moth damage in apple orchards. In this sense, the conservation of complementary parasitoid species through biodiversity-friendly actions should be combined with the control of apple production at orchard and landscape scale.

INTRODUCTION

The biological control of agricultural pests by natural enemies can offer effective solutions for avoiding crop damages while reducing the negative environmental and health impacts of chemical pesticides (Landis et al., 2000; Crowder and Jabbour, 2014; Demestihas et al., 2017). Among these natural enemies, parasitoids (Hymenoptera) are considered a highly effective group for biological control, thanks to their high diversity and specialization degree (Mason and Huber, 1993; Macfadyen et al., 2015). By impairing and ultimately killing individual hosts (Mills, 2005), parasitoids can limit pest populations (Lacey and Unruh, 2005), finally decreasing crop damages and providing an ecosystem service valued at billions of dollars annually (Losey and Vaughan, 2006; Crowder and Jabbour, 2014). Importantly, the richness within parasitoid assemblages may be relevant for modulating the potential of biological control, as different species may render additive and complementary roles in hampering pests (Straub and Snyder, 2006; Peralta et al., 2014). In fact, several studies have evidenced positive effects of parasitoid richness on the magnitude and the temporal stability of parasitism rates (Ives et al., 2005; Snyder et al., 2006; Tylianakis et al., 2006).

Understanding the role of parasitoids as agents of biological control requires going beyond the top-down forces expected in the parasitoid-pest interactions. In fact, pest population dynamics are frequently regulated by bottom-up forces via their host plants, with the availity of food resources (i.e. crops) being a limitant for pest population growth (Singer and Stireman, 2005; Vidal and Murphy, 2018; Walker et al., 2008). Therefore, a crop management which decreases access of pests to specific food resources, as for example by increasing within-crop species or genetic diversity, may lead to reduced pest damage (Root, 1973; Costello and Daane, 2003). Thus, establishing effective measures of biological control of crop pests, involving parasitoids, requires an integrative understanding of both top-down and bottom-up mechanisms simultaneously operating in the three-level parasitoid-pest-plant interactions (Singer and Stireman, 2005; Peralta et al., 2014).

A complicating factor in these trophic interactions between plant, pest and its parasitoids is the heterogeneity inherent in agricultural landscape at different spatial scales. The effects of local-scale and landscape variability on pests and parasitoids can influence their populations and their trophic interactions, so the relative effects of bottom-up and top-down relationships are likely to vary (Hunter and Price, 1992; Maalouly et al., 2013; Šigut et al., 2018). Insect species involved in active displacement at local and landscape scales are determined by the occurrence of more or less connected habitats of different size and qualities (Dennis et al., 2003; Hiebeler and Morin 2007). For instance, adjacent semi-natural habitats or floral strips whitin the crop provide plants that attract parasitoids with nectar and pollen resources (Dib et al., 2012) which could increase their populations, foster their efficiency and finally reinforce their effect on various pests.

Codling moth (*Cydia pomonella* L.) is one of the most detrimental and economically important pests in apple (*Malus* x *domestica* Borkh) and pear (*Pyrus communis* L.) orchards worldwide (Beers et al., 2003; Mills, 2005). In the absence of management, codling moth, a multivoltine species that may attack the fruit several times before harvesting, can lead to almost complete loss of apple crops (Mills, 2005). Its control is, thus, mostly based on broad-spectrum insecticides and mating disruption pheromones (Reyes et al., 2007; Witzgall et al., 2008). A varied assemblage of parasitoids has been described for codling moth in apple orchards (e.g. Mills, 2005; Maalouy et al., 2015) but, in general, their effect on biological control in intensive orchards is considered ineffective due to insufficiency (Thorpe et al., 2016) or dependency on the environmental context (Maalouy et al., 2013). Nevertheles little is known on the potential for biological control of codling moths in low-input orchards, where the minimization of the use of chemicals (both pesticides and fertilizers) may strongly condition the functioning of the parasitoid-codling moth-apple interaction.

In the present study, we explore parasitoid top-down and apple bottom-up effects on codling moth abundance and its damage in low-input cider apple orchards (Asturias, N Spain). Both trophic forces are evaluated taking into account the potential effects of landscape and local-scale factors. Specifically, we seek to explore: (1) the codling moth abundance and its associated damage to apple production across years and orchards; (2) the bottom-up effects of host apple plant on codling moth abundance and its associated damage; (3) the parasitoid assemblage attacking the codling moth across years and orchards; and (4) the top-down effects of parasitoid richness on parasitized codling moth larvae. We then interpret these questions in terms of management guidelines for promoting pest control by natural enemies with increased farmers' confidence.

MATERIAL AND METHODS

Study system and spatial design

The study was conducted in the cider apple (*Malus x domestica*) crop area of central Asturias (N Spain) (**Fig. A1**). In this region, cider is a valuable traditional product, highly ingrained in society, linked to tourism, gastronomy, leisure and an important source of income. The majority of cider apple orchards are relatively small (most cover between 0.5 and 4 ha), extensively or semi-extensively managed and comprised of local cultivars. Extensive traditional orchards of randomly distributed cultivars are growing on seedling rootstocks (100-250 trees/ha), but new orchards are growing on semi-dwarfing rootstock (500-650 trees/ha).

Orchards are embedded in a highly variegated traditional landscape, containing a fine-grained mosaic of land-uses, such as orchards, livestock pastures, other fruit plantations (e.g. blueberry, kiwi), timber (mainly eucalyptus) plantations, semi-natural woody vegetation patches (e.g. temperate broad-leaved forest, riparian forest), and human infrastructures. At the small scale of their immediate neighbourhoods, apple orchards are typically surrounded, either totally or partially, by natural woody vegetation in the form of hedgerows. In addition, farmers have a cultural tolerance to pests and diseases, because aesthetical damage is not relevant for cider apple production. Besides, farmers use local cultivars tolerant to most common apple pests and diseases (e.g. canker, scab, powdery mildew, rosy apple aphids), and thus, the use of pesticides is very low because aesthetic damage is not relevant for cider apples. As a consequence, most pests are not perceived as severe threats to productivity (Martínez-Sastre et al., 2020). Farmers control pests according to their own perceptions and following personal schemes. However, the number of codling moths reached in almost all the orchards suggests limited and weak control of codling moth by farmers.

Between 2015 and 2016, sampling was conducted in 26 cider apple orchards distributed over 600km^2 (**Fig. A1**). Orchards were chosen to represent a gradient of variability in the environmental conditions within apple orchards (i.e. tree trunk diameter, orchard size, canopy cover) and in the surrounding landscape (i.e. cover of semi-natural habitats, pastures, apple orchards). In each orchard, we established a 25m radius sampling station within the plantation, at least 25m far from orchard edge. In each sampling station, ten trees were randomly selected.

Sampling of codling moth, crop damage and production, and parasitoids

We sampled codling moth larvae using traps made of 10cm wide corrugated cardboard bands wrapped around the trunk of selected trees (40cm above the ground and always under the first branch) (**Fig. B1**). Traps intercept larvae when moving from apples to the ground, and cardboard spaces are used by larvae as shelter for overwinter. We covered all traps by a plastic mesh until collection, to protect them from moisture and animals (e.g. snails). Traps were installed in mid-July and collected in mid-December. Traps were stored at 5ºC until mid-February allowing larvae to diapause.
Then, we counted codling moth larvae collected, differentiating between males and females by the presence or absence of male gonads, visible through the tegument (MacLellan, 1972). In addition, we identified other group of codling moth larvae with small size (hereafter, small size larvae). These larvae have small size because their development has been blocked due to parasitism (Reed-Larsen and Brown, 1990). Apart from larvae cocoons, ectoparasitoid cocoons were also identified in the cardboard traps and were counted, collected and stored in individual vials for rearing.

In each orchard, the average number of codling moth larvae per tree per orchard (hereafter, *CM abundance*) was estimated across cardboard traps from the sum of alive codling moth larvae (females, males and small size larvae), dead codling moth larvae (by different unknown causes), ectoparasitoid cocoons (as each ectoparasitoid comes from a codling moth larva), and pecking marks by birds. The signs of pecking by birds were scarce. However, to obtain the number of larvae that could have been eliminated, we calculated the number of larvae per unit area in the undamaged part of cardboard trap and estimated the number of bird-predated larvae considering the cardboard surface damaged by pecks.

To estimate apple damage rate caused by codling moth (hereafter *CM damage*) per orchard and year, we randomly collected from each focal tree 10 apples from the tree canopy and 10 apples from the ground below the tree. Then, all apples were cut in half in situ to look for signs of codling moth damage (e.g. larvae inside, galleries, frass). Finally we calculated the average percentage of apples damaged per tree.
We quantified apple production per orchard per year, estimated as the average crop size of the 10 selected trees within each sampling station. Crop sizes were estimated before harvest from the average number of apples in 10 branches extrapolated to the total number of branches per tree.

In order to determine the level of parasitism (i.e. how many larvae were attacked by parasitoids), from codling moths collected from traps in each orchard, we selected a subsample of 50 females, 50 males and 50 small size larvae per orchard. The three types of larvae were placed in different plastic containers with new corrugated cardboard bands for sheltering, and reared at 25 ± 1ºC and a 16h/8h light/dark photophase. Samples were monitored periodically until the emergence of both codling moth and parasitoid adults. Emerged parasitoids were kept individually in Eppendorf tubes at -20 ºC until species identification (Athanassov et al., 1997; Graham, 1969; Peters and Baur, 2011).

We estimated the total number of parasitized codling moth larvae per orchard (hereafter, *number of parasitized larvae*). For this, firstly, we extrapolated the proportion of parasitoids emerged from the reared male and female codling moth subsamples (number of parasitoid emerged / parasitoid emerged + codling moth emerged) (Miñarro and Dapena, 2004; Maalouly et al., 2013) to the female and male codling moth larvae counted in that orchard. Secondly, all small size larvae were also considered as parasitized codling moth (Reed-Larsen and Brown, 1990), independently of their parasitoid emergence from each subsample after rearing. Then, we quantified the total number of parasitized codling moth larvae per orchard as the cumulative number of estimated male and female parasitized larvae, plus the number ofsmall size larvae, plus the number of recorded ectoparasitoids. We also estimated a *parasitism rate*, as the percentage of parasitized larvae in relation to the total number of overwintering codling moth larvae per orchard. Finally, the richness of parasitoid per orchard and year (hereafter, *parasitoid richness*) was estimated as the cumulative number of parasitoid species emerged from larvae samples and that of ectoparasitoid species of each orchard.

Landscape and local-scale features

Landscape structure was quantified by means of a Geographic Information System of the study area (GIS, ArcGIS9.3) based on 1:5000- scale orthophotographs (2014). Different types of cover were digitized in order to include four main habitats assumed to potentially affect codling moth and parasitoids: (1) semi-natural woody vegetation, (2) pastures (mainly livestock pastures and mowing grasses), (3) apple plantations and (4) exotic tree plantations (mainly eucalyptus). Semi-natural woody vegetation included forest patches of variable size, hedgerows, and isolated trees, but excluded scrubland patches. We estimated the availability of the different habitats within a circular plot of 1km radius centered on the sampling station of each orchard. This spatial scale fits to long flight distances of parasitoids and codling moth adults (Yu et al., 2009; Pajač et al., 2011).

As local-scale features that can affect codling moth and parasitoids, we measured: (1) orchard size, (2) the amount of cover by apple tree canopy in each sampling station (hereafter, apple canopy cover; from a GIS layer of apple canopy projection), (3) apple tree trunk diameter (average from 25 trees within each sampling station), (4) the proportion of surrounding hedgerows and, (5) the proportion of apple plantations, both within a circular plot of 125m radius centered on the sampling station (hereafter, hedgerows R125 and apple plantation R125 respectively; from a GIS layer).

Statistical analysis

We compared CM abundance and CM damage among orchards by using Kruskall-Wallis tests (trees as sampling units) and between years with paired t-tests (orchards as sampling units). Parasitoid richness and parasitism rate per orchard were compared between years with paired Wilcoxon tests, whereas the number of parasitized larvae per orchard was compared between years with a paired t-test. All variables were checked for normality prior to tests, and CM abundance (sqrt) and number of parasitized larvae (log) were transformed. Analyses were performed using functions in the package *stats* (R Core Team, 2013).

We sought to analyse the different trophic interactions between apple crop, codling moth and parasitoids, taking into account potential environment effects. To do this, we applied Generalized Linear Mixed Models (GLMM; Bolker et al., 2009), considering CM abundance (sqrt), CM damage and number of parasitized larvae (log) as different response variables (all of them were checked for normality, and thus models considered Gaussian distribution and identity link). Trophic interactions were first analyzed by means of simple "trophic models" searching for observational evidences of bottom-up and top-down forces. These simple trophic models included an specific interaction between pest-plant or parasitoid-pest and the potential effects of landscape or local-scale features. Hence, one model searched for bottom-up (plant→pest) effects on codling moth by checking the relationships between apple production per orchard (predictor) and the CM abundance and CM damage (response variables). Another model searched for bottom-up (pest→parasitoids) and top-down (parasitoids→pest) effects between codling moth and parasitoids, by checking the relationships between the number of parasitized larvae per orchard (response) and the CM abundance (bottom-up predictor) and parasitoid richness (top-down predictor).

To evaluate the role of the environment, we widen the previous trophic models by incorporating, as additional predictors, landscape and local-scale variables. Because of the large number of environmental variables, we did not include all variables at once in single extended models (Frost, 2019; see Ricci et al., 2009, for a similar rationale). Thus, for each response variable, a "local-scale" extended model included, as additional predictors, orchard size, hedgerows R125, apple plantation R125, apple canopy cover, tree trunk diameter, and apple production. Similarly, a "landscape" extended model included, as additional predictors, the covers of apple plantation, semi-natural habitat, pastures and exotic trees. All main predictors were initially included in the full extended models, but, to avoid over-parameterization and overfitting, those terms that were non-significant ($P > 0.05$) were excluded in a backward stepwise procedure to select the simplest model, using likelihood ratio tests. Finally, we combined for each trophic interaction the selected "local-scale" and "landscape" significant variables in a last generalized linear mixed model.

All Generalized Linear Mixed Models (GLMMs, Bolker et al., 2009) included year as a fixed factor and orchard identity as a random factor given that all orchards were replicated across years (Bolker et al., 2009). The marginal and conditional R^2 were calculated to assess the amount of variance explained by the fixed and random effects, respectively (Nakagawa and Schielzeth, 2013). Means are shown ± Standard Error (SE). Generalized Linear Mixed Models were performed using the package *nlme* (Pinheiro et al., 2012).

All statistical analyses and graphs were performed using the software package R, version 3.5.3.

RESULTS

Codling moth abundance and crop damage

A total of 16,536 (7,618 in 2015, 8,918 in 2016) larvae were collected from the cardboard traps. CM abundance per cardboard trap ranged from 1 to 99 (32.43 ± 27.00; mean ± SD) in 2015 and 1 to 89 (37.26 ± 25.87) in 2016. CM abundance was similar between years, although it varied significantly between orchards each year (**Table D1, Fig. C1**).

Codling moth damage to apples varied significantly between orchards and years (**Fig. C1; Table D1**). CM damage per orchard ranged from 1.50% to 49.00%

in 2015 and from 14.58% to 70.93% in 2016. Damage was higher in 2016 (42.75% ± 16.39; mean ± SD) than in 2015 (21.40% ± 15.76).

Determinants of codling moth abundance and crop damage

The best model searching for bottom-up effects on codling moth populations, after taking into account local-scale and landscape factors (**Table F1** and **F2**), showed a positive significant response of CM abundance to apple production, apple plantation R125 and year (2016) (**Table 1**, **Fig. 1 A** and **B**).

In terms of possible bottom-up trophic effects on apple damage, last model (**Table F1** and **F2**) showed a negative significant effect of apple production (**Table 1**, **Fig. 1C**) and a positive significant effect of year (2016) (**Table 1**) on CM damage.

Table 1. Final Generalized Linear Mixed Models evaluating bottom-up effects on codling moth abundance and damage taking into account local-scale and landscape factors (Gaussian distribution, identity link). The variance (±SD) estimate for orchard identity, considered as a random factor, is also shown.

CM abundance	$\mathbf{R^2m}$ 0.282**;** $\mathbf{R^2c}$ 0.630		
Predictors	**Estimate± SE**	**t**	**p**
Intercept	1.192 ± 1.132		
Apple production	0.003 ± <0.001	3.469	0.002
Apple plantationR125	3.993 ± 1.833	2.179	0.039
Year (2016)	1.805 ± 0.566	3.188	0.005
Orchard (random factor)	1.317 ± 1.360		
CM damage	$\mathbf{R^2m}$ 0.400**;** $\mathbf{R^2c}$ 0.721		
Predictors	**Estimate± SE**	**t**	**p**
Intercept	0.343 ± 0.058		
Apple production	-0.001 ± <0.001	-2.727	0.013
Year (2016)	0.143 ± 0.043	3.320	0.003
Orchard (random factor)	0.111 ± 0.103		

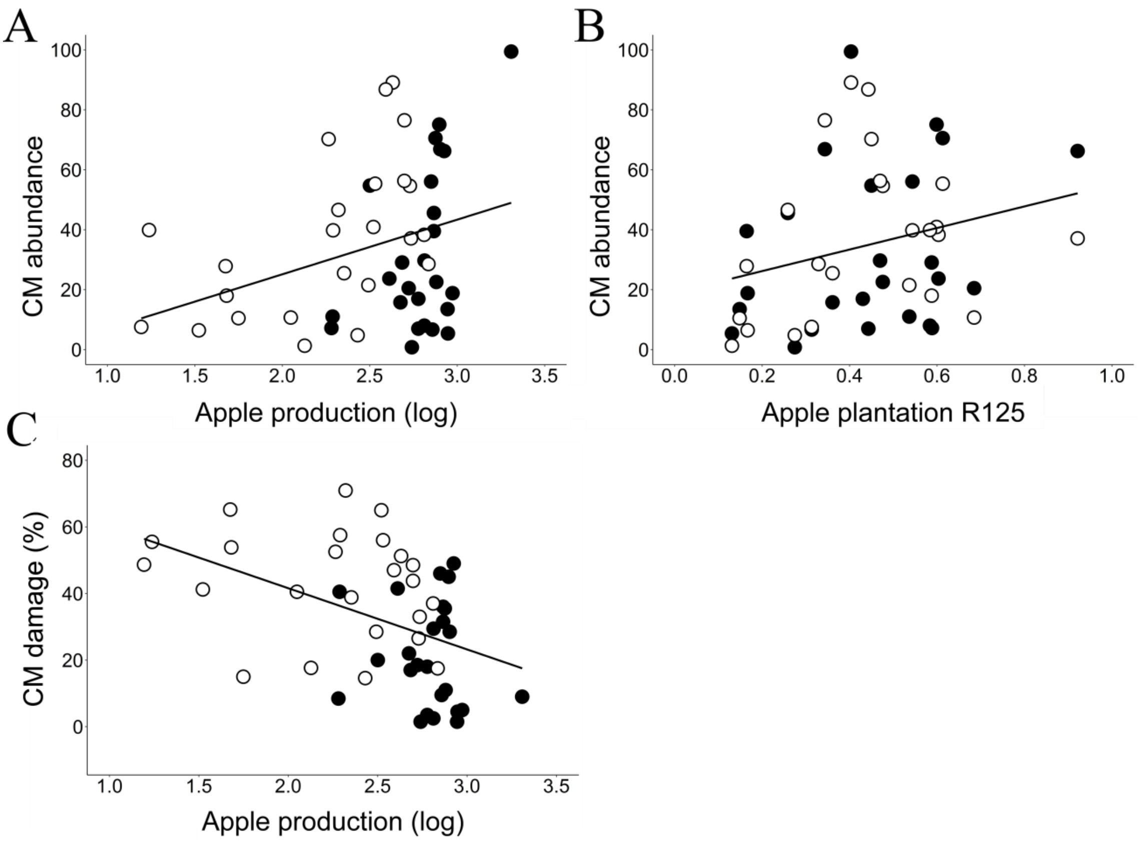

Figure 1. Significant effects of apple production and local-scale variables on codling moth abundance and codling moth damage. Colours indicate different years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variable.

Codling moth parasitoid assemblage

We found seven parasitoid hymenoptera species from four families (**Table 2**). Three species accounted for 94.9% of individuals of the parasitoid assemblage and were widerspread across orchards: *Ascogaster quadridentata* (Wesmael) (1,148 individuals, 66.3% of individuals, 25 orchards); *Pristomerus vulnerator* (Panzer) (298, 17.2%, 9 orchards in 2015 and 14 in 2016); *Trichomma enecator* (Rossius) (197, 11.4%, 13 orchards in 2015 and 11 in 2016) (**Figs. F1-F2**). Less frequent species, which included *Liotryphon caudatus* (Ratzeburg) (45 individuals), *Nippocryptus vittatorius* (Jurine) (31), *Dibrachys cavus* (Walker) (5) and *Perilampus tristis* (Mayr) (8) accounted for 5.1% of individuals (**Figs. F1-F2**).

Table 2. Number of larvae of codling moth (percentages in brackets) parasitized by different parasitoid species per year.

Specie	**Family**	**2015**	**2016**	**Total**
Ascogaster quadridentata	Braconidae	318 (49.6%)	830 (76.1%)	1148 (66.3%)
Pristomerus vulnerator	Ichneumonidae	152 (23.6%)	146 (13.4%)	298 (17.2%)
Trichoma enecator	Ichneumonidae	128 (20.1%)	69 (6.4%)	197 (11.4%)
Liotryphon caudatus	Ichneumonidae	13 (2.0%)	32 (2.8%)	45 (2.6%)
Nippocryptus vittatorius	Ichneumonidae	26 (4.1%)	5 (0.5%)	31 (1.7%)
Perilampus tristis	Perilampidae	0 (0.0%)	8 (0.7%)	8 (0.5%)
Dibrachys cavus	Pteromalidae	4 (0.6%)	1 (0.1%)	5 (0.3%)
Total		641 (100%)	1091 (100%)	1732 (100%)

We found a total of 1,732 larvae parasitized (641 in 2015, 1,091 in 2016) (**Table 2**). The number of parasitized larvae ranged from 0 to 190 per orchard and year (mean= 35.44 ± 43.85) (**Fig. F2)**. No differences in the number of parasitized larvae were detected between years (**Table D1**). The number of parasitoid species found in 2015 and 2016 was 6 and 7, respectively. Althought there were no significant differences between years in parasitoid richness (**Table D1**, **Fig. F1**), parasitism rate was significantly higher in 2016 (14.55 ± 11.91%, mean ± SD; range: 0 - 42,45%) than in 2016 (8.57 ± 7.15%; 0 - 24,12%) (**Table D1; Fig. C1).**

Determinants of the number of parasitized larvae

The number of parasitized larvae per orchard was positively affected by richness parasitoid richness as well as CM abundance (**Table 3, Fig. 2**), suggesting the occurrence of simultaneous top-down and bottom-up effects on codling moth parasitism. No effects of local-scale or landscape variables were detected (**Table E1 and E2**).

Table 3. Final Generalized Linear Mixed Model evaluating bottom-up and top-down effects on number of parasitized larvae taking into account local-scale and landscape effects (Gaussian distribution, identity link). The variance (±SD) estimate for orchard identity, considered as a random factor, is also shown.

Number of parasitized larvae	**R^2m** 0.680; **R^2c** 0.680		
Predictors	**Estimate± SE**	**t**	**p**
Intercept	0.638 ± 0.258		
Parasitoid richness	0.701 ± 0.099	7.110	<0.001
CM abundance	0.014 ± 0.005	2.744	0.013
Orchard (random factor)	0.003 ± 0.803		

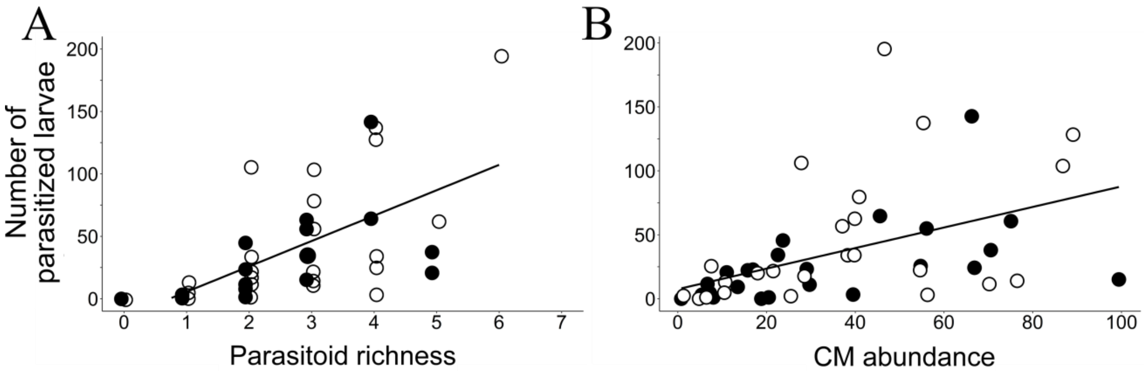

Figure 2. Significant effects of codling moth abundance (A) and parasitoid richness (B) on the number of parasitized larvae. Colours indicate different years, 2015 (black) and 2016 (white). Linear fits predicted by Generalized Linear Mixed Models are shown for each combination of predictor and response variable.

DISCUSSION

In this work, we disentangle the trophic interactions between apple, codling moth and its parasitoids in cider apple orchards while simultaneously searching for landscape and local-scale features that affect these interactions. In 26 cider apple orchards monitored during the two years, codling moth populations were able to reach high densities per tree, damaging up to 70.9% of the apple tree crops. Seven parasitoids parasitized codling moth, reaching parasitism rates of 42,5% in certain orchards. By analyzing each trophic interaction we detected positive effect of resource availability (i.e. apple production and apple plantations) on codling moth abundance. However, the damage of this pest proportionally decreased with apple production, suggesting a satiation of the pest under high resource availability. Moreover, codling moth parasitism increased with parasitoid richness and codling moth abundance. Our study suggests that simultaneous top-down and bottom-up forces across the interaction triad parasitoids-pest-plant could be important and actually necessary pieces for controlling codling moth in apple crops. We discuss below the possible consequences of these interactions in low-input systems, in relation to the promotion of biological control by parasitoids with potential benefits for cider apple production.

Codling moth abundance and crop damage

Codling moth reached 99 larvae per tree in certain orchards. These high values are inconceivable in intensive orchards, where the abundance of codling moth reaches a few larvae per tree (Ricci et al., 2009, Monteirto et al., 2013). Moreover, we can assume that codling moth abundance is even higher that the number of individuals trapped by cardboard bands. Many natural enemy species can attack different stages of codling moth before overwintering (Lacey and Unruh, 2005) and according to Blomefield and Giliomee (2012) there are more codling moth larvae overwintering on side and primary branches than in trunks. Such a high local abundances, stable across years and variable between orchards each year, is not surprising given the lack of regulated chemical treatments among cider apple orchard by farmers and the specialism of this pest in apple crops (Bengtsson et al., 2001).

Regarding landscape and local-scale effects on codling moth abundance, our results only showed how orchards with high proportion of apple orchards in the surroundings (125m radius) and large apple productions had higher numbers of codling moth. Both of them can be considered a measure of host density (availability of resources) and understood as two possible bottom-up effects at different spatial scales. At landscape level, the availability of apples generated by the orchard itself is reinforced by the presence of more orchards in the surroundings (Ricci et al., 2009; Monteiro et al., 2013) which in turn promotes the spread of the pest among orchards (Margaritopoulos et al., 2012; Monteiro et al., 2013). At local-scale, apple production determines the reproductive success of codling moth and the stability of their populations (Bengtsson et al., 2001; Beers et al., 2003).

Both bottom-up effects can be explained by the fact that the codling moth is a specialist pest (Bengtsson et al., 2001). It is well known that codling moth looks for apples to lays its eggs (Wearing, 1975) and can detect volatile compounds from branches with leaves, and from apples (Bengtsson et al., 2001). For instance, in temperate forest, canopy features of the trees (i.e. canopy structure, canopy level and leaf area) have been proved to influence the abundance of herbivores (Šigut et al., 2018). Therefore, it may be that the apple tree canopy or the size of the trees influences their location by the codling moth. Nevertheless, the proximity between orchards favors the dispersion of this pest due to the magnitude of the codling moth dispersal distance (Tyson et al., 2007; Ricci et al., 2009).

Despite a stable codling moth population across years, apple damage observed was higher in 2016 (42.7% of the apples per tree) than in 2015 (21.3%), with differences between orchards. The orchard with the highest attack reached 70.9 % of damaged apples. Our results proved codling moth damage capacity in low-input apple orchards, Mills (2005) reported similar percentages of damage in untreated organic orchards in California. These annual differences in the percentage of apple damaged while the populations remain stable reinforce the influence of apple production on codling moth damage. This result is related with the intrinsic biennial bearing patterns of alternating high and low apple productions intrinsic to apple orchards (Clark and Gage, 1997). Codling moth, as other insects that exploit fruiting structures of plants (Solomon, 1981; Williams et al., 2001), may suffer satiation due to surplus of their food resource (Rhainds and English-Loeb, 2003). As a consequence, the feeding impact of codling moth is most intense when food resources are limited, that means this pest would be more detrimental in years with low apple production. During these years low apple production inhibits codling moth and prepare the crop for the subsequent "mast" (Knudsen et al., 2008), where the probability of attack per apple is reduced. Therefore, years of less apple production drive codling moth to seek alternative host plants, where again the proximity of other orchards is key to prevent the spread of the pest (Knudsen et al., 2008).

From farmers' point of view these relationships between availability of resources and codling moth could interfere with the "worst years" of apple production, producing large economic losses. In any case, for low-input apple orchards embedded in highly patched landscape, such as the case of Asturias, farmers' coordination at landscape and local-scale level to avoid codling moth dispersion between orchards is essential to make effective treatments and management practices against codling moth populations (Monteiro et al., 2013).

Codling moth parasitoids

The codling moth was attacked by a parasitoid assemblage that included seven species. The number of parasitoid species in the orchards did not vary between years. Maalouly et al. (2015) reported lower richness but also stable communities across years and sites in French apple orchards. In terms of composition, *A. quadridentata* was identified as the most abundant and most ubiquitous parasitoid (96% of the orchards). Among the seven parasitoids emerged from codling moth larvae, we found two hyperparasitoids, *P. tristis* and *D. cavus.* Although they can parasitize codling moth, they can also parasitize other parasitoids of codling moth, eventually decreasing the ecosystem service of biological control provided by the parasitoid assemblage (Rosenberg, 1934; Bogenschütz, 1991). Biological control by parasitoids in these low-input cider apple orchards reached high parasitism rates, with a maximum value of 42.5% of parasitized larvae. Such as high parasitism rates and high local richness were only observed in non intensive orchards (Maalouly et al., 2013; Ismail and Albittar, 2015; Walker et al., 2017), intensive ones have reported very low parasitism rates (<5% in average) (Maalouly et al., 2013; Monteiro et al., 2013) mainly due to the use of pesticides applications (Mates et al., 2012). Besides, conventional orchards and their associated chemical control practices have been proved to decrease parasitism rates in surrounding orchards (Ricci et al., 2009; Monteiro et al., 2013). Therefore, to promote a rich community of parasitoids able to help in codling moth suppression, we need to decrease the use of harmful chemical inputs, one of the most important drivers of entomofauna loss (Sánchez-Bayo et al., 2019).

The coexistence of these seven species represents a wide gradient of behavioural, morphological and physiological variability that suggest a high functional diversity of parasitoids and an explicit niche separation between them competing for the codling moth. The developmental mode and the use of resources might explain the community structure of parasitoids in the orchards, as a consequence, they can avoid spatial and temporal constraints due to lack of resources: ectoparasitism versus endoparasitism, koinobiosis versus idiobiosis, the number of host orders potentially utilized and the developmental stage of the host they attack (egg, larva, prepupa, pupa) (Rosenberg, 1934; Wharton, 1993; Shaw, 1994). In fact, our results are in line with others that suggest that these parasitoids are not absolutely specialized in one particular host species nor generalist to the point of damaging the stability of the parasitoid community (Rosenberg, 1934; Wharton, 1993; Shaw, 1994).

This high functional diversity of parasitoids and our results regarding how the number of parasitized larvae increased with parasitoid richness enable us to interpret top-down forces exerted by diversity of parasitoids related with a better provision of pest control (Hassell, 2000; Finke and Snyder, 2008; Peralta et al., 2014). In other orchards, the lack of a high functional diversity of parasitoids, for instance, parastisim of different codling moth stage, revealed an insufficient and incomplete biological control of this pest by parasitoids (Walker et al., 2017).

Finally, we observed that the number of parasitized larvae increased with higher abundances of codling moth. Therefore our results allow us to infer possible bottom-up effects on number of parasitized larvae by CM abundance. Such relationship is not surprising given that parasitoids are very sensitive to host population changes because of their small population sizes and the high dependence on host abundance (Hassell, 2000). We also infer that higher abundances of codling moth would be able to increase the number of parasitized larvae due to there is more availability of hosts. However, in many parasitoid-host relations, parasitism reaches a plateau as the host abundance increases (saturating functional response; Holling, 1965; Umbanhowar et al., 2003), in our case we did not appreciate this decelerating parasitoid response.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

To improve the success of codling moth biological control by parasitoids in apple orchards we recommend: at landscape level, more distance between low-input orchards should be promoted to prevent the colonization of the codling moth because large areas of apple plantations attract and spread them. However, higher density of conventional orchards can be promoted due to the intensity of conventional treatments that affect the surrounding orchards (Monteiro et al., 2013). At orchard level, management strategies to control the codling moth should be implemented effectively every year since codling moth is positively related with fruit resources availability. Years of high production codling moth can increase their numbers of overwintering larvae for the next year, when it will be more harmful in proportion to the apple production. However, years of low production force codling moth to look for other orchards to lay their eggs, dispersing the pest and increasing their populations in other orchards. Bottom-up effects on codling moth abundance and damage by the availability of food resources in low-input cider orchards are key factor for successfull management strategies.

Despite the high levels of codling moth in low-input cider apple orchards, this study has proved the parasitoid capacity as natural enemies of codling moth. Although they do not protect the fruit the same year they emerge, in certain trees they can parasitize 42.5 % of codling moth larvae. Top-down effects by parasitoids regulating codling moth abundance can be enhanced by richer species and more functionally diverse parasitoid communities. However, our results suggest that parasitoids as the only measure to control codling moth is not enough, but their effects can help to regulate CM populations in low-input apple orchards. The combination between parasitoids and other codling moths natural enemies promotion with several control strategies at different spatial scales (e.g. trapping of diapausing larvae, use of mating disruption and post-harvest recovery of attacked fruit) (Judd et al., 2005), may enhance the biological control of this important insect pest in the long term. Biological control of codling moth can help to mitigate the negative consequences of agricultural intensification on diversity and ecosystem services. We suggest that parasitoid enhancement should be included in new agri-environment schemes for a more sustainable farming, taking into account population fluctuations (parasitoids and their hosts) across orchards and time.

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Chapter 3

Farmers' perceptions and knowledge of natural enemies as providers of biological control in cider apple orchards

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ABSTRACT

While the importance of biological control for crop production is widely acknowledged, research on how farmers perceive on-farm natural enemies remains scarce. This paper examines cider apple farmers' perceptions and knowledge of the concept of biological control and the specific organisms underpinning its provision (i.e. natural enemies) in the cider apple orchards of Asturias (N Spain). Although these orchards host a high diversity of natural enemies, certain pests continue to be a problem, e.g. the codling moth and the fossorial water vole. By conducting 90 face-to-face surveys, we found that farmers "under-estimated" the importance of biological control and the role played by natural enemies in suppressing pests from cider apple orchards. Furthermore, farmers were particularly unaware of the indirect benefits of biological control, such as the increased quality and yield of product. Farmers also perceived that different taxa of natural enemies contribute to biological control to differing extents, for example, birds, such as buzzard, robin and tit, were perceived as the most important natural enemies, while arachnids and insects (excluding ladybug) were perceived as less important. This perceived difference in the biological control contribution of vertebrates and invertebrates could be influenced by farmers' local knowledge, acquired on-farm through daily experiences, as well as from external sources. In addition, we found that farmers did recognize many interactions between natural enemies and pests, although there were serious misconceptions and knowledge gaps. Finally, we revealed that education level, being a full-or part time farmer rather than a 'hobby' farmer, time spent working in agriculture, and orchard size are all factors that positively influence farmer's perception of natural enemies. Our results provide insights for a future management of cider apple orchards which promotes biological control through: (1) creating initiatives to develop farmers' knowledge regarding biological control and natural enemies, (2) fostering traditional farming systems that contribute to preserving local ecological knowledge of biological control, and (3) establishing networks of farmers so they can learn from each other and share local knowledge.

INTRODUCTION

Crop production depends on several regulating ecosystem services, such as pollination (Garibaldi et al., 2011), biological control (Bommarco et al., 2013) and the maintenance of soil fertility (Zandbergen et al., 2017). However, despite their importance, these regulating services, in particular biological control, have been underexplored in ecosystem service research pertaining to agroecosystems (Nieto-Romero et al., 2014; Fagerholm et al., 2016). Biological control is understood as the reduction of one organism population by another one (Cock et al., 2010). Van Lenteren et al. (2018) described four types of biological control: natural, conservation, classical, and augmentative. In this paper, we focus on natural biological control (*hereafter* biological control) because this refers to those situations whereby naturally occurring beneficial organisms reduce the occurrence of pest organisms without any human intervention.

Biological control is an efficient, profitable and sustainable alternative to chemical means of pest control to reduce crop losses (Bale et al., 2007; Bommarco et al., 2013; Losey and Vaughan, 2006). At the farm-level, biological control not only reduces pest outbreaks, but also has a positive economic impact (Naranjo et al., 2015). In addition, it leads to other positive social-ecological outcomes, such as reducing human health risks (Sarwar, 2015) and conserving biodiversity (Boatman et al., 2007; Gibbs et al., 2009; Isenring, 2010). As such, biological control has been extensively promoted over the past decade, yet its farm-level adoption is slow and hampered by multiple factors (Hajek and Eilenberg, 2018). In fact, biological control is decreasing worldwide (MA, 2005; IPBES, 2018) because of the impact of several drivers, such as land-use change (Chaplin-Kramer et al., 2011; Rusch et al., 2016), climate change (Oliver et al., 2015) and the intensification of farming systems (Emmerson et al., 2016).

A wide range of organisms deliver ecological functions to provide biological control including insectivorous birds (García et al., 2018), bats (Puig-Montserrat et al., 2015), ladybugs (Jacobsen et al., 2019), spiders (Happe et al., 2019; Hong-xing et al., 2017), anthocorids (Jacobsen et al., 2016), nematodes (Nermut' et al., 2019), parasitoids

(Hong-xing et al., 2017) and microorganisms (Van Lenteren et al., 2018). Increasing on-farm biodiversity of natural enemies is known to enhance biological control (Dainese et al., 2019; Gurr et al., 2003; Ives et al., 2000; Wilby and Thomas, 2002). For example, a greater richness and abundance of natural enemies ensures more mechanisms by which different prey are consumed across environments and over time (Letourneau et al., 2009; Tscharntke et al., 2005; Vance-Chalcraft et al., 2007). However, the uneven effectiveness of natural enemies for pest suppression does need to be taken into account (Greenstone et al., 2010; Loreau et al., 2001; Straub and Snyder, 2006). For example, the spined soldier bug (*Podisus maculiventris*) preys more on Colorado potato beetle (*Leptinotarsa decemlineata*) than other predators (Greenstone et al., 2010).

Although there is considerable ecological research on the organisms underpinning biological control (Chaplin-Kramer et al., 2011), little social research on perceptions of biological control and the organisms involved has been conducted (Rawluk and Saunders, 2019). Farmers' agro-ecological knowledge of biological control and their perceptions of the contribution on-farm biodiversity makes to pest control have, for example, been routinely overlooked. Most studies have, instead, focused on the motivation and attitude of farmers who adopt biological control measures (Abdollahzadeh et al., 2016; Goldberger and Lehrer, 2016). Others have focused more generally on the farmers' perceptions of pesticide use, insects as natural enemies (Wyckhuys et al., 2019), pests (Sekamatte and Okwakol, 2007; Van Mele et al., 2009) and pest management (Midega et al., 2016; Morales, 2002; Okonya and Kroschel, 2016).

Understanding farmers' perceptions of biological control can shed light on their motivation to apply, or not, farming practices that support natural enemies (Abdollahzadeh et al., 2016). In turn, this information impacts on any potential implementation of sustainable management practices and informs policy-makers about what is required to support and encourage farmers in the uptake of such practices (Savary et al., 2017). This is particularly relevant in the European context, where the Common Agriculture Policy (CAP) advocates agri-environment schemes through which farmers support biodiversity and biological control (Bengtsson et al., 2005; Van Buskirk and Willi, 2004).

The main objective of this paper is to examine farmers' perceptions and knowledge of the biodiversity underpinning biological control in cider apple orchards in Asturias (N Spain), specifically: (1) the importance they consider biological control to have, for croplands in general as well as for their own orchards; (2) their ability to recognize various natural enemies and their knowledge of the degree to which each contributes to pest control in their own cider apple orchards; and (3) their knowledge of the specific interactions between natural enemies and pests. In addition, (4) we assess whether there is a relationship between farmers' perceptions and knowledge of natural enemies as providers of biological control and, certain farming and socio-economic characteristics of the farmers themselves.

The remainder of the manuscript is organized as follows: The second section describes the characteristics of the cider apple region in Asturias, including relevant pests and pest control practices commonly in use. Section three describes the data collection and analysis procedures. The results in relation to each aim of the research are in section four, while section five describes farmers' perceptions and knowledge about the importance of biological control, natural enemies and their interactions with pests and the farming and socio-economic characteristics behind these perceptions. Also in this section, we suggest ways to enhance farmers' understanding of the importance of natural enemies. The concluding section provides insights for the management of cider apple orchards in order to promote biological control.

OVERVIEW OF CIDER APPLE ORCHARDS

The research was conducted in the cider apple region of Asturias (N Spain) (**Fig. 1**), across six municipalities (Colunga, Nava, Sariego, Siero, Villaviciosa and the rural areas of Gijón). Asturias, with its extensive and semi-extensive orchards, is the most productive region of cider apple (*Malus x domestica* Borkh) in Spain, the crop covering 4131 out of the total 8245 ha that comprise the region (INE, 2018). Orchards are relatively small, between 0.5 and 2.0 ha, surrounded by hedgerows and embedded in a traditional landscape mosaic of multiple land-uses (e.g. livestock pastures, eucalyptus plantations, natural forests): an optimal system for preserving beneficial animals for pollination and biological control (Miñarro and Prida, 2013; García et al., 2018).

The management of Asturian cider apple orchards remains to a great extent traditional (Dapena and Fernández-Ceballos, 2007), although cultivars have been locally and historically selected to tolerate common apple diseases (scab, canker and powdery mildew) (Dapena and Blázquez, 2009). The most detrimental and economically important pests are the fossorial water vole (*Arvicola scherman*), which attacks the roots and may cause tree death (Somoano et al., 2017), and the codling moth (*Cydia pomonella*), which damages the fruit (Peisley et al., 2016). Other pests of note are the apple aphid (e.g. *Dysaphis plantaginea*, *Aphis* spp.), which harms young shoots (Miñarro et al., 2010), and the apple blossom weevil (*Anthonomus pomorum*), which damages blossom (Miñarro and García, 2018). Within the six municipalities selected, only 51% of farmers use pesticides, and this only when they consider it necessary, treatment generally consisting of spraying diflubenzuron against codling moth (*own data, not shown*).

Much pest control in Asturian cider apple orchards, then, relies on natural enemies. Previous research has demonstrated the importance of birds (e.g. tits, thrushes, robin, woodpeckers) for biological control in the region (García et al., 2018), as well as the essential roles played by birds of prey (e.g. buzzard, owls), carnivorous mammals (e.g. mustelids), a wide variety of insects (e.g. ladybug, earwig, hoverflies) and arachnids (spiders) (Miñarro et al., 2011).

The Asturian region is sparsely populated. The six municipalities selected have a total rural population of 103,115 inhabitants, with an average population density of 4.1 inhabitants per hectare. Fifty-nine per cent of the population is aged between 25 and 65, 21.0% is over 65 and 20.0% below 25. The active population in the area is principally employed in service industries (12.9%), manufacturing and building (7.9%), tourism (3.8%) or agriculture (2.5%). Tourism related to cider apple orchards, cider production and the cider culture and its gastronomy is becoming increasingly important economically (INE, 2018).

MATERIAL AND METHODS

Data collection

Between January and July 2018, we conducted 90 face-to-face surveys with cider apple farmers over 18 years of age, randomly selected from across the 6 municipalities of the study area. The sample size is representative of the rural population in the region (see above) at the 95% level, with a sampling error < 10%. Surveys were carried out either in quiet public spaces or in farmers' own orchards. We pre-tested the questionnaire with six other farmers ensure all questions were understood by respondents.

The final questionnaire had four sections, each linked to a specific aim of this research: (1) farmers' perceptions of the importance of biological control for croplands in general (*hereafter* croplands) and their own cider apple orchard(s) specifically. This was based on a set of open and closed questions; (2) farmers' knowledge of organisms that act as natural enemies in cider apple orchards. This was ascertained through farmers' responses to a table asking if they had ever sighted (at any time in the area), knew about (were aware through local hearsay, folk culture, information provided publically or on courses, or their own search for information) or recognized as a natural enemy 14 taxa, each of which was illustrated with an image of a representative species. Only ten of the taxa are known natural enemies in the area (García et al., 2018; Miñarro et al., 2011) (**Table B1**); (3) farmers' perceptions on the interactions between natural enemies and pests in cider apple orchards, based on ratings of importance for the ten known local natural enemies, and on direct questions relating to which natural enemies controlled a list of local pests in cider apple orchards; and (4) farming and socio-economic details of the respondent elicited through direct questions. The complete questionnaire can be found in Appendix A.

Data analyses

First, we conducted descriptive analyses to assess the importance farmers consider biological control to have, for croplands in general as well as for their own orchards. For this, farmers' responses were classified according to whether they spoke about direct benefits resulting from biological control (e.g. elimination of pests) or indirect benefits (such as increased yield or quality) benefits. In addition, descriptive analyses were also conducted to determine the percentage of farmers that had sighted, knew about and recognized the different taxa they were asked about in the questionnaire as natural enemies.

Second, to measure the importance farmers ascribed to each taxon in terms of providing biological control, we created a *biological control index,* a measure of the average capacity of a particular natural enemy to provide biological control as perceived by farmers. Then, we conducted Spearman's correlation tests to ascertain whether there was a relationship between each species' rating in the *biological control index* and the percentage of farmers that had sighted it, knew what it was and/or recognized it as natural enemy.

Third, we estimated the contribution of each taxon to biological control according to farmers' perceptions of pest-natural enemy interactions using network analysis. In the network, nodes represent pests and natural enemies. For natural enemies, we calculated (1) the weighted degree, i.e. the number of relationships between two nodes weighted by the size of the edges (Borgatti and Everett, 1997) and (2) the betweenness, i.e. how many times a node relates to other nodes to which it would otherwise not be connected (Freeman, 1978; Scott et al., 1996). We used Gephi software to create the networks (Bastian et al., 2009) and NodeXL for their visualization (Smith et al., 2010). To test the association between farmers' perceptions of the importance of each natural enemy and their perceptions of interaction between natural enemies and pests, we conducted Spearman's correlations between the *biological control index* and the weighted degree and betweenness. All Spearman's correlation tests were performed with the 'cor.test' function in the 'stats' (version 3.3.2) package, using the statistical software R version 3.3.3 (www.r-project.org).

Fourth, to analyze what effect the farming and socio-economic characteristics of the respondents had on their perception of natural enemies as providers of biological control, we used generalized linear models (GLMs) and redundancy analysis (RDA).

Table 1 shows the explanatory variables used in the two analyses. To conduct the GLM, we created the dependent variable *Natural enemy awareness*, a measure of the number of taxa farmers correctly recognized as natural enemies in their own cider apple orchards. We performed a stepwise-forward regression procedure to identify the best model according to Akaike (Zhang, 2016). We used the 'glm' function in the package 'stats' (version 3.3.2).

Table 1. Description of farming and socio-economic variables. (Y = Yes; N = No; nl = natural logarithm).

Farming and socio-economic variables	Description
Full-time farmer	Works full time, only in agriculture (Y/N)
Part-time farmer	Also has another job not related to agriculture (Y/N)
Farms for leisure and tradition	Cultivates apples for tradition and hobby reasons (Y/N)
Time working in agriculture	Years spent working in aspects of agriculture (nl)
Home-gardener	Cultivates fruit and vegetables for self-supply (Y/N)
Market for produce	Destination of the harvest: mass marketing, local scale, self-supply (rank 1 to 3)
Orchard size	Orchard area in hectares (nl)
Education level	Educational qualifications achieved by farmers (rank 1 to 5)
Membership of association	Membership of association or organization of agriculture nature (Y/N)
Herbicide use	Under trees (some farmers) or in the whole orchard (Y/N)
Insecticide use	Use of insecticides to control various pests (Y/N)
Use of chemical fertilizers	Use of chemical fertilizers to improve yield (at least once a year) (Y/N)

The RDA examined the relationships between the *biological control index* estimated for all natural enemies (dependent variables) and farming and socio-economic characteristics (explanatory variables; see **Table 1**). To find the best model, we used automatic stepwise model building based on permutation tests (Blanchet et al., 2008). Two variables were omitted: (1) *membership of an association* and (2) *use of chemical fertilizers*. The significance of the RDA was tested with a Monte Carlo permutation test (999 iterations). The RDA was performed with the 'rda' function in the package 'vegan' (version 2.4-2).

Before applying both the GLM and the RDA we tested for linear dependencies among the explanatory variables using the variance inflation factors (VIF) (Belsley, 1991). To avoid heteroscedasticity, we log-transformed the continuous explanatory variables (*time working in agriculture* and *orchard size*).

RESULTS

Importance of biological control and natural enemies

Most farmers (90%) considered natural enemies important for croplands, while only 55.6% of farmers considered them important for their own cider apple orchards. The most important benefits of natural enemies were considered to be that they killed pests and were an alternative to pesticides, both of them direct benefits. Some indirect benefits were, however, also mentioned by a small number of respondents: to improve crop quality, to increase yield and that they were essential for production (**Fig. 2**).

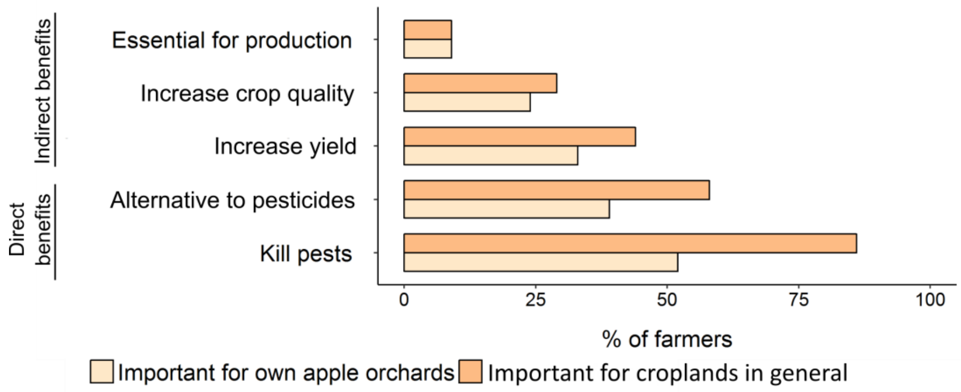

Figure 2. Benefits of natural enemies identified by farmers for croplands in general and in their own cider apple orchards.

The percentage of natural enemy taxa that farmers had seen was higher than the percentage they knew about or recognized as natural enemies (94.3%, 88.7% and 57.7% of farmers, respectively). Earwig (*Forficula auricularia*) was the taxon that farmers had seen least in their orchards (77.8%) and hoverfly, tit and earwig were those farmers least knew about (17.8%. 64.4% and 66.7%, respectively). Earwig and hoverfly were also the least recognized natural enemies (12.2% and 7.8% respectively). By contrast, the ladybug (*Coccinella septempunctata*) and the vertebrates were the most recognized natural enemies (ranging from 61.1% to 93.3%). Interestingly, all taxa that are not natural enemies, except the land slug (*Arion ater*), were mistakenly identified by some farmers as natural enemies: stag beetle (*Lucanus cervus*) (by 12.2%), bumblebee (*Bombus terrestris*) (7.8%) and magpie (*Pica pica*) (24.4%) (**Fig. 3**). Finally, 37.8% of farmers also named other species they considered important for biological control: 26.0% mentioned nocturnal raptors (e.g. *Tyto alba*, *Strix aluco*, *Athene noctua*) and bats, and 13.3% mentioned various other mammals (e.g. *Mustela nivalis, Mustela erminea, Martes martes/foina, Meles meles* and *Erinaceus europaeus*) (**Fig. 3**).

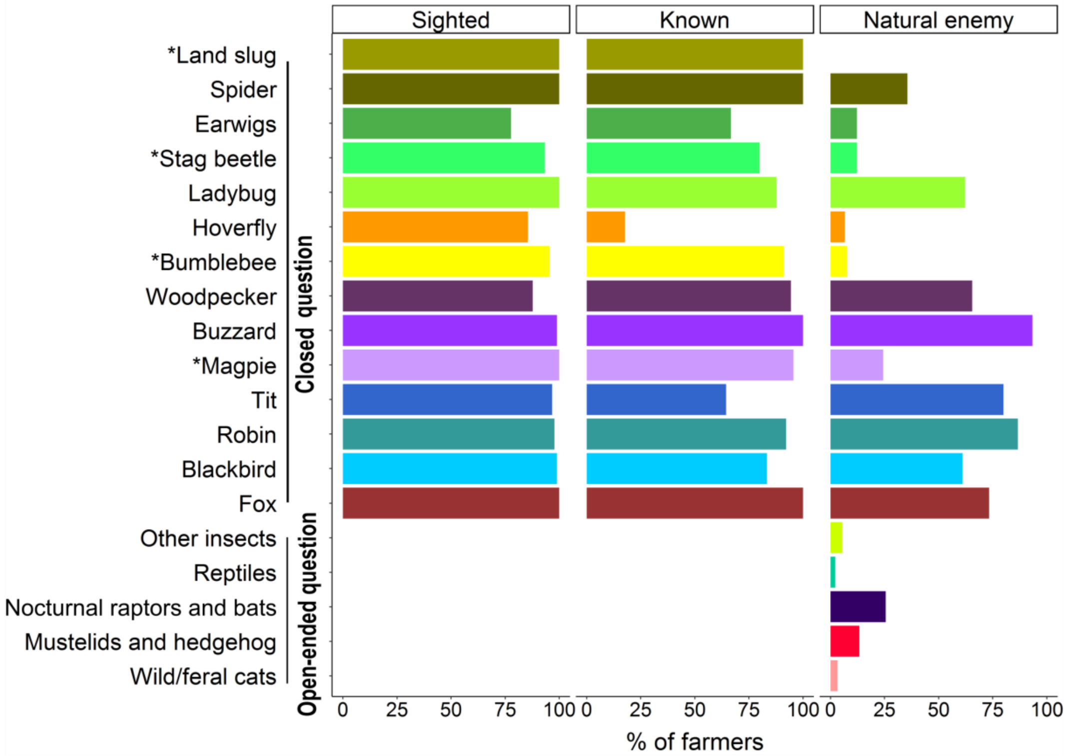

Figure 3. Bar diagram representing, above, the percentage of farmers that had seen and/or knew about each taxon and/or considered it to be a natural enemy (information from closed question) and, below, other taxa mentioned as being natural enemies (open-ended question). The different colors and shades indicate taxonomic affinity: olive green – Gastropods; dark olive green – Arachnids; shades of bright green, orange and yellow – Insects; shades of blue – Birds; shades of reds- Mammals. * indicates a taxon that is not actually a natural enemy.

Perceptions of natural enemies as providers of biological control

Birds (except blackbird and woodpecker) and ladybug were the natural enemies with the highest *biological control index.* By contrast, hoverfly, earwig and spider had the lowest (**Fig. 4**). Whilst *biological control index* of a taxon was not correlated with the percentage of farmers who had seen it (*Spearman's rho* = 0.375, p = 0.288; **Fig. 4a**) or knew about it (*Spearman's rho* = 0.313, p = 0.381; **Fig. 4b**), it was, however, significantly positively correlated with the percentage of farmers who recognized it as a natural enemy (*Spearman's rho* = 0.927, $p < 0.001$; **Fig. 4c**).

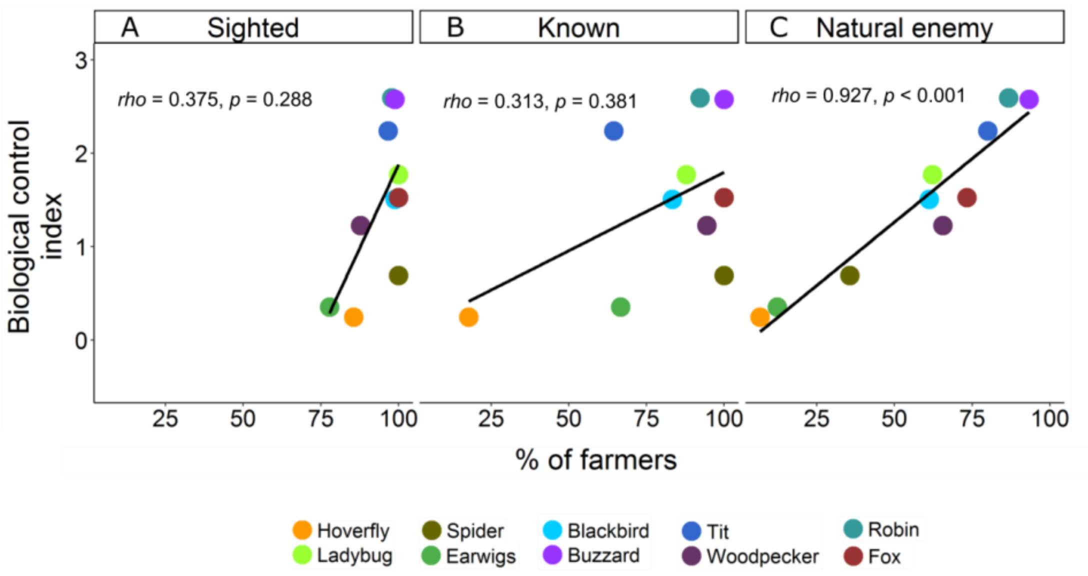

Figure 4. Correlations between *biological control index* (i.e. perceived importance of natural enemy as biological control) and percentage of farmers that (A) had seen and/or (B) knew of the taxon and (C) considered it a natural enemy.

The network in **Fig. 5** shows that farmers perceived a high number of connections between natural enemies and pests. Based on the network, farmers perceived the robin (*Erithacus rubecula*), tit, buzzard and ladybug as the most important natural enemies and the fossorial water vole, rosy apple aphid, green aphid and woolly apple aphid as the most serious pests (**Fig. 5a**, **Table B2** for more details). A clique comprised of two natural enemies -buzzard and fox (*Vulpes vulpes*) - and two pests - fossorial water vole and roe deer (*Capreolus capreolus*) is also evident. In addition, we found that farmers perceived trophic interactions that do not in fact exist, such as between magpie, blackbird or woodpecker and several invertebrate pests (e.g. aphids, green weevil and blossom weevil) (**Fig. 5a**).

The taxa with the highest weighted degrees were robin and tit, while buzzard and tit had the highest betweenness (**Fig. 5b** and **c**). We found significant correlations between the weighted degree and betweenness and *biological control index* (Weighted degree: *Spearman's rho* = 0.818, p = 0.007; Betweenness: *Spearman's rho* = 0.790, p = 0.006; **Fig. 5b** and **c**).

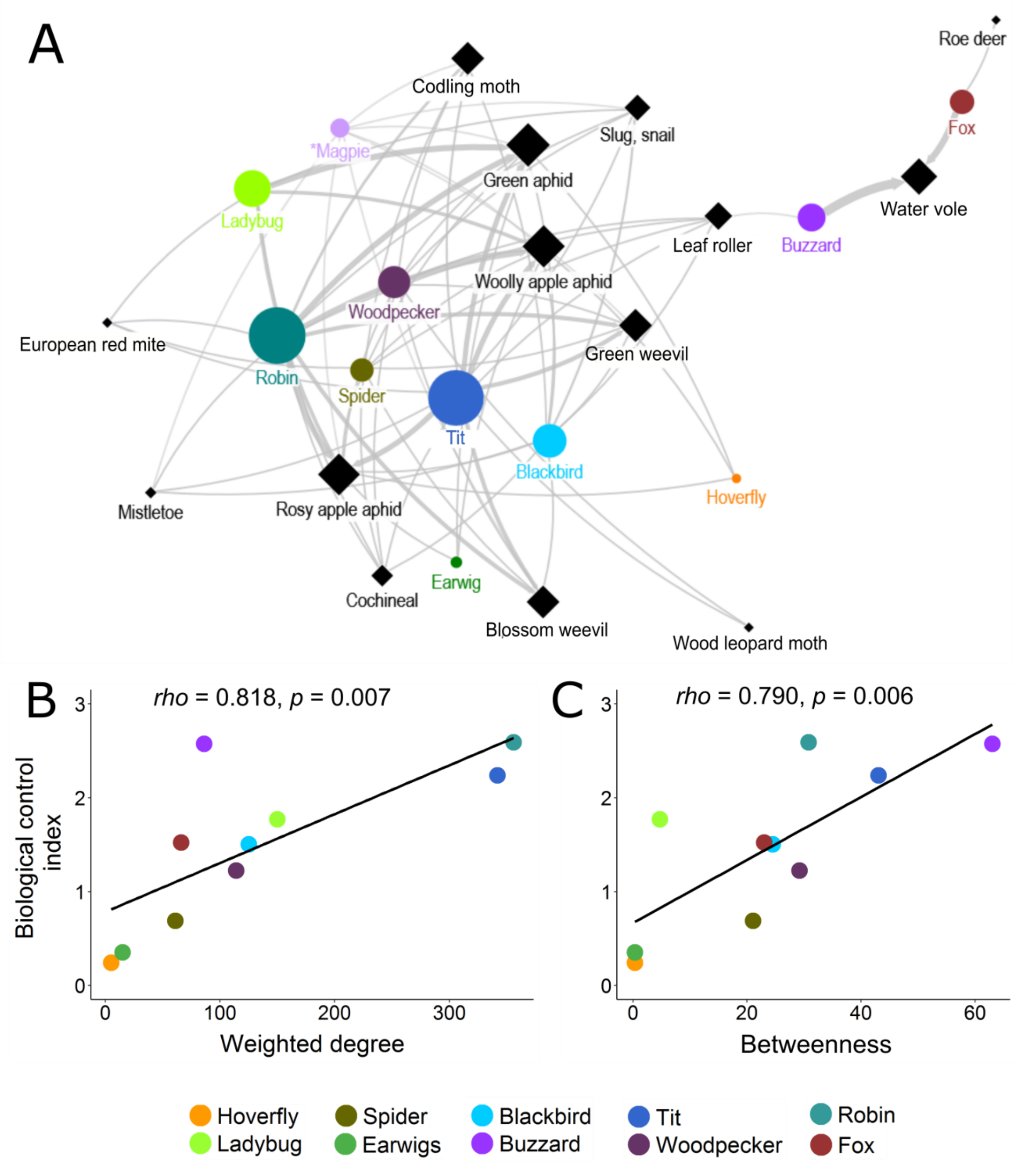

Figure 5. (A) Network created from farmers' perceptions of the contribution of different natural enemies to pest control (circles represent natural enemies, diamonds represent different pests; the size of the node represents the weighted degree; the line width is proportional to the number of farmers that mentioned the predation relationship). (B and C) Correlations between the *biological control index* of each taxon and (B) weighted degree and (C) betweenness of nodes (i.e. natural enemies) calculated from network analysis.

Farming and socio-economic characteristics

Natural enemy awareness was significantly affected by the farming and socio-economic characteristics of the farmers surveyed (F = 8.557, p < 0.001) (**Table 2**). *Education level*, *time working in agriculture* and *being a full- or part time farmer* had a positive effect on *natural enemy awareness* (**Table 2**).

Table 2 Results of the multivariate regression analysis of farmers' *Natural enemy awareness*.

	Full model		**Reduced model**	
Variables	Coefficient + (SD)	Significance	Coefficient + (SD)	Significance
Full-time farming	0.402 (0.161)	0.015	0.464 (-0.137)	0.001
Part-time farming	0.281 (0.111)	0.013	0.346 (0.1)	0.001
Time working in agriculture	0.119 (0.075)	0.118	0.179 (0.069)	0.011
Education level	0.123 (0.0334)	< 0.001	0.131 (0.029)	< 0.001
Insecticide use	-0.171 (0.104)	0.102	-0.158 (0.091)	0.084
Farms for leisure and tradition	0.231 (0.131)	0.082		
Home-gardener	0.001 (0.109)	0.994		
Market for produce	0.03 (0.075)	0.685		
Orchard size	0.093 (0.072)	0.2		
Membership of association	0.057 (0.099)	0.568		
Herbicide use	0.103 (0.105)	0.33		
Use of chemical fertilizers	-0.159 (0.102)	0.123		
R^2	0.388		0.337	
Adjusted R^2	0.292		0.298	
F	4.060	< 0.001	8.557	< 0.001
AIC	112.933		106.001	

The RDA showed statistically significant associations between farming and socio-economic characteristics and *biological control index* (p = 0.007, from 999 permutations). The first two axes explained 61.6% of the total variance (**Table 3**). The first RDA axis (34.9% of the variance) showed an association between the *biological control index* of tit, robin, ladybug, spider, earwig and fox (in the positive scores) and working in larger orchards and using herbicides. The second axis (26.7% of the variance) represented in its positive scores the association between the *biological control index* of robin with part-time farmers who have worked for longer periods in agriculture. The negative scores of the second axis represent an association between the *biological control index* of blackbird, woodpecker, buzzard and hoverflies with farmers working in larger orchards (**Table 3**).

Table 3 Results of the redundancy analysis showing the influence of farming and socio-economic characteristics on *biological control index* estimated for different taxa perceived as natural enemies by farmers. Explanatory variables with a *p*-value <0.05 after stepwise model building are in bold.

Dependent variables	**Axis 1**	**Axis 2**
Tit	**0.631**	0.278
Blackbird	0.275	**-0.434**
Woodpecker	0.198	**-0.397**
Robin	**0.607**	**0.599**
Buzzard	0.289	**-0.452**
Ladybug	**0.482**	-0.245
Hoverfly	0.079	**-0.081**
Spider	**0.309**	-0.078
Earwig	**0.184**	-0.034
Fox	**0.310**	-0.181
Explanatory variables		
Full-time farming	0.187	0.001
Part-time farming	0.014	**0.077**
Farming for leisure and tradition	-0.106	0.239
Time working in agriculture	-0.076	**0.261**
Home-gardener	-0.202	0.009
Market for produce	0.176	-0.009
Orchard size	**0.331**	**-0.206**
Education level	0.268	-0.134
Herbicide use	**0.329**	0.135
Insecticide use	0.007	-0.091
RDA statistics		
Eigenvalue	0.420	0.321
Variance explained (%)	34.910	26.714
Cumulative variance (%)	34.910	61.624

DISCUSSION

In this study we characterized farmers' perceptions and knowledge of different natural enemies and the contributions each makes to biological control in Asturian cider apple orchards. These cider apple orchards are extensive or semi-extensive agroecosystems where various taxa contribute to biological control (i.e. insects, arachnids, birds, mammals; Miñarro et al., 2011). However, the results of the survey showed that farmers considered biological control to be less important in cider apple orchards than in croplands in general (**Fig. 2**). This difference might be explained by the fact that for cider production, a degree of damage to the apples is permissible, meaning that farmers tolerate a greater level of pests in apple orchards than they would tolerate (or would expect others to) in other crop production systems. In addition, not all cider production in this region is professionalized and home production and consumption is common. A similar tolerance for pests was found by Morales and Perfecto (2000), who concluded that some farmers do not consider insects as a pest until the damage they cause results in economic loss. Nevertheless, awareness of biological control in cider apple farmers is higher than in many of those working with other crops around the world given that nearly 70% of farmers worldwide have no knowledge of the concept (Wyckhuys et al., 2019).

We found that a higher number of farmers perceived the direct benefits (i.e. kill pests and alternative to pesticides) of natural enemies than the indirect benefits (i.e. increase yield and improve quality) (**Fig. 2**). This might lead to an underestimation of the role of natural enemies for biological control in orchards and their contribution to cider production. Previous research has found that an increased awareness of the benefits derived from ecosystem services can contribute to enhancing biodiversity conservation (Bennett, 2016). Future campaigns from government agencies, training providers and farming associations should promote farmers' awareness of the benefits, both direct and indirect, provided by natural enemies in cider apple orchards.

We found that the recognition of animals as natural enemies varies across taxonomic groups (i.e. birds, mammals, insects, arachnids). While farmers easily recognized birds and mammals as natural enemies, arachnids and insects were poorly recognized (with the exception of the ladybug) (**Fig. 3**). This is in line with previous research that found that vertebrates are easier to observe than invertebrates (Martín-López et al., 2007; Willemen et al., 2015), which is due not only to body size but also to the former's greater capacity for movement (Tscharntke et al., 2008). For example, birds spill-over into crop fields from surrounding habitat patches and vice versa, often using orchards for several resources (i.e. nesting, feeding, protection) (García et al., 2018). Some vertebrates are also easily recognized because they are part of the local folk culture (Berlin, 1992), meaning knowledge of on-farm animals is probably shaped not only by the conspicuousness of the animal itself, but also by farmers' cultural knowledge (Bentley and Rodríguez, 2001; Bentley and Baker, 2005). However, in fact, in this work recognition of a taxon as a good natural enemy was not correlated with having seen or knowing about the creature involved, but rather with farmers' knowledge and ability to recognize it as a provider of biological control (**Fig. 4**). This supports previous research on perceptions of regulating services provided by scavengers (Morales-Reyes et al., 2018).

In addition, we found that within each large taxonomic group, identification of the individual taxa as natural enemies varied considerably. For instance, whilst robin and tit were recognized as very important natural enemies, the importance given to woodpecker was much less (**Fig. 4**). These differences could be explained by farmers' daily interactions with biodiversity in cider apple orchards and their local ecological knowledge. First, farmers probably notice those natural enemies that are more abundant and thus more visible (Okonya and Kroschel, 2016; Wyckhuys and O'Neil, 2007). For example, robin and tit were frequently recognized and well valued as natural enemies, and, in fact, these are the most abundant species in these cider apple orchards (García et al., 2018). In addition, abundant species tend to contribute more to the provision of a particular ecosystem service than rare species (Díaz et al., 2011; Winfree et al., 2015).

In addition to the effect of certain traits of an animal (e.g. body size or abundance) on farmers' perceptions of organisms as natural enemies within the orchard, knowledge acquired from external sources, such as scientific outreach, newspaper coverage, and social media, may also have an effect. For example, an outreach campaign by García et al. (2018), which included seminars for apple farmers and articles in the press, might have contributed to raising awareness of the importance of insectivorous birds as providers of biological control. In addition, certain species are more likely to feature in press coverage on biological control and this may well affect farmers' perceptions. For example, ladybug appears more often in magazine articles related to biological control than other invertebrates (Riddick, 2017), and since 'people care about what they know' (Balmford et al., 2002, pp. 2367), this may explain why we found that ladybug was more often recognized as a natural enemy than other invertebrates. Newspaper and media coverage is also known to impact on public perceptions of biodiversity and the social acceptance of wildlife (Schakner et al., 2019; Fernández-Gil et al., 2016), and the higher likelihood of vertebrates rather than invertebrates featuring in news coverage and social media (Kidd et al., 2018; Willemen et al., 2015) might also play its part in explaining our results. Reassuringly, some authors have identified ways of enhancing farmers' knowledge of biological control by using external sources and channels of communication: digital apps (Van Mele et al., 2018), outreach videos (Bentley et al., 2019), and participatory and transdisciplinary research approaches (Šūmane et al., 2018).

The results of this work show that Asturian apple farmers have a complex understanding of the interactions between natural enemies and pests (**Fig. 5a**). Those taxa perceived as more important for biological control also had higher weighted degree and betweenness (**Fig. 5b** and **c**). For example, the robin and the tit were identified as important natural enemies and were considered to prey on many pests. This is in accordance with research demonstrating that both species are generalist natural enemies (Ceia and Ramos, 2016). The buzzard, on the other hand, while considered by the respondents to be important for biological control, had low weighted degree but the highest betweenness. This may be because the farmers knew that the buzzard preyed on fossorial water vole, which is the most serious and well-known pest in local apple folk culture (**Table B2**), but mistakenly thought that it also predates leaf roller, resulting in its high betweenness value and it connecting the clique comprised by mammals with the main network (**Fig. 5**). Farmers also "over-estimated" the biological control capabilities of certain organisms: for example, blackbird and woodpecker preying on aphids and magpie preying on various arthropods. However, at the same time they also "under-estimated" the potential of specific taxa: for example, earwig and spider are perceived to predate on a limited number of pests despite them being generalists (Cross et al., 2015) and hoverfly is not perceived as a natural enemy by farmers. Both cases show that farmers critically misunderstand the role of those organisms for biological control.

Furthermore, we found that farming and socio-economic characteristics also influence farmers' perception of and knowledge about biological control and natural enemies. Time spent in agriculture and working full- or part time in farming increased the number of taxa correctly identified as natural enemies (**Table 1**). This is in line with other works where farming experience has been identified as key to the local ecological knowledge required for sustainable agricultural practices (Gómez-Baggethun et al., 2010; Iniesta-Arandia et al., 2015; Oteros-Rozas et al., 2013), and those investigating farmers' knowledge of ecosystem services in Spain (Morales-Reyes et al., 2018, 2019). In addition, we found that farmers with higher educational qualifications correctly identified more taxa as natural enemies (Caballero-Serrano et al., 2017; Lewan and Soderqvist, 2002; Martín-López et al., 2012), confirming the findings of Wyckhuys and O'Neil (2007) that to improve farmers' knowledge of natural enemies, environmental education programs are essential.

Finally, our results also support the idea that both knowledge systems, formal and local ecological knowledge, are important for building perceptions of natural enemies (**Table 2**). For example, owners of larger orchards who used herbicides correctly identified a wider variety of taxa as providers of biological control. Assuming that owning bigger orchards means the farmers are more likely to work full- or part time on the land, rather than, for example, seeing it as a hobby, they most likely have acquired considerable knowledge, either formally (courses, trade magazines or workshops) or informally (local ecological knowledge). This might mean that the hybridization between formal and local ecological knowledge might allow farmers to recognize the biological control importance of more species. These results support the recent claims of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystems Services (IPBES) that both types of knowledge need to be addressed in order to support environmental management and biodiversity conservation (Hill et al., 2017; Tengö et al., 2014).

This study shows that the consideration of farmers' perceptions and knowledge in scientific research of natural enemies can shed light on how farmers engage in actions to foster biodiversity conservation and sustainable food production in agroecosystems (Rawluk and Saunders, 2019). Yet, this study has some limitations to achieve the above-mentioned goal since it does not consider other relevant aspects, such as level of empowerment, engagement and trust (Kusnandar et al., 2019). A second limitation is that perceptions are often contextual, they can change and being influenced by different forces (e.g. markets, industries, global trends). In fact, perceptions are often dismissed in conservation and environmental management because they are considered inaccurate place-based "experiential knowledge" (Bennett, 2016). Yet, we argue that studies about farmers' perceptions can provide important insights of understandings and interpretations of ecosystem services and the ways by which biodiversity provide them. In addition, studies about farmers' perceptions can contribute to understand how to promote acceptability of environmental management (Bennett, 2016). To overcome the limitations posed by the research of perceptions, future studies should also research other social components, such as attitudes, behaviour, norms and governance (Bennett et al., 2017). In the context of the EU Common Agricultural Policy beyond 2020, it is urgent to understand how farmers interpret ecosystem services, how they are willing to engage in sustainable agricultural practices and how institutions can reinforce sustainable behaviours.

CONCLUSIONS

Asturian cider apple farmers are aware of the importance of natural enemies and biological control for general crop production. However, they "under-estimate" the importance of biological control for their own cider apple orchards. Key benefits provided by natural enemies, such as improving crop quality and increasing yield are not acknowledged by many farmers. Although they clearly had knowledge of many of the taxa that act as natural enemies, we found some important knowledge gaps and misunderstandings. While farmers identified certain taxa (i.e. robin, great tit, buzzard, fox, ladybug) as important for biological control, they also did not recognize other important taxa related to cider apple production (i.e. woodpecker, hoverfly, spider, earwig). Thus it can be seen that prevailing perceptions (farmers' ecological knowledge) are inadequate and insufficient to tackle certain pests (e.g. woolly apple aphids or codling moth) using biological control. Our findings show that those farmers economically dependent on cider apple orchards (working full-or part time in the sector), with higher educational levels and knowledge acquired through working in cider apple orchards recognized a higher number of natural enemies. Although farmers' perceptions of biological control and natural enemies are complex and influenced by multiple factors, our results suggest that their perceptions are shaped by both their local ecological knowledge and external sources. Based on these results and in order to promote biological control in cider apple 9 orchards, we suggest that future actions pertaining to orchard management should take into account improving farmers' knowledge of biological control and natural enemies, particularly for those that are less visible (for example insects) or more difficult to identify. In addition, orchard management practices should promote traditional farming systems that contribute to preserving local ecological knowledge and support the setting up or maintenance of farmer networks through which knowledge regarding biological control can be shared.

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General Discussion

The current agricultural landscape has gone through large changes as a result of land use conversion to agriculture and intensification (Foley et al., 2011). This has led to many negative effects on environment such as loss of soil fertility, habitat destruction, air and land pollution (FAO, 2017). The expansion of food production is one of the main drivers for biodiversity loss (Newbold et al., 2016; MA, 2005).

Biodiversity should be conserved for ethical reasons but also for all the benefits that it provides us. The provision of ecosystem services by biodiversity can decrease the use of chemical and mechanical inputs applied to maintain high crop productivity and profitability. These inputs end up generating negative effects on the environment and human health (Geiger et al., 2010; FAO, 2017). Besides, biodiversity declines in agroecosystems have negative feedbacks for productivity.

The need of more sustainable ways of agriculture is a current urgent goal. As I suggest in this thesis, the solution may partially lie in the biodiversity that we have been destroying. Agriculture is based on biodiversity and it influences biodiversity (Thrupp, 1997; Riffell et al., 2009). The mutual and complex interactions between biodiversity and agricultural production could be the key for a more sustainable agriculture, where preserving biodiversity and the ecosystems are compatible with sufficient and safe food delivery and human well-being. Farmers, stakeholders and researchers expect to discover how to enhance biodiversity for the provision of several ecosystem services simultaneously in a same crop (Bennett et al., 2009; Biggs et al., 2012). After reading this thesis, there is one question that has to be easily answered: Can we maximize pollination and biological control within apple orchards?

Overall, this thesis contributes to the vital need for scientific understanding of the links between landscape structure, local-scale features, biodiversity, and ecosystem services in order to develop management tools that can promote sustainable agriculture based in biodiversity. While numerous conceptual frameworks have been put forward for understanding ecosystem services and implementing this knowledge to improve sustainable agricultural managements (Fahrig et al., 2011; Kremen et al., 2012; Huang et al., 2015), very few have combined the simultaneously study of the links between landscape structure, local-scale features, biodiversity, and several ecosystem services in a same real agroecosystem. Here, we describe the community patterns of insectivorous birds, codling moth parasitoids and wild pollinators as landscape structure and local-scale features varies across 26 low-input cider apple orchards (**Chapter 1 and 2**). Simultaneously we evidence the potential of these animal biodiversity groups for the compatible provision of biological control and pollination (**Chapter 1 and 2**).

Such integrative research on how farming and landscape constrict or foster biodiversity, and on the relationship between biodiversity and ecosystem services is uncommon for specific biodiversity groups and ecosystem services (Tscharntke et al., 2012). However, focusing in these biodiversity groups for the provision of these two key ecosystem services we can reinforce our general knowledge to design more specific and successful management practices in agriculture. However, to ensure a successful implementation of our results, we also performed a participatory study to examine the weaknesses and strengths of farmers regarding their perceptions and knowledge of biological control and natural enemies (**Chapter 3**) and of pollination and pollinator insects (Hevia et al., 2020).

LANDSCAPE AND LOCAL-SCALE DRIVERS OF ANIMAL BIODIVERSITY THAT OPERATE IN CIDER APPLE ORCHARDS

A large number of insectivorous bird, pollinator insect and codling moth parasitoid individuals and species were found in Asturian cider apple orchards. These high local richness were not found in other European studies focus on conventional orchards, but can be found in orchards under environmental-friendly managements (for birds see Bouvier et al., 2011; Myczko et al., 2013, for codling moth parasitoids see Maalouly et al., 2013; Ismail and Albittar, 2015, for pollinator insects see Power and Stout, 2011; Samnegard et al., 2019). Moreover, Asturian cider apple orchards are surrounded by hedgerows and embedded in a traditional landscape mosaic of multiple land-uses, which complement an optimal system for preserving these beneficial organisms (Miñarro and Prida, 2013; García et al., 2018). As we present forward, these species-rich assemblages of birds, pollinators and parasitoids are possible within orchards under specific levels of habitat availability driven by regional land-use and farming management.

In **Chapter 1** insectivorous birds and pollinator insects positively covaried with habitat structural features related to the availability of tree and woody cover at landscape and local-scale. Forests, scattered trees, shrubby hedgerows and apple tree canopy provide shelter against predators, alternative feeding resources, overwintering places and nesting sites (Castro-Caro et al., 2014, Garfinkel and Johnson, 2015; Alomar et al., 2018; Mestre et al., 2018). However, in **Chapter 2,** despite all the studies that prove the tightly relationship between parasitoids and the availability of different habitats and resources at different spatial scales (Landis et al., 2000; Wratten et al., 2012; Molina et al., 2019), we did not find any influence of landscape and local-scale feature on parasitoids - codling moth interactions. We only found effects of proportion of apple plantations (125m radius) on codling moth populations and codling moth damage.

By contrast, we noted that the number of parasitized larvae was positively affected by the abundance of codling moth. Therefore, parasitoid populations are strongly linked to the availability of hosts (food resources). This strong “bottom-up” relationship between the pest and their parasitoids can be the reason for the masking of landscape and local-scale effects (e.g. Ricci et al., 2009; Geiger et al., 2010). Regarding codling moth populations, its abundance was also “bottom-up” determined by apple plantations and fruit production. Thus, we can influence in codling moth populations through changes in the configuration and connectivity of apple plantations.

Unlike pollinator insects or insectivorous birds, parasitoids have very specific requirements. Host species diversity, host stage, host size, host densities, and intraguild predation determine the preferences, specificity and effectiveness of parasitoids (Rezaei et al., 2019). For adult parasitoids, finding host is essential for reproductive purposes. In order to maintain high reproductive success they have to optimize all their behaviours to finding hosts. This means, effectively covering their short-term nutritional needs. Therefore, the specific low-input features of these orchards (i.e. lack of regular and planned chemical treatments against the codling moth, flowers on the ground cover) and the landscape surrounded them, may cause minimal disruption of their host foraging processes. As a consequence, the “bottom-up” relationships between pest and parasitoids would be reinforced. Being the availability of host on annual basis the main drivers of codling moth parasitoids populations in Asturian cider apple orchards.

Therefore, the status of parasitoid hosts should be periodically monitored; otherwise changes at landscape and orchard level to improve parasitoids diversity would probably be a worthless effort.

Nevertheless, our results are in line with other studies that prove the positive effects of semi-natural woody habitats and tree cover on animal communities in crops (Tscharntke et al., Bianchi et al., 2006; 2005; Mestre et al., 2018). Insectivorous bird, pollinator insect and codling moth parasitoid communities are positively affected by low-input cider apple orchard features and the structure of Asturian landscape surrounding the orchards. Insectivorous birds and pollinators were directly favored by the availability of resources in these habitats. However, parasitoids were only favored by the availability of codling moth and codling moth abundance was favored by the availability of apple tree cover and fruit production. Therefore, **Chapter 2** showed us that landscape and local-scale features, understood as the amount and type of habitats, are not the only drivers that should be considered to study certain ecosystem services, such as biological control of specific pests (i.e. codling moth). Interspecific interactions can also determine their population dynamics. Environmentally-friendly managements performed by farmers and agricultural landscapes rich in habitats and different resources may favor the importance of these interactions.

Alternatively, we should be aware that landscape composition, configuration and connectivity were not considered in our studies. The positive effects of semi-natural woody habitats landscape and local-scale features on biodiversity could be also related with these landscape metrics. Regional landscapes composed of diverse not highly anthropized land uses can avoid strong agricultural drivers of biodiversity loss such as habitat loss, fragmentation and alteration (Tscharntke et al., 2005; Newbold et al., 2015; Stanton et al., 2018). For instance, these drivers might disassociate flowering and nesting resources in space and time that can seriously impact bees and parasitoids (Winfree et al., 2009; Kennedy et al., 2013). In North America, these drivers decreased bird abundance, survival and reproduction, sentencing 40% of farmland insectivorous birds to disappear in just twenty years (Stanton et al., 2018). In fact, in European countries has been well established the linkage between agricultural intensification and periods of major avian declines (Newton, 2004).

In this context, low-input agroecosystems can supply quality habitats for biodiversity, but also link different semi-natural habitats across the agricultural landscape (Kennedy et al., 2013; Garibaldi et al., 2017; Mellink et al., 2017). They play an important role supplying essential resources that allow the establishment of biodiversity in the orchards and the movement of biodiversity between other patches of the landscape (Rusch et al., 2010; Kennedy et al., 2013; Mellink et al., 2017). Therefore, insectivorous birds, pollinator insects and codling moth parasitoids conservation will depend on both maintenance of semi-natural habitats at landscape level and on local management practices that favor sustainable orchards.

MANAGEMENT RECOMMENDATIONS AT LANDSCAPE AND LOCAL-SCALE

Finding common management practices which are capable of enhancing simultaneously insectivorous birds and pollinator insects is not an easy task. Besides, in **Chapter 2**, we realized that specific interactions between natural enemies and pests should be also considered, in combinations with landscape and local-scale features, as important drivers of biodiversity. Insectivorous birds compared with pollinator insects and codling moth parasitoids are very different animal groups, with different movement capacities, behaviours or diets. Therefore, due to the fact that insectivorous birds inhabit very different ecological niches, we assumed that find common points in their resources requirements at small scales would be hard. More specific management practices at local-scale level should be found to effectively promote simultaneously insectivorous birds, pollinator insects and codling moth parasitoids in apple orchards.

According to this thesis, insectivorous birds, wild insect pollinators and parasitoids can be attracted to apple orchards through several strategies. As landscape enhancement, we recommend promoting semi-natural woody habitats (i.e. forest patches, isolated trees, hedgerows). And, in order to control codling moth, more distance between orchards should be promoted to prevent the emergence of large and stable populations, while we prevent its expansion to new orchards. As local-scale enhancement, we recommend to maintain a wide and continuous apple tree canopy cover in relation with the provision of different resources for each animal group (i.e.

nectar and pollen for pollinator insects, host resources and protection against predators for codling moth parasitoids, safe foraging for insectivorous birds).

However, from field experience and supported by a wide number of research, we can extend these measures. On the one hand, landscape enhancements that could be considered are: 1) managing landscape composition, configuration and connectivity (Bianchi et al., 2006; Steckel et al., 2014; Carrara et al., 2015), for instance, conserving extant patches of native forests or even allowing rewilding; 2) reintroducing native species in degraded landscape patches (Kross et al., 2016); and 3) reducing invasive species' impacts on target species (McClure et al., 2015), for instance, the damage caused by the Asian hornet (Vespa velutina, Lepeletier) on pollinator communities or the negative effects of the introduction of bumblebees and honeybees colonies on other crops in the agricultural landscape.

On the other hand, local-scale enhancements that could be considered are: 1) providing critical structures and materials like perches, nest boxes and roosts (for insectivorous birds see Rey Benayas et al., 2017; for bees see Magalhães and Freitas, 2013), 2) maintaining wildflower strips (reduce tillage) or growing a rich ground cover of flowers (for bees see Campbell et al., 2017; for parasitoids see Dib et al., 2012), 3) providing food resources in times of shortage (for bees see Rosa-García and Miñarro, 2014; for birds see Xu et al., 2015), 4) promoting hedgerows (for parasitoids see Maalouly et al., 2013; for bees see Miñarro and Prida, 2013; for birds see Heath et al., 2017), 5) transforming field margins to semi-natural habitats (Bischoff et al., 2016), 6) keeping scattered native trees (for birds see Manning et al., 2006), 7) leaving crop areas with bare soil to promote ground solitary bees (Nichols et al., 2020).

REVEALING THE RELATIONSHIP BETWEEN BIODIVERSITY AND THE PROVISION OF ECOSYSTEM SERVICES

The relevance of biodiversity-ecosystem service relationships on agriculture has been widely proved (Tscharntke et al., 2005). Insect pollination, pest control by birds and parasitism rate increase according to the richness and abundance of their respective communities (Winfree, 2013; Maas et al., 2016; Tylianakis et al., 2006). In this context, **Chapter 1 and 2**, likewise these studies, explain the importance of biodiversity understood through the positive link between animal diversity and ecosystem functioning (BEF link) (Duncan et al., 2015). Our results, in line with this idea, showed a consistent positive effect of biodiversity on the provision of ecosystem services in a given crop type.

The differences in the ecosystem services supply between orchards were caused by the differences in the animal communities within them. As we have seen before, these differences are due to environmental drivers, such as local-scale features and landscape structure. Using this framework, we can link landscape and local-scale managements to improve animal biodiversity with the final enhancement of ecosystem services in the crop. In **Chapter 1 and 2**, the relationship between biodiversity and the ecological function have been examined through observational and empirical studies. Across the 26 low-input cider apple orchards we observed the positive effects of animal biodiversity on pest control and pollination. We thus found a consistent positive BEF link across animal groups and functions performing in apple orchards.

Simultaneously we noted that there are different mechanisms to explain these positive patterns between animal biodiversity and ecosystem functioning. For instance, we argue that through functional complementarity, sampling effects and interspecific interactions; insectivorous birds, pollinator insects and codling moth parasitoids can provide better ecosystem services in apple crops (Winfree 2013, Peralta et al., 2014; Tscharntke et al., 2005). These mechanisms can happen simultaneously within each animal group and between different animal groups providers of different ecosystem functions (Classen et al., 2014).

Focusing on species that belong to a same animal group, first, we can note sampling effects. It occurs when there is a greater chance of including a species of greatest inherent productivity for the ecosystem service in a community that is more diverse (Winfree et al., 2013; Tscharntke et al., 2005; Tylianakis et al., 2006). However, this assumption should be studied carefully because the abundance of some species can dilute the effects of richness on the ecological function. For instance, in our communities there are very abundance species, such as *A. quadridentata* for parasitoids, *E. rubecula* for birds or *E. tenax* for pollinators. Therefore, in cider apple orchards the provision of pollination and biological control could be more influenced for few dominant species than for the community richness (Hillebrand et al., 2008).

Second, functional complementarity assumes that the ecological effects of different species can be additive and synergetic (Brittain et al., 2012; Peralta et al., 2014). For instance, wild pollinator insects can exhibit temporal complementarity, as emergence dates, tolerance to different weather conditions and foraging periods vary. They also differ according to spatial complementarity thorough different preferences for plants species, varieties or foraging location (Brittain et al., 2013). By comparison, insectivorous birds represent a wide gradient of morphological and behavioural variability, for instance, we can find from small-sized foliage gleaners (e.g. firecrests) to trunk, bark and ground gleaners (e.g. woodpeckers). Moreover, bird community composition changes according to seasonal species, present in the cider apple orchards for breeding (e.g. red-backed shrike) (García et al., 2018). Finally, codling moth parasitoid communities have a wide range of hosts, different life cycles and different food requirements (Dib et al., 2012; Maalouly et al., 2013; Peralta et al., 2014). All these complementary mechanisms allow improving biological control and pollination in agricultural landscapes trough richer biodiversity communities.

Third, interspecific interactions in relation with BEF link explain how different species can increase their ecological function when they interact with each other or when they try to avoid negative interactions between them. For instance, the co-occurrence of different species ends in the use of different ecological niches and species specialization (Fründ et al., 2013). In other situations, a given species may benefit from interspecific interaction (Cusumano et al., 2016). For instance, multiple species of bees may directly interact with one another and affect each other’s pollen load, pollen deposition rates and floral constancy (Delaplane and Mayer 2000). As a result the quality or quantity of pollen deposition is enhanced.

All these mechanisms are related to the structure and functioning of animal communities. In **Chapter 1 and 2,** the response of biological control and pollination in apple orchards was positively influenced by biodiversity. We argued that insectivorous bird, wild pollinator and codling moth parasitoid diversity can promote ecosystem services through positive functional responses. In this sense, we suggest that the combined activity of insectivorous birds, pollinator insects and codling moth parasitoids will have a positive net effect on apple production. Farmers will perceive the benefits in the form of higher yields and profitability. However, the relationship between the ecological variables measured here and explicit yield and economic parameters were not performed. Therefore, we cannot confirm the ultimate agronomic role of these biodiversity groups on apple crops.

However, different authors have been proved the agricultural benefits of these animal groups in apple orchards: lower pest damage and enhanced pollination benefit farmers in the form of higher yields (Mols and Visser, 2002; Mallinger and Gratton, 2015), increased harvest quality (Garrat et al., 2014; Peisley et al., 2016), and increased profitability, for instance, due to decreased expenditure on insecticides (Cross et al., 2015).

Nevertheless, these results of **Chapter 1 and 2** are in line with the idea of biodiversity-farming win-win scenarios in cider apple orchards. Once again, the promotion of multiple animal-mediated ecosystem services not only could generate agricultural benefits, but also helps to preserve the environment, biodiversity and improves human well-being (MA, 2005). **Chapter 1** evidences strong potential, on the basis of animal biodiversity, for the compatible provision of generalist ecosystem services (i.e. biological control and pollination). But **Chapter 2** suggests that parasitism rates are not enough to control codling moth in Asturian cider apple orchards. However, the occurrence of positive host density dependence suggests that parasitoids can play an essential role to control codling moth (Maalouly et al., 2013; Jonsson et al., 2012). In this way, the availability of resources for codling moth and for parasitoids can show us the right moment and the best management strategy for enhancing parasitoid populations and decreasing damages in apple production. The combination between parasitoids and other codling moths natural enemies promotion with several control strategies at different spatial scales (e.g. trapping of diapausing larvae, use of mating disruption and post-harvest recovery of attacked fruit) (Judd et al., 2005), may enhance the biological control of this important insect pest in the long term.

SEEING THROUGH FARMERS' EYES

There are many measures implemented at farm-level (e.g. field margins, hedgerows and surrounding habitats changes), and farmers are the only people who will make the last decision. Current changes in agriculture are occurring very fast (e.g. social, environmental, institutional, and market-related dynamics). Farmers grow their crops within a risky and uncertain context, but even so, they should be able to cope and adapt being confident about their decisions (Singh et al., 2016). Therefore, a first step toward achieving a better understanding and acceptance of new management practices is to co-work whit farmers. What is the point of all the scientific advances about biological control if farmers do not apply them?

In **Chapter 3,** we contributed toward filling the gap between science and farmers. In applied studies, as **Chapter 1 and 2**, it is essential to include the factors that influence the decision-making process of farmers. Thus, it has become a policy objective to involve farmers in the new agro-environmental schemes that try to promote a more sustainable agriculture and conserve biodiversity (Kampmann et al., 2012). To that end, in a first step we tried to thoroughly understand farmers' perceptions and current knowledge about the concept of biological control. However, when delving deeper into farmers' perception and knowledge about biological control, we realized that it was also important to considerer specific species identities. In fact, this is the first study about farmers' perception and knowledge of specific species identities belonging to different taxa (i.e. birds, mammals, insects, arachnids) able to provide biological control in agroecosystems.

During the process of creating the questionnaire, constant doubts arose us about the comprehension of the questions by farmers. However, after concluding the meetings, I realized that farmers have a very high understanding about the topic. Their perceptions and knowledge are developed through long-term interactions with the natural environment, generating a deep understanding of the surrounding ecology (Aswani et al., 2018). Previous studies on perceptions of biodiversity showed that most people have a rich interpretation of biodiversity, from species to habitats (Fischer and Young, 2007; Soini and Aakkula, 2007). Asturian apple farmers sometimes answered several questions contradictory; however, it was not due to incomprehension but to a misunderstanding. These kinds of contradictions can illustrate that in many cases new agricultural measures are not well accepted not because of famers' knowledge but because of the way we approach the presentation of our new strategies. After all my meetings with farmers, I can say that there was not any miscommunication stemmed from the specific encounter between a research and a farmer. The results of the questionnaires certainly reflect relevant information for the management of nature in agriculture. Asturian apple farmers are an example about the importance of local ecological knowledge for biodiversity management. They know very well the ecosystems in which they work and they have relevant perception about biodiversity, surprisingly, a more functional point of view (Fischer and Young, 2007; Soini and Aakkula, 2007).

Focusing in the results of the survey, farmers considered biological control to be more important in other croplands than in their cider apple orchards. In addition to what was discussed in **Chapter 3** in relation to this point, during the interviews, some farmers stated their concern about biological control in open agroecosystems embedded in an agricultural landscape. They thought that their management actions would have no positive effect in attracting natural enemies. Most of them thought that natural enemies would rather be in other semi-natural habitats than within their own cider apple orchards. This fear is understandable and can be explained by the "intermediate landscape complexity hypothesis" from Tscharntke et al. (2012) and empirically supported by Jonsson et al. (2015). This hypothesis explains that in complex landscapes, natural enemies can meet their requirements in natural habitats of the landscape and spill-over into orchard regardless of the practices done. Local-scale practices to promote, for instance, natural enemies will only increase the biological control measurably when the orchard is located in a landscape of intermediate diversity. Therefore, farmers' doubts about the possibility of loss natural enemies in the landscape were justified. This hypothesis, combined with farmers' idea about the possibility of pest promotion by semi-natural habitats or certain managements (Bianchi et al., 2006), should be taken into account when new management practices are implemented in agricultural landscapes.

Furthermore, when we tried to study if the recognition of an organism as a natural enemy was correlated with having seen it before or knowing about it, the results did not show any correlation. However, we realized that the ability to recognize a natural enemy as a provider of biological control was associated with a previous farmers' knowledge about the natural enemy. This is a very important point because they can understand or perceive some kind of link between the ecological functions or the ecosystem services with biodiversity. This is an unknown field of study where more research needs to be done. If farmers need a prior knowledge to understand that certain biodiversity can control pests in their agroecosystem, do farmers have the knowledge to associate biodiversity with other important ecosystem services? Can we improve farmers' knowledge about the links among biodiversity, ecosystem functions and ecosystem services? Can farmers change their perception of biodiversity to a more functional point of view? How farmers perceive functional biodiversity? Finding the answer to those questions would help to improve farmers' understanding of agroecosystems, their components, their processes and even their flows of energy.

We demonstrated that farmers' knowledge about natural enemies and biological control is built from farmers' daily interactions with biodiversity that complement their local ecological knowledge (e.g. beliefs, heritage and cultural knowledge), and from external formal sources (e.g. newspaper coverage, magazines, social media, television). Therefore, our findings reinforced that farmers' knowledge and perceptions can be influenced by several channels of information. Researchers, as well as the agricultural policies that will implement their results, should invest time and money in increasing the dissemination channels of information. Nowadays, any farmer in the world has access to a mobile phone where they can watch videos and read about new agricultural management practices. In many cases, they also ask each other for quick solutions. Some platforms such as Twitter or mobile apps are being used to transmit information and increase farmers' knowledge in many developing countries (see www.accessagriculture.org). As other author noted, shared beliefs and knowledge, competencies, habits and socio-demographic characteristics are important factors that influence the way individuals perceive biodiversity and their associated processes (Vatn, 2005).

As we have seen in this thesis science and scientists have an important role to play for the future of sustainable food security but in order to have more impact they have to go beyond research and improve in the ways they collaborate with farmers. How can scientists reach farmers to transfer new knowledge?

A communication gap exists between farmers and scientists. However, there are different structures and mechanisms to bridge this gap: 1) Participatory approaches, such as workshops, interviews and meeting points, enables farmers to play an active and influential part in decision which affect their crops and the agricultural landscape (Ullmann et al., 2016; Martínez-Sastre et al., 2017). 2) Educational approaches, such as agricultural training courses, demonstration plots and handbooks, can increase the adoption of management practices that enhance biodiversity that provide ecosystem services (Ullmann et al., 2016; Cai et al., 2014). 3) Social media approaches, such as the use of Twitter, Facebook, YouTube, blogs, mobile apps, web apps or other virtual platforms that facilitate the sharing of knowledge, thoughts and information about agriculture (Cai and Abbot et al., 2013; Emeana et al., 2020).

It is clear that scientist have a wide range of possibilities to transfer their knowledges. Therefore, first we may have to promote our willingness to transfer. Academic institutions only listen to each other. Second, reinforce our communications skills and capacities. And finally, some money from project budgets should be allocated to the transmission of new knowledge.

Finally, our findings have an important message at general methodological level for scientist because they inevitable indicate the need for a participatory approach to a successful biodiversity promotion in agroecosystems. Without such an approach, the wide range of benefits derived from biodiversity and most of the natural enemy species may not be identified. Therefore, the real potential of biodiversity may be undervalued both in individual and collective decisions concerning agricultural management practices at landscape and local-scale level. However, we also claim that biodiversity conservation and sustainable agriculture need to be more shared, society-wide responsibility. We have to start reinforcing farmers' positive aptitudes and continue with more stakeholders and society. This research created an opportunity for farmers to identify the natural enemies relevant in the biological control of apple orchards. But this is only the beginning. More socio-ecological aspect should be study to facilitate farmers' decision making processes to adopt or adapt agricultural managements at different scale to promote ecosystem services. For instance, farmers' willingness for the new proposals (Boonstra et al., 2011) and famers' understanding of the possible effects of agricultural practices on the provisioning of ecosystem services (Smith and Sullivan, 2014).

Reinforcements and future perspectives

LANDSCAPE AND LOCAL-SCALE DRIVERS OF ANIMAL BIODIVERSITY THAT OPERATE IN CIDER APPLE ORCHARDS

To a successful promotion of ecosystem services mediated by biodiversity in agricultural landscapes more integrative and multi-scaled studies are needed. Landscape structure should be measure not only as the amount and type of habitats, but also as a matrix of habitats (e.g. composition, configuration, connectivity). I suggest that the resources that determine these habitats (e.g. alternative food resources, nesting places), their distribution and how they affect the movement of species in the agricultural landscape should be also assessed.

Furthermore, semi-natural habitat, as a driver of biodiversity, is a generic term that can be understood and applied in various ways. Hence, this variable could be divided into more specific habitats for the development of more precise management strategies (Mestre et al., 2018). In turn, depending on the agricultural landscape, other different types of semi-natural habitats should be considered as important drivers for pollinators and natural enemies (Mestre et al., 2018). Moreover, it could be interesting for governments and policymakers to know what percentage of semi-natural habitat or what amount of resources (e.g. nesting places, food, overwintering sites) are needed for a minimum provision of certain ecosystem services. This could better justify the protection and promotion of beneficial habitats for biodiversity conservation throughout agricultural landscapes.

At local-scale level, manipulative studies could be a very important source of information about which resources requirements must be promoted to simultaneously attract several animal groups within the crop. Therefore, more studies on specific manipulative measures and their relation to landscape and biodiversity should be studied in agroecosystems. Local-scale measures such as intercropping, planting flower strips, growing bushes and flowers in field margins, setting up roosts and nesting boxes can be solutions to encourage a viable sustainable agriculture.

Considering that our results can be applied directly by farmers or landscape managers, I suggest completing our study determining the applicability and profitability of the practices suggested in this thesis. Farmers expect to know the costs associated with the new measures and what direct and indirect benefits they will get.

Finally, the biodiversity studied in this thesis can be considered as relevant for a sustainable food production. However, I encourage extending the study to more relevant animals groups. For instance, anthocorids, earwigs, hoverflies or spiders should be studied to achieve a better biological control in Asturian cider apple orchards.

REVEALING THE RELATIONSHIP BETWEEN BIODIVERSITY AND THE PROVISION OF ECOSYSTEM SERVICES

The link between biodiversity and ecosystem services is not just a matter of abundance and richness of animals groups. To better assess whether changes in biodiversity lead to changes in ecosystem functioning and what shape the potential relationship might have, we should extend the concept of biodiversity. How species redundancy within functional groups affect ecosystem functioning? What is the effect of specific species? Are they important because of their functional traits or because of their abundance? How the pool of species interact each other? Does ecosystem functioning respond when some species suffer relative declines? What happens when some species become dominant?

Alternatively, we have only considered the positive effects that insectivorous birds, pollinator insects and codling moth parasitoids bring to agroecosystems. However, could they generate any damage to apple orchards? For instance, insectivorous birds can damage the fruit (Pejchar et al., 2018), consume pollinator insects (Gonthier et al., 2019) or even predate upon other natural enemies (e.g. intraguild predation) (García et al., 2018). Pollinators could interfere with each other via resources competition (e.g. nesting cavities) (Russo et al., 2016) and changes in plant communities (Mallinger et al., 2017). Besides, the disease transmission among then can also affect the overall supply of pollination (Vanbergen et al., 2018). Codling moth parasitoids can also parasitize beneficial organisms as other parasitoids of pests (e.g. hyperparasitoids) (Mills, 2005). Future research should consider the possible ecosystem disservice associated with insectivorous birds, codling moth parasitoids and wild pollinators. In particular agroecosystems, the overall positive result of these functionally important biodiversity could be very affected by these ecosystem disservices.

We must also acknowledge that interactions between ecosystem services are possible and they have important practical implications for any strategy aimed at increasing the supply of multiple ecosystem services for human well-being (Seppelt et al., 2011). Synergetic interactions allow for the simultaneous enhancement of more than one ecosystem service. Increasing the supply of one ecosystem service can enhance the supply of others (Michalet and Pugnaire et al., 2016). More efforts should be devoted to study positive interactions among ecosystem services in agroecosystems.

Regarding codling moth parasitoids, more research should be done to characterize the composition of the codling moth parasitoid community and their specific interactions with codling moth populations. Both codling moth-parasitoids and plant-codling moth interactions are spatially and temporally structured and require more study, for instance, codling moth density was estimated at the end of the fruit apple growing season based on diapausing larvae, which did not allow us to study the real moment where parasitoids may respond to host density. And even more to distinguish different behaviours among parasitoid species.

SEEING THROUGH THE FARMERS' EYES

Regarding the participatory study performed in this thesis, it could be interesting to compare the ecological knowledge of farmers with the ecological knowledge assessed in scientific research. For instance, we can compare the network based in farmers' perceptions of pest-natural enemy interactions with results from ecological assessments. By this way, we can examine the reliability of farmers' knowledge in biodiversity management.

Besides, to facilitate farmers' decision making processes, farmers' motivations and perceptions about possible sustainable environmental measures should be studied. Moreover, farmers' expectations of sustainable measures profit, risk and social acceptance cannot be overlooked.

After proving the importance of communication between scientists and farmers, more efforts need to be made to determine the effectiveness of information channels. The successful implementation of new agricultural measures to promote ecosystem services in agricultural landscapes depends on a proper understanding of scientific results by farmers.

Finally, the need for a participatory study on farmers' perception and knowledge of pollinator insects as provider of pollination in cider apple orchards is undeniable.

Conclusions

1. Asturian cider apple orchards are low-input agroecosystems rich in insectivorous birds, codling moth parasitoids and wild pollinators.

2. Animal biodiversity positively affects biological control and pollination in apple orchards. Insectivory responds positively to higher richness and abundance of insectivorous birds. Parasitoid richness increases the number of parasitized codling moth larvae. Richness and abundance of wild bees increase fruit set, and abundance of wild pollinators improves seed set.

3. Simultaneous management of landscape and local-scale features will foster animal biodiversity. More semi-natural woody habitats around orchards and a wider apple canopy cover within orchards increase pollinator insects and insectivorous birds.

4. Simultaneous “top-down” and “bottom-up” forces across the interactions triad parasitoids-pest-plant determine parasitoids and codling moth populations in Asturian cider apple orchards.

5. Biodiversity win-win scenarios can take place in cider apple orchards by simultaneously promoting valuable ecosystem services such as biological control by insectivorous birds and parasitoids, and pollination by pollinator insects.

6. Farmers in cider apple orchards recognize the importance of biological control but only some of the benefits derived from it.

7. Farmers easily recognize predatory birds and mammals as natural enemies, whereas predatory arachnids and insects are poorly recognized. Farmers also recognize some prey-pest interactions, although there are knowledge gaps.

8. Farmers' perceptions are shaped by both their local ecological knowledge and external sources. Farmers’ recognition of natural enemies can be enhanced through different channels of information.

9. The study of farmers' perception and knowledge of natural enemies is one of the first steps to make science more participative. To achieve success agricultural policies and management practices is essential to co-work with farmers.

A personal view of the way forward

Developing and implementing sustainable strategies that enhance ecosystem services through biodiversity and related food production technologies will be one of the great challenges facing agriculture in the 21st century and beyond. However, the vision of many is to hide direct and indirect damage that agriculture generates in the environment by implementing some "environmental-friendly" practices. When at the same time, they continue squeezing the agroecosystems to produce more. I do not want to be pessimistic but, although some sustainable measures are implemented, the agroecosystems will remain high-input, resource-intensive systems. Otherwise, the right approach would be to achieve high food productions with low costs by designing, to each situation, specific agricultural systems that mimic natural systems. That means real sustainable agroecosystems that are able to maintain profitable productions based on biodiversity and minimal use of human inputs.

Low-input agroecosystems can be the key to help us to understand more about the structure and functioning of natural and agricultural systems. We have endeavored throughout this thesis to provide results that will advance our understanding about the link among landscape and local-scale features with pollination and biological control in cider apple orchards. Also we proved the positive effects of both ecosystems services within the crop. And finally, we developed a participative researching approach that encourages integration of farmers' knowledge with scientific knowledge.

However, we are still far to understand the mechanisms that explain the potential of agriculture to improve crop productivity while protecting the environment. The link between biodiversity and ecosystem services supply in agricultural landscapes is not just a matter of biophysical relations. Management strategies carry out by farmers and nature management policies on large scales play essential roles. Until there is a united front among farmers, scientists and policy makers, the progress towards sustainable production will be limited, weak and incomplete.

Firstly, at the political level, a lack of demonstrated cost-effectiveness of sustainable programmes based on biodiversity has not encouraged governments to invest in agricultural ecosystem services research and development. This in turn has led to reduced interest from academics to carry out research or educate students in agricultural biodiversity as supplier of ecosystem services. Secondly, at the grower level, farmers and land managers who have not been well engaged in the sustainable programmes based on biodiversity may see only slow progress or no initial impact on biological control or pollination. Farmers may feel that their efforts are not providing enough rewards to them compared with conventional agriculture that seems more reliable and predictable.

Therefore, we must call government´s attention on the importance of sustainable agriculture. This will bolster private investments, public research and education on an agriculture that allows people to consume more and better products while halting and reversing environmental degradation. Besides, training farmers about their role in agricultural landscapes and engagement of farmers in scientific research should be another priority. What would happen if farmers were more participative in agricultural research? They are going to test scientific results in real agroecosystems. Our results are not absolute truths. Each agroecosystem is characterized by specific local conditions. Farmers are going to adapt the scientific knowledge and to innovate using our recommendations based on their thoughts and prior experience.

Finally, if we really want to make progress towards a more sustainable agriculture we also need the involvement of society. After the occurrence of coronavirus disease (Covid-19), that has shocked the planet. I was hopeful that society would change some of its current patterns of life, among them, the current model of globalized food consumption. I started to see renewed emphasis upon a “local” link between production and consumption. However, like a temporary fashion, the motivation also disappeared. Governments should encourage consumers to buy local products. Governments should facilitate rural entrepreneurs who want to produce sustainable food. By this way, we help farmers to produce in a sustainable way, selling their products at fairer prices, reducing rural abandonment and reducing the distance travelled from source of supply to retailer. Making direct connections between food production and consumption generates huge economic, social and environmental benefits.

Resumen y conclusiones

INTRODUCCIÓN

La agricultura ocupa más de un 40 % de la superficie terrestre. Sin embargo, el crecimiento exponencial de la población humana, así como la hambruna que asola muchas partes del planeta, obligan a una expansión continua de la producción de alimentos. Es nuestra responsabilidad elegir la manera en la que incrementamos tanto la superficie como la producción de nuestros cultivos a fin de hacer frente a las necesidades del futuro. Tanto en el pasado como en la actualidad, la expansión agrícola sigue estando asociada a un fuerte deterioro medio ambiental y una gran pérdida de biodiversidad.

Aunque los daños producidos por la agricultura son claros y se aboga por sistemas de producción más responsables con el medio ambiente, la mayoría todavía mantienen un alto uso de insumos de origen humano como el petróleo, los agroquímicos y la maquinaria industrial. La combinación de esta agricultura intensiva unida a la influencia de multinacionales agroalimentarias y mercados globalizados, así como al consumo indiferente de alimentos por gran parte de la sociedad, refuerza los efectos negativos de la agricultura sobre el medio ambiente y la biodiversidad.

La necesidad de conducir la agricultura hacia sistemas de producción más sostenibles que conserven el medio ambiente se ha convertido en una prioridad. Pero producir más con menos de una manera sostenible requiere entender los posibles mecanismos capaces de mejorar la producción de alimentos mientras se detiene y/o se invierte la degradación del medio ambiente. Los sistemas de producción de bajos insumos podrían ser capaces de alcanzar estos objetivos. Estos sistemas de producción disminuyen la contaminación de la tierra y las aguas subterráneas al reducir el uso de agroquímicos, minimizando al mismo tiempo los gastos para los agricultores. Al contrario de lo que se piensa, los sistemas de bajos insumos pueden incrementar a corto y largo plazo la rentabilidad de los cultivos.

La definición de agrosistema incluye cualquier tipo de ecosistema modificado por el ser humano con el objetivo de optimizar el suministro de servicio ecosistémicos de producción: como son los alimentos, fibras, biocombustibles y otros materiales de origen biótico. Por otro lado, los servicios ecosistémicos se definen como los beneficios directos e indirectos que los ecosistemas proporcionan al bienestar humano.

Dependiendo del grado de intensificación de los agrosistemas, la dependencia y demanda de servicios ecosistémicos suministrados por la biodiversidad pueden ser muy altas. Usando los servicios ecosistémicos como marco de estudio podemos destacar cómo la biodiversidad, presente en el agrosistema o en los paisajes circundantes, provee una serie de servicios ecosistémicos que mejoran el bienestar humano y son claves para una producción más sostenible de alimentos.

Sin embargo, el marco de los servicios ecosistémicos puede resultar problemático. Considerar la naturaleza como un flujo continuo de beneficios puede simplificar los estudios de los agrosistemas hasta el punto de desequilibrarlos en pos de uno o muy pocos servicios ecosistémicos (ej. provisión). De esta manera olvidamos otros aspectos relevantes que se interconectan en los agrosistemas, como los ecológicos, económicos, políticos y sociales.

A su vez, los agrosistemas son sistemas socio-ecológicos definidos como ecosistemas adaptativos y dinámicos compuestos por entidades humanas y ecológicas que interactúan constantemente. La sociedad, y en concreto los agricultores, juegan un papel esencial en el devenir de los agrosistemas. Por lo tanto, la inclusión de los agricultores en la ciencia se considera fundamental para conseguir una sostenibilidad agrícola que cubra la demanda actual de alimentos. Los agricultores son quienes tienen la última palabra para aceptar o rechazar cambios en sus cultivos. Los estudios participativos sobre servicios ecosistémicos y variables que relacionen los componentes humanos y naturales de los agrosistemas pueden aportar información muy valiosa sobre el devenir de los paisajes agrícolas. Además, de esta manera se promueve una mayor aceptación de estas medidas agrícolas así como un incremento del interés y del conocimiento que los agricultores poseen sobre sus cultivos, lo que puede derivar en una mejor comprensión del papel que juega la ciencia en la agricultura.

En la Unión Europea, donde la agricultura se basa en la Política Agraria Común, se diseñan medidas específicas para mejorar la provisión de servicios ecosistémicos por la biodiversidad en los agrosistemas. Entre ellas existen una serie de recomendaciones para fomentar cultivos menos dañinos con la biodiversidad y los hábitats circundantes. Estas recomendaciones van desde diversos manejos, como puede ser dejar áreas con vegetación natural dentro y alrededor del cultivo, disminuir el uso de insecticidas o incorporar estructuras que atraigan fauna beneficiosa; hasta simplemente conservar o regenerar hábitats naturales situados en las proximidades. De esta manera, se pretende asentar diferentes comunidades de animales beneficiosos para la producción de alimentos y conseguir que los agricultores sean “protectores y vigilantes” del medio ambiente.

El papel de la biodiversidad en el funcionamiento ecosistémico, que resulta en la provisión de servicios ecosistémicos en los cultivos, ha captado la atención de los científicos en los últimos años. Acorde a este paradigma teórico que relaciona biodiversidad y funcionamiento ecosistémico (vinculo BFE) encontramos que existe un efecto positivo de la biodiversidad animal sobre diferentes servicios ecosistémicos. La estructura y el funcionamiento de las comunidades animales, en relación con sus abundancias relativas y sus nichos ecológicos, afectan a la magnitud de los servicios ecosistémicos resultantes. En este marco se plantean diferentes mecanismos principales para explicar por qué una mayor biodiversidad animal conduce a funciones ecológicas más estables y beneficiosas, entre los que se encuentran la complementariedad funcional, las interacciones interespecíficas y los efectos de selección.

Por otro lado, para intentar manejar los efectos de la biodiversidad sobre el funcionamiento del agrosistema necesitamos entender qué factores modulan la biodiversidad. La estructura del paisaje circundante al agrosistema, así como las prácticas agrícolas implementadas en él, pueden considerarse como agentes moduladores de la biodiversidad a diferentes escalas. Estas dos aproximaciones están relacionadas con el suministro de recursos clave para el asentamiento de diferentes grupos animales como son los sitios de nidificación e hibernación, refugios frente a depredadores y fuentes alternativas de alimentos.

Por lo tanto, para conseguir un cuadro completo de cómo el paisaje y las características de los cultivos pueden fomentar la biodiversidad a fin de maximizar el suministro de servicios ecosistémicos necesitamos: comprender las relaciones entre el paisaje y las prácticas agrícolas con la biodiversidad y entender la compleja relación existente entre la biodiversidad y los servicios ecosistémicos.

En esta tesis doctoral nos centramos en dos servicios ecosistémicos que son el control biológico de plagas y la polinización, ambos de vital importancia para los cultivos. El 75 % de los cultivos necesitan de la polinización animal y todos ellos requieren una gestión adecuada de las plagas para conseguir una producción rentable y sostenible de alimentos. Los beneficios de promover ambos grupos animales van más allá del rendimiento económico, pues a través de ellos disminuimos también el uso de químicos perjudiciales para la salud, detenemos la degradación del medio ambiente e impedimos la pérdida de biodiversidad.

OBJETIVOS Y ESQUEMA GENERAL

El objetivo de esta tesis doctoral es proporcionar conocimientos acerca del suministro simultáneo de los servicios de control biológico de plagas y de polinización en la zona por excelencia del cultivo de manzana de sidra (*Malus x domestica* Borkh) en Asturias (España). Para ello, en primer lugar, la tesis se centra en los impulsores de la biodiversidad que operan en estos paisajes agrícolas. En segundo lugar, trata de revelar las relaciones entre la biodiversidad y los dos servicios ecosistémicos elegidos. Y, en tercer lugar, evalúa las percepciones y el conocimiento de los agricultores sobre el control biológico y los enemigos naturales que amenazan sus cultivos. En concreto abarca tres estudios:

El primero evalúa en profundidad los principales efectos ambientales (paisaje y características a escala local) que impulsan simultáneamente la avifauna insectívora y los insectos polinizadores en 26 plantaciones de manzana de sidra. Asimismo, demuestra la relación positiva entre esta biodiversidad y el suministro de los servicios de control biológico y de polinización. Durante dos años se muestreó la riqueza y abundancia de aves insectívoras e insectos polinizadores mediante censos y capturas. Por su parte, la insectivoría se estimó mediante experimentos de exclusión y señuelos de plastilina que imitaban la plaga más problemática del manzano, la carpocapsa (*Cydia pomonella* L.). El servicio de polinización se estimó mediante el cuajado de frutos y la formación de semillas.

El segundo estudio también aborda los principales efectos medioambientales que impulsan a las poblaciones de carpocapsa y a sus parasitoides. Sin embargo, en este caso las interacciones tróficas ("bottom-up" y "top-down") dentro del sistema parasitoides-carpocapsa-manzano parecen gobernar el parasitismo y el daño en la producción de manzana generado por la carpocapsa. Durante dos años, en las mismas veintiséis plantaciones de manzana, se recogieron carpocapsas hibernantes mediante bandas de papel corrugado sujetas a los troncos. El seguimiento en laboratorio de las carpocapsas proporcionó el número y las especies de parasitoides capaces de controlar esta plaga. A su vez, el número de carpocapsas parasitadas indicó la magnitud del servicio ecosistémico proporcionado por los parasitoides, mientras que el daño producido por la carpocapsa se estimó en campo a través de manzanas dañadas tanto en la copa como en el suelo.

Finalmente, el tercer estudio, a través de 90 encuestas “face-to-face” y diferentes análisis (ej. correlaciones, GLMs, RDA y análisis de redes), intenta comprender los conocimientos y percepciones que poseen los agricultores de manzana de sidra sobre el control biológico y los enemigos naturales. En colaboración con ellos, tratamos de proporcionar conocimientos para una gestión exitosa de las plantaciones de manzano de sidra a través del control biológico que, a su vez, disminuya la distancia existente entre científicos y agricultores.

RESULTADOS Y DISCUSIÓN

Esta tesis contribuye a la necesidad de comprender las relaciones existentes entre la estructura del paisaje, las características locales de las plantaciones de manzano, la biodiversidad y los servicios ecosistémicos al tiempo que promovemos medidas sostenibles en la agricultura basadas en la biodiversidad. Sin embargo, para tener éxito en la implementación de las medidas resultantes es fundamental trabajar con los agricultores para conocer sus percepciones y conocimientos acerca de los servicios ecosistémicos estudiados y su biodiversidad asociada.

Las plantaciones de manzana de sidra asturianas demostraron contener una alta diversidad de aves insectívoras (32 especies), insectos polinizadores (82) y parasitoides de carpocapsa (7). Como veremos más adelante, esta riqueza y abundancia de especies se debe en parte a las características de las plantaciones y del paisaje circundante. De acuerdo con otros estudios, estos valores de riqueza y abundancia solo se encuentran en plantaciones no convencionales de bajos insumos, las cuales minimizan el uso de pesticidas, fertilizantes químicos y maquinaria agrícola.

Mediante un enfoque integrador, combinando aproximaciones empíricas y participativas basadas en la teoría que vincula la biodiversidad con el funcionamiento ecosistémico y el marco de los servicios de los ecosistemas, los resultados de esta tesis sugieren que las aves insectívoras y los insectos polinizadores pueden promoverse simultáneamente si se aumentan los hábitats leñosos semi-naturales alrededor de las plantaciones y se favorece un dosel continuo y extenso de manzanos dentro de ellas. Ambas medidas están relacionadas con el suministro de diferentes recursos como lugares de nidificación, refugios contra depredadores y fuentes de alimento alternativas.

Por el contrario, a pesar de los estudios que prueban la relación entre los parasitoides y las poblaciones de carpocapsa con la disponibilidad de distintos hábitats y recursos a diferentes escalas, nuestros resultados no muestran ninguna influencia del paisaje ni de las características a escala local; a excepción de la proporción de plantaciones de manzano en un radio de 125m alrededor del cultivo. Esta variable podría influir en las dinámicas poblacionales de la carpocapsa, por ejemplo, favoreciendo su dispersión y colonización de nuevas plantaciones. Sin embargo, los resultados mostraron como la producción de manzana influía "bottom-up" sobre la abundancia de carpocapsas y su daño generado en las plantaciones.

Por otro lado, los parasitoides ejercieron una fuerte presión "top-down" sobre las poblaciones de carpocapsa, siendo capaces de llegar a parasitar en algunas plantaciones hasta el 42,5 % de las larvas de carpocapsa recogidas en las bandas de cartón. Sin embargo, conviene resaltar que los parasitoides por si solos no fueron capaces de controlar esta plaga tan dañina, por lo que abogamos por el uso de varias técnicas de control (ej. parasitoides, confusión sexual, trampas de feromonas).

En el caso de las poblaciones de parasitoides, estas también se vieron relacionadas con la disponibilidad de larvas de carpocapsa. Esta fuerte relación entre plaga y enemigo natural ("bottom-up") podría enmascarar los efectos del paisaje y de las características de la plantación sobre las poblaciones de parasitoides. Asimismo, las características del paisaje mosaico circundante y las características de las plantaciones de sidra (ej. uso mínimo de pesticidas, presencia de cubiertas vegetales y setos) podrían cubrir ampliamente las demás necesidades a corto plazo de las comunidades de parasitoides, como son la búsqueda de néctar y refugio contra los depredadores. Como consecuencia, la relación entre plaga y enemigo natural se vería reforzada. Siendo la búsqueda de hospedadores para continuar el ciclo reproductivo el factor limitante de las poblaciones de parasitoides de carpocapsa en las plantaciones de manzana de sidra asturianas.

Encontrar recomendaciones de manejo comunes a estos grupos de biodiversidad estudiados no es tarea fácil. Además de aumentar la disponibilidad de hábitats semi-naturales y doseles de manzanos a fin de fomentar la presencia de aves insectívoras y polinizadores, en relación a los parasitoides no podemos confirmar ninguna medida práctica ya que su interacción con la carpocapsa es la que determina sus poblaciones. Sin embargo, con la intención de prevenir la expansión de la carpocapsa y el aumento de sus poblaciones se podría ampliar la distancia entre las futuras plantaciones de manzano en la zona. Otros estudios basados en observaciones de campo abogan por otras medidas para fomentar esta biodiversidad animal como: 1) introducir estructuras de nidificación, perchas y refugios, 2) favorecer la vegetación floral espontánea, ya sea disminuyendo el uso de herbicidas o el número de veces que se siegan las calles, 3) dejar remanentes florales y de vegetación todo el año en algunas zonas de la plantación, y 4) promover setos entre fincas y transformar las lindes hacia composiciones vegetales naturales.

El estudio de las relaciones entre la biodiversidad y el funcionamiento ecosistémico (vínculo BFE) reveló que el control biológico y la polinización responden positivamente a la biodiversidad de aves insectívoras, insectos polinizadores y parasitoides de carpocapsa. Una mayor riqueza y abundancia de estos grupos animales proporcionan mejores servicios ecosistémicos. Por lo que, finalmente, obtenemos el cuadro completo: las diferencias en las comunidades de estos grupos animales se deben a diferencias en el paisaje y en las características de la finca, las cuales podemos manipular para mejorar las comunidades de animales y así mejorar los servicios ecosistémicos que estos proveen. En el caso del control biológico de la carpocapsa, la disponibilidad de recursos alimentarios, tanto para ella como para sus parasitoides, es esencial para comprender la dinámica de ambas poblaciones y controlar eficazmente esta plaga.

Para explicar estas relaciones positivas entre la biodiversidad y el funcionamiento ecosistémico planteamos diferentes mecanismos. En primer lugar, desarrollamos la complementariedad funcional, entendida como las sinergias y efectos aditivos que pueden surgir cuando se encuentran diferentes especies en el agrosistema. Este mecanismo puede generar tanto complementariedad espacial como temporal entre diferentes especies. Un ejemplo de complementariedad funcional lo encontramos en las aves insectívoras que se alimentan en distintas partes de los manzanos para disminuir la competencia entre ellas: unas se alimentan de insectos en las hojas de las copas, otras en el tronco y otras realizando vuelos de captura alrededor de los árboles. En segundo lugar, exponemos los resultados beneficiosos que pueden surgir de las interacciones interespecíficas entre diferentes especies. Por ejemplo, las interacciones entre especies de abejas pueden favorecer la polinización cruzada y mejorar la composición del polen transportado, lo que repercute en un mejor servicio de polinización. Finalmente, encontramos los efectos de muestreo, **c**uanto mayor es el número de especies encontradas mayores probabilidades hay de que aparezcan especies más eficientes en la comunidad con un mayor peso en la provisión del servicio ecosistémico.

Cabe resaltar que, pese a comprender la relación positiva entre estos grupos animales y la provisión de los servicios ecosistémicos de polinización y control de plagas, y sugerir su mejora a través de cambios en el paisaje y en las características de cada plantación, en esta tesis no hemos estudiado la relación directa entre estos servicios ecosistémicos y las mejoras en las cosechas. Por ello, no podemos afirmar incrementos en las rentabilidades de este cultivo como consecuencia de estas modificaciones. Sin embargo, otros estudios prueban los papeles agronómicos de estas especies, capaces de crear beneficios en la cantidad y calidad de las cosechas en diferentes cultivos.

Por último, muchas de las medidas planteadas para conseguir una agricultura más sostenible deberán ser aplicadas por los agricultores, por lo que el estudio de los factores que influyen en la toma de decisiones es clave para tener éxito en las políticas agrarias. Estudiar los conocimientos que los agricultores poseen acerca del control biológico, y en concreto, de las especies animales que proveen este servicio en las plantaciones de manzana es uno de los primeros pasos para desarrollar políticas agrarias relevantes.

El estudio participativo realizado con 90 agricultores de manzana de sidra reveló que estos subestimaban el control biológico en sus plantaciones respecto a los beneficios que este generaba en otros cultivos. Por otro lado, demostró que conocían mejor a los enemigos naturales vertebrados que a los invertebrados y que su capacidad para reconocer a un enemigo natural estaba asociada a conocimientos previos sobre el organismo (ej. conocimientos ecológicos locales y formales). En cuanto a las percepciones sobre las interacciones enemigos naturales-plaga, estas mostraron que los agricultores necesitaban corregir ciertas lagunas en sus conocimientos. Estos resultados nos aportan información esencial a la hora de lograr políticas agrícolas y prácticas de gestión exitosas en relación con el suministro de servicios ecosistémicos en los paisajes agrícolas. Lo que a su vez prueba la necesidad de combinar estudios empíricos y participativos en marcos integradores.

Centrándonos en la habilidad de los agricultores para reconocer enemigos naturales como proveedores del servicio de control plagas, encontramos una relación directa entre los conocimientos previos de los agricultores y la capacidad de reconocer dicho enemigo natural. La posible percepción de un nexo entre la función ecológica o el servicio ecosistémico y la biodiversidad por parte de los agricultores abre la puerta a novedosos campos de estudio imprescindibles para mejorar y transformar las actuales políticas agrarias. La posibilidad de orientar las políticas hacia medidas sostenibles más comprensibles que además capaciten a los agricultores es algo fundamental, pues serán ellos quienes suplan la demanda actual de alimentos al tiempo que protegen y fomentan paisajes agrícolas sostenibles.

Asimismo, en este tercer capítulo, demostramos que los conocimientos de los agricultores acerca del control biológico y los enemigos naturales provenían de diferentes fuentes: por un lado, de sus propias experiencias cotidianas en las plantaciones y por el otro, de fuentes externas como periódicos, revistas, medios sociales o la televisión; los cuales influencian sus conocimientos y las percepciones. La ciencia debe llegar a los agricultores y a la sociedad por lo que una mejora en la transmisión de conocimientos es necesaria. Diferentes estudios han confirmado la posibilidad de mejorar esta transmisión a través de acercamientos participativos, educativos y del uso de diferentes redes sociales.

Finalmente y a modo de resumen esta tesis ofrece, en primer lugar, una perspectiva integradora sobre el suministro de los servicios de control biológico de plagas y de polinización en cultivos de manzana por diferentes grupos de biodiversidad (aves insectívoras, parasitoides de carpocapsa e insectos polinizadores). En segundo lugar, prueba que esta biodiversidad está condicionada por el paisaje y factores a escala local y por último, demuestra que los estudios participativos son esenciales para diseñar estrategias de gestión exitosas. Las plantaciones de manzana de sidra asturianas pueden ser un ejemplo de una agricultura basada en prácticas agrícolas sostenibles y en la biodiversidad, demostrando la existencia de otros modelos de producción que pueden satisfacer la demanda futura de alimentos y reducir al mismo tiempo los daños en el medio ambiente y la pérdida de biodiversidad.

CONCLUSIONES

1. Los plantaciones de manzanas de sidra asturianas son agrosistemas de bajos insumos, ricos en aves insectívoras, parasitoides de carpocapsa y polinizadores silvestres.

2. La biodiversidad animal influye positivamente en el control biológico y la polinización. La insectivoría responde positivamente a la riqueza y abundancia de aves insectívoras. La riqueza de parasitoides aumenta el número de larvas de carpocapsa parasitada. La riqueza y abundancia de abejas silvestres aumenta el cuajado de los frutos, y la abundancia de polinizadores silvestres mejora la formación de semillas.

3. La gestión simultánea del paisaje y de las características locales pueden fomentar la biodiversidad animal. Un mayor número de hábitats leñosos semi-naturales alrededor de las plantaciones y una mayor cobertura del dosel de los manzanos favorecen los insectos polinizadores y las aves insectívoras.

4. Efectos simultáneos “top-down” y “bottom-up” a lo largo del sistema parasitoide-carpocapsa-manzano determinan tanto las poblaciones de parasitoides como las de carpocapsa.

5. En las plantaciones de manzanas de sidra la conservación de la biodiversidad y la producción agrícola pueden ir de la mano a través de los servicios ecosistémicos de control biológico por aves insectívoras y parasitoides, y la polinización por insectos polinizadores.

6. Los agricultores de la manzana de sidra reconocen la importancia del control biológico, pero sólo algunos de los beneficios derivados de ella.

7. Los agricultores reconocen fácilmente a las aves y mamíferos depredadores como enemigos naturales, mientras que las arañas e insectos depredadores son menos reconocidos. Los agricultores también perciben varias de las interacciones entre enemigo natural-plaga, aunque desconocen muchas de ellas.

8. Las percepciones de los agricultores están determinadas por sus conocimientos ecológicos locales y de fuentes externas. El reconocimiento de los enemigos naturales por los agricultores puede reforzarse a través de diferentes canales de información.

9. El estudio de la percepción y el conocimiento de los agricultores sobre los enemigos naturales es uno de los primeros pasos para que la ciencia sea más participativa. Para lograr políticas agrarias y medidas de gestión exitosas es esencial colaborar con los agricultores.

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Appendices

Appendix **Chapter 1**

Appendix **Chapter 2**

Appendix **Chapter 3**

Appendix Chapter 1

Appendix A. List of animal species recorded in cider apple orchards

Table A1. List of species of insectivorous birds recorded in cider apple orchards in this study.

Scientific name	Common name
Aegithalos caudatus	Long-tailed tit
Anthus trivialis	Tree pipit
Certhia brachydactyla	Short-toed treecreeper
Cettia cetti	Cetti's warbler
Cyanistes caeruleus	Eurasian blue tit
Dendrocopos major	Great spotted woodpecker
Erithacus rubecula	European robin
Ficedula hypoleuca	European pied flycatcher
Fringilla coelebs	Common chaffinch
Garrulus glandarius	Eurasian jay
Hippolais polyglotta	Melodious warbler
Lanius collurio	Red-backed shrike
Lophophanes cristatus	European crested tit
Oriolus oriolus	Eurasian golden oriole
Parus major	Great tit
Periparus ater	Coal tit
Phoenicurus phoenicurus	Common redstart
Phylloscopus collybita/ibericus	Common/Iberian chiffchaff
Picus viridis	Green woodpecker
Prunella modularis	Dunnock
Regulus ignicapilla	Common firecrest
Regulus regulus	Goldcrest
Sitta europaea	Eurasian nuthatch
Sylvia atricapilla	Eurasian blackcap
Sylvia borin	Garden warbler
Sylvia communis	Common whitethroat
Troglodytes troglodytes	Eurasian wren
Turdus iliacus	Redwing
Turdus merula	Common blackbird
Turdus philomelos	Song thrush
Turdus pilaris	Fieldfare
Turdus viscivorus	Mistle thrush

Table A2. List of species of pollinators identified in cider apple orchards in this study. Classified as either honey bee (HB), wild bee (WB), bumblebee (BB), hoverfly (HF), fly (F), beetle (B), or other (O).

Scientific name	Group	Scientific name	Group
Apis mellifera	HB	*Nomada succinta*	WB
Bombus pascuorum	BB	*Osmia bicornis*	WB
Bombus pratorum	BB	*Cheilosia pagana*	HF
Bombus terrestris	BB	*Chrysotoxum festivum*	HF
Andrena bicolor	WB	*Episyrphus balteatus*	HF
Andrena cyanomicans	WB	*Eristalis arbustorum*	HF
Andrena dorsata	WB	*Eristalis interrupta*	HF
Andrena flavipes	WB	*Eristalis pertinax*	HF
Andrena fulva	WB	*Eristalis similis*	HF
Andrena haemorrhoa	WB	*Eristalis tenax*	HF
Andrena humilis	WB	*Eupeodes corollae*	HF
Andrena lathyri	WB	*Helophilus pendulus*	HF
Andrena leptopyga	WB	*Melanostoma mellinum*	HF
Andrena minutula	WB	*Melanostoma scalare*	HF
Andrena nigroaenea	WB	*Meliscaeva auricollis*	HF
Andrena nitida	WB	*Neoascia podagrica*	HF
Andrena pilipes	WB	*Parhelophilus sp.*	HF
Andrena similis	WB	*Platycheirus albimanus*	HF
Andrena thoracica	WB	*Sphaerophoria scripta*	HF
Andrena trimmerana	WB	*Syrphus ribesii*	HF
Eucera sp.	WB	*Syrphus vitripennis*	HF
Halictidae sp1.	WB	*Volucella bombylans*	HF
Halictus (Seladonia) sp.	WB	*Xanthandrus comtus*	HF
Halictus crenicornis	WB	*Bombylius major*	F
Halictus scabiosae	WB	*Empis* sp.	F
Halictus tumulorum	WB	*Molobratia teutonus*	F
Lasioglossum calceatum	WB	*Neomyia cornicina*	F
Lasioglossum fulvicorne	WB	*Sarcophaga* sp.	F
Lasioglossum lativentre	WB	*Stevenia deceptoria*	F
Lasioglossum limbellum	WB	*Tricogena rubricosa*	F
Lasioglossum littorale	WB	*Zophomyia temula*	F
Lasioglossum lucidulum	WB	*Agrypnus murinus*	B
Lasioglossum malachurum	WB	*Hoplia hungarica*	B
Lasioglossum morio	WB	*Oedemera nobilis*	B
Lasioglossum pallens	WB	*Oxythyrea funesta*	B
Lasioglossum parvulum	WB	*Rhagonycha fulva*	B
Lasioglossum pauperatum	WB	*Trichius zonatus*	B
Lasioglossum pauxillum	WB	*Tropinota squalida*	B
Lasioglossum punctatissimum	WB	*Valgus hemipterus*	B
Lasioglossum puncticolle	WB	*Panorpa* sp.	O
Lasioglossum zonulum	WB	*Tenthredo koehleri*	O

Appendix B. Details of sentinel model experiment

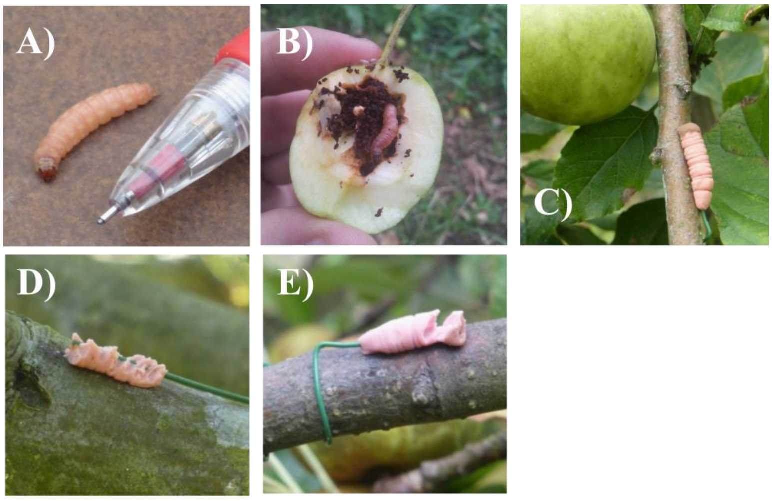


Figure B1. A-B) Views of codling moth larvae on cider apple; C) Plasticine sentinel model representing the codling moth caterpillar, attached to a cider apple branch; D-E) examples of sentinel models with signs of attack (pecking) by birds. Images by Daniel García (A, C-E) and Carlos Guardado (B).

Appendix C. Details of Principal Components Analysis (PCA) of landscape composition

Table C1. Results of Principal Components Analysis (PCA) accounting for the variability in the six general ground cover types in R1000 plots across orchards. PCAs were calculated based the percentages of cover of different ground cover types in R1000 plot around each orchard (quantified by GIS, ArcGIS9.3). PCA factor scores were obtained from the three first (Varimax) rotated eigenvectors of each analysis. The percentage of variance accounted for by each eigenvector, as well as the loadings of rotated factors (correlations, coefficients ≥ |0.700| highlighted in bold) are shown.

General ground cover types in R1000 **Factor**	**PCA1**	**PCA2**	**PCA3**
% Variance	42.41	25.39	14.37
Exotic tree plantations	**0.973**	0.143	-0.083
Fruit tree plantations	0.156	0.104	**0.740**
Other habitats	-0.010	-0.187	**0.822**
Pastures	**-0.846**	-0.205	-0.331
Semi-natural woody habitats	0.050	**0.942**	-0.201
Urbanized ground	-0.429	**-0.805**	-0.184

Appendix D. Comparison between pollination treatments

Table D1. Results of Generalized Linear Mixed Models evaluating the effects of pollination treatments (hand vs. open pollination) on fruit set and seed set. Models included the variance (±SD) estimate for tree and orchard identity, considered as random factors. Response variables were fitted by considering a binomial error distribution (logit link).

Fruit set			
Predictors	**Estimate ± SE/SD**	**z**	**P**
Intercept	-0.109 ± 0.127	-0.857	0.391
Treatment (Open-pollination)	-0.886 ± 0.027	-33.353	<0.001
Tree [Orchard] (random factor)	0.276 ± 0.525		
Orchard (random factor)	0.321 ± 0.567		
Seed set			
Predictors	**Estimate ± SE/SD**	**z**	**P**
Intercept	1.554 ± 0.068	22.74	<0.001
Treatment (Open-pollination)	-0.795 ± 0.022	-36.85	<0.001
Tree [Orchard] (random factor)	0.141 ± 0.375		
Orchard (random factor)	0.066 ± 0.256		

Appendix E. Non-linear response of bird biodiversity to semi-natural woody vegetation.

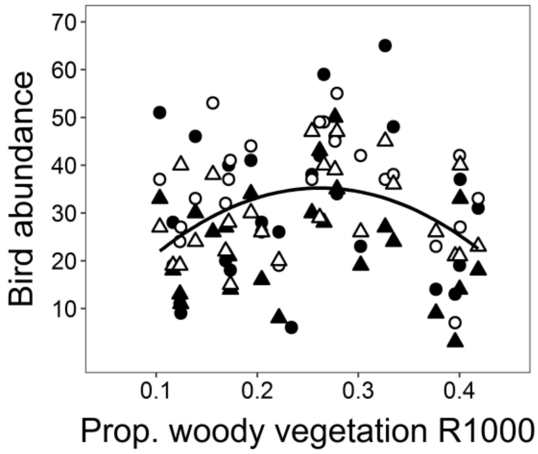


Figure E1. Results of polynomial (quadratic) regression model relating the proportion of semi-natural woody vegetation cover in a 1000-m radius around apple orchards with the abundance of forest insectivorous birds. Colors indicate different years, 2015-2016 (black) and 2016-2017 (white). Seasons are indicated with different shapes for Autumn-Winter (circles) and Spring-Summer (triangles).

Table E1. Generalized Linear Mixed Model evaluating the effect of the cover of semi-natural woody habitat (SNWH, 10000 m radius centered on the sampling station of each orchard) and its quadratic term on the abundance of forest insectivorous birds (Gaussian distribution, identity link). The variance (±SD) estimate for orchard identity, considered as a random factor, is also shown.

Bird abundance **Predictors**	**Estimate ± SE/SD**	**t**	**P**
Intercept	1.62 ± 14.06	0.12	0.909
SNWH	250.01 ± 118.92	2.10	0.048
$SNWH^2$	-476.17 ± 225.18	-2.11	0.047
Orchard (random factor)	68.54 ± 60.60		

Appendix F. Trade-offs between biodiversity groups and between ecological functions.

Table F1. Pearson **c**orrelation coefficients (r) between abundance/richness of insectivorous birds and pollinator insects (spring 2016), as well as between ecological functions, measured as insectivory and fruit set (spring 2016)

	r	**N**	**P**
Wild bee abundance & Bird abundance	0.380	21	0.090
Wild bee abundance & Bird richness	0.520	21	0.016
Wild bee richness & Bird abundance	-0.060	21	0.800
Wild bee richness & Bird richness	0.130	21	0.580
Wild pollinator abundance & Bird abundance	-0.190	21	0.410
Wild pollinator abundance & Bird rich	-0.131	21	0.571
Wild pollinator richness & Bird abundance	-0.22	21	0.340
Wild pollinator richness & Bird richness	-0.083	21	0.720
Fruit set & Proportion of attacked caterpillar models	0.364	21	0.105

Appendix Chapter 2

Appendix A. Study area.

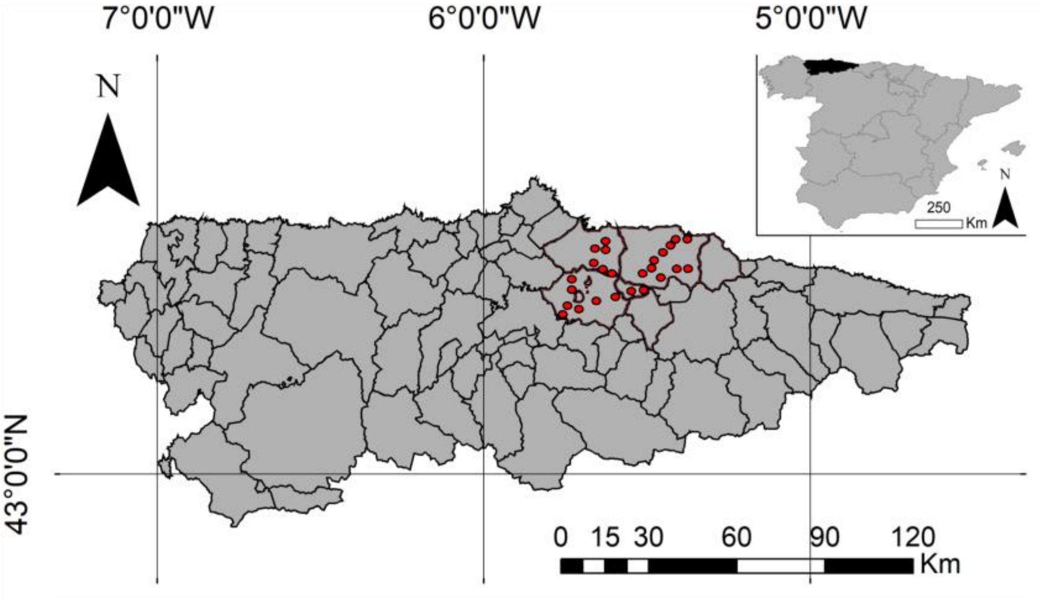


Figure A1. Study area. Inset shows location within Spain of Asturias region. Larger image shows Asturias, with the cider apple orchards selected for this study depicted in red points.

Appendix B. Details on cardboard trap experiment.

Figure B1. Cardboard trap under the first branch and 40 cm above the ground. Image by Daniel García.

Appendix C. Codling moth abundance, crop damage and parasitism rate between years.

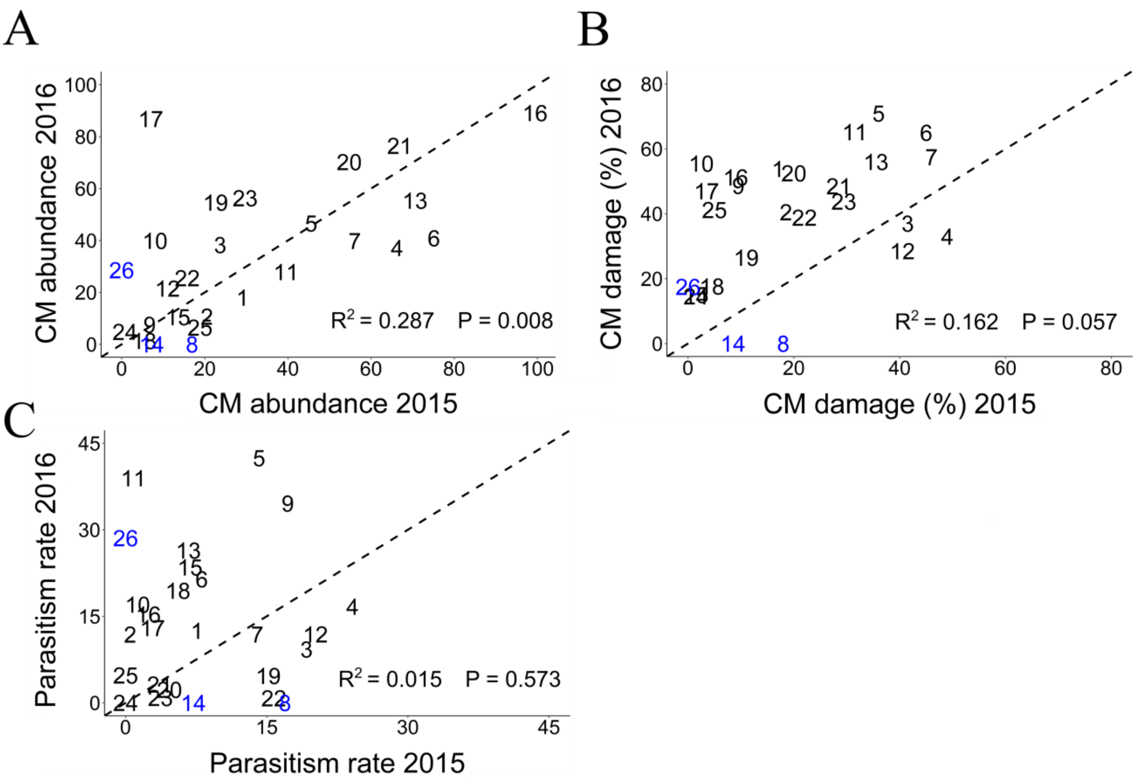


Figure C1. Relationship between the average of codling moth abundance per cardboard trap, codling moth damage and parasitism rate at the 26 cider apple orchards for the years 2015 and 2016 (black numbers: cider apple orchards sampled two years; blue numbers: cider apple orchards sampled just one year). Coefficient of determination and significance level from correlation tests between years are also shown.

Appendix D. CM abundance, CM damage and number of parasitized larvae across years and orchards.

Table D1. Results for accounting the differences in CM abundance, CM damage, number of parasitized larvae and parasitoid richness across years and orchards. T-test was performed on CM abundance, CM damage and number of parasitized larvae to compare between years. Kruskal-Wallis test was performed on CM abundance and CM damage among orchards. Wilcoxon test was performed on parasitoid richness between years.

	Variable	**Df**	**Statistical test value**	**p-value**
CM abundance	Year	22	t = -0.791	0.437
	Orchard (2015)	24	χ^2 = 166.600	<0.001
	Orchard (2016)	22	χ^2 = 159.230	<0.001
CM damage	Year	22	t = -5.955	<0.001
	Orchard (2015)	24	χ^2 = 178.230	<0.001
	Orchard (2016)	22	χ^2 = 119.520	<0.001
Number of parasitized larvae	Year	22	t = -1.523	0.142
Parasitism rate	Year	22	z = -6.026	<0.001
Parasitoid richness	Year	22	z = -1.625	0.104

Appendix E. Model selection process following a step-wise procedure.

Table E1. Models included in the procedure of backward step-wise deletion of non-significant (p>0.05) fixed factors from full local-scalemodels, for response variables of CM abundance, CM damage and No of parasitized larvae. Values of Akaike Information Criterion (AIC) for the different full and nested models, and the results of likelihood ratio tests comparing nested models to their corresponding full model are shown. Non-significant predictors detected to be removed in the step-wise process are shown in bold.

CM abundance(local-scale model)	**df**	**AIC**	**BIC**	**logLik**	**L.Ratio**	**p-value**
Apple production + hedgerow R125 + apple plantation R125 + Orchard size + **Apple canopy cover** + Diameter + Year	10	210.372	229.084	-95.185		
Apple production + **hedgerow R125** + apple plantation R125 + Orchard size + Diameter + Year	9	208.375	225.215	-95.187	0.003	0.957
Apple production + apple plantation R125 + Orchard size + **Diameter** + Year	8	206.390	221.360	-95.195	0.019	0.991
Apple production + apple plantation R125 + **Orchard size** + Year	7	205.057	218.155	-95.528	0.685	0.877
Apple production + apple plantation R125 + Year	6	203.617	214.845	-95.809	1.246	0.871
CM damage (local-scale model)	**df**	**AIC**	**BIC**	**logLik**	**L.Ratio**	**p-value**
Apple production + **hedgerow R125** + apple plantation R125 + Orchard size + Apple canopy cover + Diameter + Year	10	-40.251	-21.539	30.125		
Apple production + apple plantation R125 + **Orchard size** + Apple canopy cover + Diameter + Year	9	-42.155	-25.314	30.077	0.096	0.756
Apple production + apple plantation R125 + **Apple canopy cover** + Diameter + Year	8	-43.663	-28.693	29.831	0.588	0.745
Apple production + apple plantation R125 + **Diameter** + Year	7	-44.592	-31.494	29.296	1.658	0.646
Apple production + **apple plantation R125** + Year	6	-43.425	-32.198	27.713	4.826	0.306

Apple production + Year	5	-42.466	-33.110	26.233	7.785	0.169
Number of parasitized larvae (local-scale model)	**df**	**AIC**	**BIC**	**logLik**	**L.Ratio**	**p-value**
Parasitoid richness + CM abundance+ hedgerow R125 + apple plantation R125 + Orchard size + **Apple canopy cover** + Diameter + Year	11	129.202	149.785	-53.601		
Parasitoid richness + CM abundance+ hedgerow R125 + apple plantation R125 + **Orchard size**+Diameter + Year	10	127.325	146.037	-53.663	0.123	0.725
Parasitoid richness + CM abundance+ **hedgerow R125**+ apple plantation R125 + Diameter + Year	9	126.172	143.013	-54.086	0.971	0.616
Parasitoid richness + CM abundance+ apple plantation R125 + Diameter + **Year**	8	124.877	139.846	-54.438	1.675	0.643
Parasitoid richness + CM abundance+ **apple plantation R125** + Diameter	7	123.662	136.760	-54.831	2.460	0.652
Parasitoid richness + CM abundance+ **Diameter**	6	124.097	135.324	-56.048	4.895	0.429
Parasitoid richness + CM abundance	5	125.105	134.461	-57.552	7.903	0.245

Table E2. Models included in the procedure of backward step-wise deletion of non-significant (p>0.05) fixed factors from full landscape models, for response variables of CM abundance, CM damage and No of parasitized larvae. Values of Akaike Information Criterion (AIC) for the different full and nested models, and the results of likelihood ratio tests comparing nested models to their corresponding full model are shown. Non-significant predictors detected to be removed in the step-wise process are shown in bold.

CMabundance(landscape model)	df	AIC	BIC	logLik	L.Ratio	p-value
Apple production + **apple plantation1000** + snwh1000 + pasture1000 + exotic1000 + Year	9	210.761	227.602	-96.380		
Apple production + **snwh1000** + pasture1000 + exotic1000 + Year	8	208.851	223.821	-96.425	0.090	0.764
Apple production + pasture1000 + **exotic1000** + Year	7	207.050	220.149	-96.525	0.289	0.865
Apple production + **pastures1000**+ Year	6	207.435	218.662	-97.718	2.674	0.445
Apple production + Year	5	206.311	215.667	-98.156	3.551	0.470
CM damage (landscape model)	df	AIC	BIC	logLik	L.Ratio	p-value
Apple production + apple plantation1000 + **snwh1000** + pasture1000 + exotic1000 + Year	9	-37.836	-20.995	27.918		
Apple production + **apple plantation1000** + pasture1000 + exotic1000 + Year	8	-39.002	-24.033	27.501	0.835	0.361
Apple production + **pasture1000** + exotic1000 + Year	7	-40.064	-26.966	27.032	1.772	0.412
Apple production + **exotic1000** + Year	6	-41.107	-29.880	26.553	2.729	0.435
Apple production + Year	5	-42.466	-33.110	26.233	3.370	0.498
Number ofparasitizedlarvae(landscape model)	df	AIC	BIC	logLik	L.Ratio	p-value
CM abundance + parasitoid richness + apple plantation1000 + snwh1000 + **pasture1000** + exotic1000 + Year	10	131.112	149.824	-55.556		
CM abundance + parasitoid richness + apple plantation1000 + **snwh1000**+ exotic1000 + Year	9	129.126	145.967	-55.563	0.0142	0.905
CM abundance + parasitoid richness + apple plantation1000 + exotic1000 + **Year**	8	127.643	142.613	-55.822	0.531	0.767
CM abundance + parasitoid richness + **apple plantation1000** + exotic1000	7	126.411	139.510	-56.206	1.299	0.729
CM abundance + parasitoid richness + **exotic1000**	6	125.268	136.495	-56.634	2.156	0.707
CM abundance + parasitoid richness	5	125.105	134.461	-57.552	3.993	0.551

Appendix F. Codling moth parasitoids and parasitism rate among orchards and years.

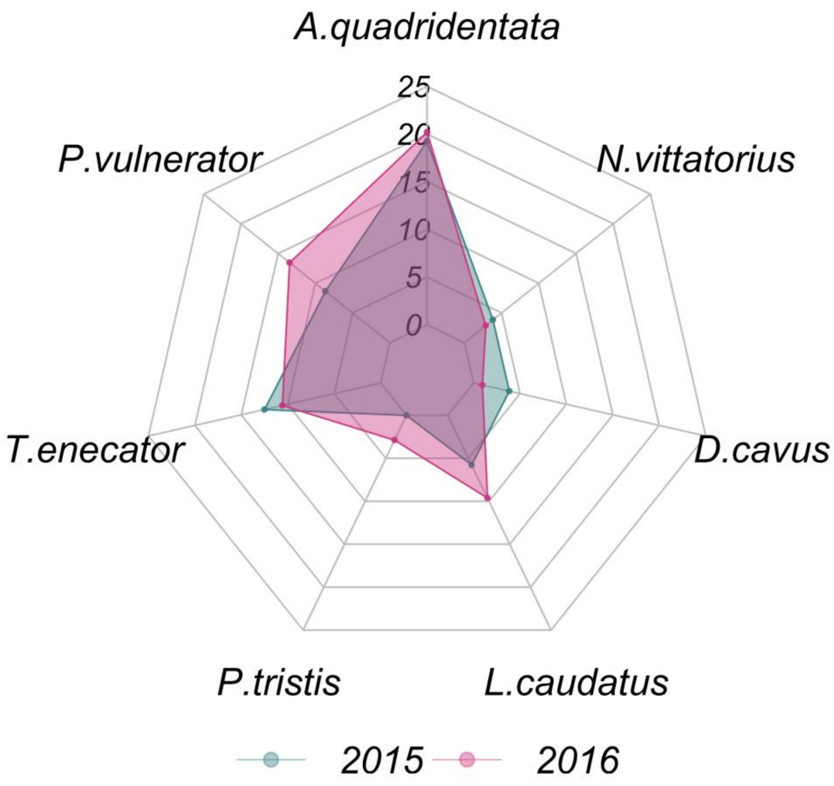


Figure F1. Number of orchards in which each parasitoid occurred.

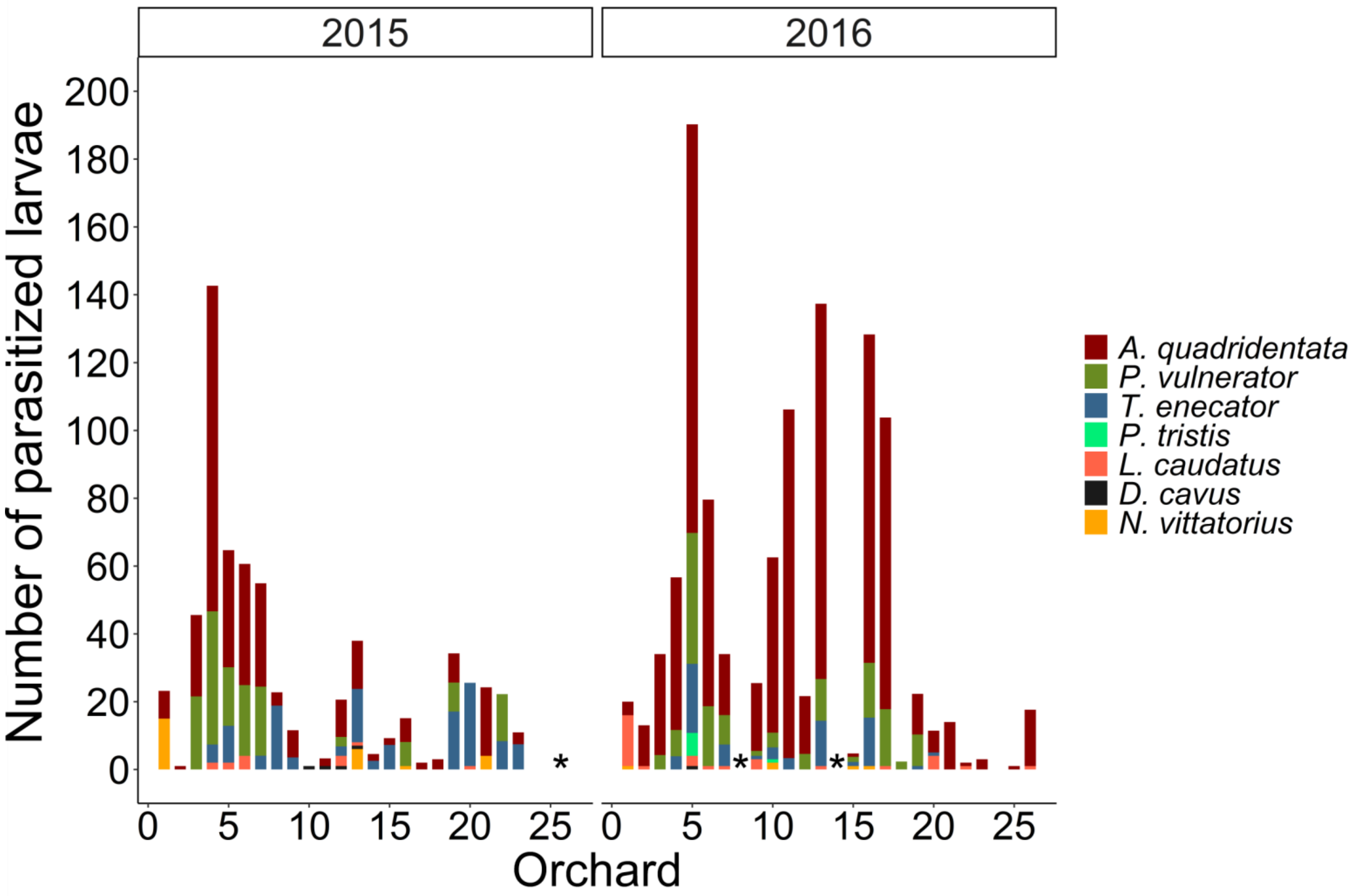


Figure F2. Number of parasitized larvae per year (2015, 2016) by the different species of parasitoids in the twenty six cider apple orchards.* indicates orchards not sampled that year.

Appendix Chapter 3

Appendix A. Final questionnaire.

DATE _____________ START TIME __________ PLACE ________________ SURVEY Nº ____

Good morning/afternoon, my name is _____. We are conducting a survey to evaluate the perception of the agricultural sector on the role of natural enemies in apple crops. The survey is completely anonymous and confidential and your information will only be used for the purposes of this study. This is a research project funded by INIA, MinEco and FEDER.

You do not need special training or even clear involvement in the subject to complete the questionnaire. There are no "right answers", simply express your opinion or knowledge after reading the questions carefully.

The survey takes between 30 and 45 minutes. Thank you very much.

I. Importance of biological control

1. What do you understand by biological control?

   What do you understand by natural enemy?

2. Do you think that natural enemies are important for crops?

   Yes ☐
   No ☐
   Why? ___________________

3. Are natural enemies important for your cider apple orchards?

   Yes ☐
   No ☐
   Why? __________________

4. Does the application of natural enemies change your agricultural production in your cider apple orchards?

   Yes ☐
   No ☐
   Why? ___________________

II. Knowledge of different natural enemies

5. From the species shown in this table, which ones do you know about and/or have you seen in your cider apple orchards? If you know the species but you haven´t seen it, how do you know about it? Which of them are natural enemies?

		Name	Known	Sighted	Not Sighted	If you know about it but you haven´t seen it, how do you know about it?
1						
2						
3						
4						
5						
6						
7						
8						
9						
10						
11						
12						
13						
14						

6. Are there other species that are considered important for pest control that are not displayed in the table?

   Yes ☐ What are they? ___________________
   No ☐

III. Knowledge of natural enemies of pests in cider apple orchards

7. How important are the species shown in the table for your cider apple orchards in terms of pest control? Value their contribution on a scale from 0 (not important) to 3 (very important).

	Species	Importance					Why is it important for pest control?
		0	1	2	3	No answer	
1							
2							
3							
4							
5							
6							
7							
8							
9							
10							

8. What is the importance of the following pests in your apple orchards? (0-not at all harmful; 1-a little harmful; 2-moderately harmful; 3-very harmful; No answer) Which natural enemies from the previous table attack each pest?

	Importance	Attacked by		Importance	Attacked by
Rosy apple aphid			Roe deer		
Woolly apple aphid			Apple proliferation		
Green aphid			Land slug		
Fossorial water vole			Wood leopard moth		
Apple blossom weevil			Cochineal beetle		
Green weevil			Leaf roller		
Codling moth			European canker		
European red mite			Mistletoe		

IV. Socio-economic characteristics

9. Where do you live? ______________________________
10. How many years have you been living there? ___________ years
11. Where were you born? ______________________________
12. What type of relationship do you have with the agricultural sector? (multi-answer)

- ☐ I am a full-time farmer
- ☐ I am a part-time farmer
- ☐ I work transforming agricultural products (secondary sector)
- ☐ I am not a professional farmer but I practice agriculture as a hobby/ for a secondary income/ to maintain family tradition/ to be able to consume my own products
- ☐ I am a member of an agricultural trade union/association
- ☐ I am a management agent/ land manager
- ☐ I am a beekeeper
- ☐ Other, which? ____

13. How many years have you been engaged in agriculture (or worked in a related field)? _____ years

14. If you grow something, what crops do you grow?

15. In your opinion, what are the main problems that you face in terms of crops and production?

16. What are the causes of the problems mentioned above?

17. What do you do with your crop production? (Multianswer)
- ☐ Home supply
- ☐ Barter or exchange
- ☐ Local direct sale
- ☐ Mass market

18. In your apple orchards,

Do you use herbicides? Yes_____ No ______
Do you use insecticides? Yes _____ No ______
Do you use chemical fertilizer? Yes _____ No ______

19. Year of birth _______________

20. How many plots of land do you work?_________ How many hectares?______________ Are they your property? Yes _____ No ______ (Some)How many of them?______

21. What is your monthly income?

a	No income	
b	Less than 600 €	
e	Between 600 and 1200 €	
f	Between 1200 and 1800 €	
g	Between 1800 and 2400 €	
h	More than 2400 €	

22. What is the highest educational qualification you have?

a	No formal studies	
b	Primary school	
c	Compulsory secondary school (16 years)	
d	Non-compulsory secondary school (18 years) or basic vocational qualification	
e	Higher vocational qualification	
f	University degree	

23. Do you currently have any other occupation/profession?

a	Work in the primary sector (farmer, shepherd, fisherman…)	
b	Work in the secondary sector (industry, energy, construction ...)	
c	Work in the tertiary sector / services (markets, hotels, tourism, transport, communications, administration, finance)	
d	Work in the quaternary sector (education, health, research, art)	
e	Retired	
h	Other:	

24. Do you belong to any associations or organizations? (Multi-answer).

Yes, to one related to…	c	Agriculture / Livestock	
	d	Environment	
	e	Politics	
	f	Culture	
	h	Other__________________	
No			

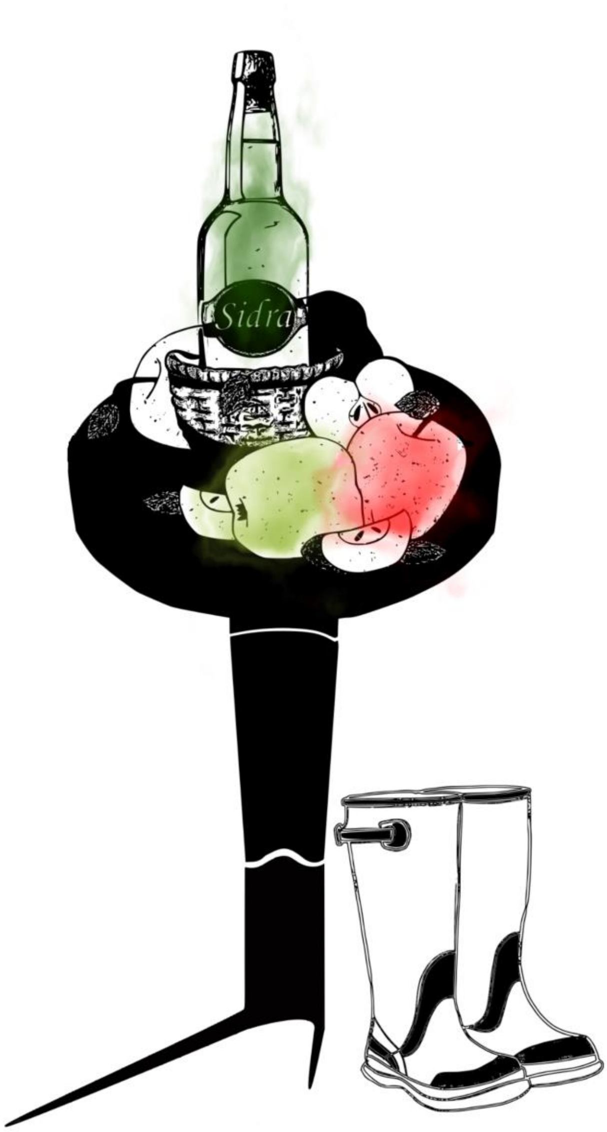
Appendix B. Natural enemies and pests in cider apple orchards.

Table B1. Description of the possible natural enemies used in the questionnaire. * indicates non-natural enemies.

Name used in the study	Common name	Scientific name	Taxonomic group	Description
Slug*	Land slug	*Arion ater* L.	Gastropods	Terrestrial slug (Mollusca; Gastropoda)
Bumblebee*	Buff-tailed bumblebee	*Bombus terrestris* L.	Insects	Widespread large social bee, distinguishable by three-color ringed abdomen
Buzzard	Common buzzard	*Buteo buteo* L.	Birds	Medium-to-large raptor, common resident in northern Spain
Ladybug	Seven-spot ladybug	*Coccinella septempunctata* L.	Insects	Also known as C-7, it is the most common ladybug in Europe
Robin	European robin	*Erithacus rubecula* L.	Birds	Common song bird, easily recognizable by its red breast
Earwig	European earwig	*Forficularia auricularia* L.	Insects	Common omnivorous insect, easily recognizable by its forceps-like pincers
Hoverfly	Dronefly	*Episyrphus balteatus* De Geer	Insects	Common and cosmopolitan hoverfly (Diptera: Syphidae)
Stag beetle*	Stag beetle	*Lucanus cervus* L.	Insects	Common large, xylophagous beetle, easily distinguishable by horn-like mandibles in males
Spider	Spider	*Lycosa sp*.	Arachnids	Non-flying arthropod with 8 joint-legs
Tit	Great tit	*Parus major* L.	Birds	Common tit (Paridae), with a ‘black tie’ being its distinguishing feature
Magpie*	Eurasian magpie	*Pica pica* L.	Birds	Widespread and common crow (Corvidae) easily distinguishable by the black and white body design and a long tail
Woodpecker	European green woodpecker	*Picus viridis* L.	Birds	Insectivorous woodpecker widespread in rural areas
Blackbird	Common blackbird	*Turdus merula* L.	Birds	Common song bird in rural and urban areas, easily recognizable by the black body and a contrasted yellow beak (in male)
Fox	Red fox	*Vulpes vulpes* L.	Mammals	Abundant medium-sized dog-like carnivore (Canidae)

Table B2. Description of the cider apple pests used in the questionnaire and the average importance given by farmers (from 0-not at all harmful to 3-very harmful).

Article and common name	**Scientific name**	**Taxonomic group**	**Area damaged on cider apple trees**	**Importance assigned by farmers (average)**
Apple blossom weevil	*Anthonomus pomorum* L.	Insects	Blossoms	1.4
Green aphid	*Aphis pomi* DeGeer *Aphis spiraecola* Patch	Insects	Leaves and shoots (especially of young trees)	0.9
Land slug	*Arion ater* L.	Gastropods	Fruits	0.4
Fossorial water vole	*Arvicola scherman* Shaw	Mammals	Roots	2.6
Apple proliferation	*Candidatus* Phytoplasma mali	Bacteria	Shoot, leaf, fruit and roots	1.3
Roe deer	*Capreolus capreolus* L.	Mammals	Trunk bark, shoots and leaves	2.2
Codling moth	*Cydia pomonella* L.	Insects	Fruits	2.0
Rosy apple aphid	*Dysaphis plantaginea* Pass.	Insects	Leaves, shoots and fruits	1.8
Woolly apple aphid	*Eriosoma lanigerum* Hausm.	Insects	Aerial and root parts	1.7
European canker	*Nectria galligena* Bres.	Fungi	Trunk and branches	1.7
European red mite	*Panonychus ulmi* Koch	Insects	Buds, leaves and shoots	0.7
Leaf roller	Several species	Insects	Leaves	0.6
Green weevil	*Polydrusus formosus* Mayer	Insects	Leaves	1.1
Cochineal beetle	Several species	Insects	Leaves and branches	0.4
Mistletoe	*Viscum album* L.	Plant	Branches	1.2
Wood leopard moth	*Zeuzera pyrina* L.	Insects	Trunk and branches	0.8


Sidra