# ECOSYSTEM SERVICES IN AGRICULTURAL LANDSCAPES

THE CASE OF FLEMISH APPLE FARMING

Robin DAELEMANS

Supervisor:

Prof. dr. ir. Olivier Honnay

Members of the Examination Committee:

Prof. dr. ir. Wim Van den Ende, Chair
Prof. dr. ir. Koenraad Van Meerbeek
Prof. dr. Tobias Ceulemans
Dr. ir. Serge Remy
Dr. Fanny Boeraeve
Dr. Willem Proesmans

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# SUMMARY

Since the second world war, agriculture in the EU has become increasingly intensive through the introduction of high-yielding crop varieties, advanced farming techniques, and the replacement of biological functions and services with high inputs of synthetic fertilizers and pesticides. While these practices have boosted agricultural production, food security, food quality, and economic development, they have also resulted in severe environmental problems. In concert with further agricultural expansions at the detriment of natural habitats, agricultural intensification has caused an alarming degradation of biodiversity and biodiversity-based ecosystem services (ES). To prevent further environmental degradation and ensure long-term food security, organic farming is increasingly being promoted as a more environmentally-friendly alternative to conventional farming, as it abandons the use of synthetic inputs and stimulates natural ecosystem functions and services to grow and protect crops.

However, despite the steady growth of the organic sector, the actual performance of organic farming in sustaining and enhancing biodiversity and the provisioning of multiple ecosystem services remains poorly understood. This is especially the case for perennial crops, where studies are relatively scarce and often report inconsistent results. Additionally, most studies to date also lack a comparison with a semi-natural benchmark, while this can provide valuable insights into the extent to which biodiversity and biodiversity-based services are affected by different types of agricultural management. Furthermore, also the lower productivity of organic farming relative to conventional farming may raise questions about its sustainability when applied across large areas. Due to lower yields, organic systems indeed require more land per unit of food produced, meaning that for similar production levels, organic systems might have a similar or even greater environmental impact than conventional systems. In summary, more insights are needed into the ecological, agronomical, and economic performance of organic farming, to better evaluate its effectiveness in stimulating environmental, agricultural, and socio-economic sustainability. In this study, we therefore quantified a set of indicators for ecological, agronomical, and economic performance in organic and integrated pest management (IPM) apple orchards, and assessed how these were affected by both local management and the landscape context. Additionally, we compared the ecological performance of both organic and IPM orchards with a semi-natural reference system to better evaluate their potential for biodiversity conservation and maintenance of ecosystem service provisioning.

First, we compared physical, chemical, and biological soil health indicators among organic orchards, IPM orchards, and semi-natural grasslands. No significant differences in soil health between the organic and IPM orchards were found, and neither farming systems showed any evidence of impaired soil health compared to the semi-natural reference, except for higher litter decomposition rates in both orchard types. This suggests that both organic and IPM apple orchards can be managed sustainably in terms of soil health. Nonetheless, the presence of spatial variability in soil health between drive rows and crop rows within orchards suggests that soil management can still be improved, especially in the crop rows of IPM orchards.

Next, we assessed the effects of organic management and the landscape context on biological pest control and pollination services. Natural enemies were more abundant in organic orchards than in IPM orchards, which had a small beneficial effect on biological control services, but overall did not affect pest infestation levels. Moreover, pest infestation levels were positively affected by organic management and the presence of semi-natural habitat in the surrounding landscape. These findings indicate that factors that enhance natural enemies can be even more beneficial to pest species, highlighting the importance of balancing ecosystem services and disservices when designing environmentally-friendly agricultural landscapes. Relative to the semi-natural reference, both organic and IPM orchards showed degraded predator communities and a lower potential for biological pest control. For pollinator communities, few differences were found between organic and IPM orchards, and these did not affect differences in pollination services or yield levels. Instead, yield levels were directly and negatively affected by organic orchard management. Pollinator communities in both organic and IPM orchards benefited from orchard edges, high landscape diversity, and the presence of semi-natural habitat, but were overall less abundant and diverse than those in the semi-natural benchmark. Furthermore, the results obtained for soil-based services, biological pest control, and pollination were combined with measures of biodiversity, yield, and farmer income to quantify overall agroecosystem multifunctionality and to identify possible synergies and trade-offs among services. Overall multifunctionality measures did not differ between organic and IPM orchards, and a clear trade-off between biodiversity and yield was found in both systems.

In conclusion, the relatively limited benefits of organic farming practices in terms of biodiversity conservation and ES provisioning, in combination with the high yield gap relative to the IPM system, indicate the need to look further than the organic/conventional dichotomy to improve orchard sustainability. Maintaining and increasing orchard edges, semi-natural habitats, and landscape complexity seems to be a more effective biodiversity conservation strategy that can also provide the required

ES. The presence of a clear trade-off between biodiversity and yield, even across management systems, and the much higher biodiversity in our semi-natural benchmark further support this conclusion. Therefore, we argue that the focus in apple orchards should be on maintaining or improving functional agrobiodiversity to safeguard ecosystem service provisioning, and that more attention should be given to the preservation of semi-natural habitats for their role in regional biodiversity conservation. Finally, our study supports the view that improving the environmental, agricultural, and socio-economic sustainability of farming requires close collaboration between different stakeholders at the landscape level and adequate policy support at regional, national, and international levels.

# SAMENVATTING

Sinds de tweede wereldoorlog is de landbouw in de EU steeds intensiever geworden door de invoering van nieuwe gewasvariëteiten met een hoge opbrengst, geavanceerde landbouwtechnieken en de vervanging van biologische functies en diensten door grote hoeveelheden kunstmeststoffen en bestrijdingsmiddelen. Hoewel deze praktijken de landbouwproductie, voedselzekerheid, voedselkwaliteit en economische ontwikkeling hebben gestimuleerd, hebben ze ook geleid tot ernstige milieuproblemen. Samen met de verdere uitbreiding van landbouwgebieden ten koste van (half)natuurlijke habitats heeft de intensivering van de landbouw geleid tot een ernstige achteruitgang van de biodiversiteit en op biodiversiteit gebaseerde ecosysteemdiensten. Om verdere degradatie van het milieu te voorkomen en voedselzekerheid op lange termijn te kunnen garanderen, wordt biologische landbouw steeds meer gepromoot als een milieuvriendelijker alternatief voor conventionele landbouw, omdat daarbij wordt afgezien van het gebruik van synthetische inputs en de natuurlijke functies en diensten van ecosystemen worden aangewend voor het telen en beschermen van gewassen.

Ondanks de gestage groei van de biologische sector is er slechts weinig geweten over de mate waarin biologische landbouw effectief bijdraagt aan de instandhouding en verbetering van de biodiversiteit en de levering van allerlei ecosysteemdiensten. Dit geldt zeker voor meerjarige gewassen, waar tot nu toe slechts weinig onderzoek naar is gedaan en vaak tegenstrijdige resultaten worden gerapporteerd. Bovendien ontbreekt in de meeste studies ook een vergelijking met een halfnatuurlijke referentie, terwijl dit waardevolle inzichten kan opleveren in de mate waarin biodiversiteit en ecosysteemdiensten worden beïnvloed door verschillende landbouwsystemen. Verder roept ook de lagere productiviteit van de biologische landbouw ten opzichte van de conventionele landbouw vragen op over de duurzaamheid wanneer dit op grote schaal zou worden toegepast. Door de lagere opbrengsten hebben biologische systemen immers meer land nodig per eenheid geproduceerd voedsel, wat betekent dat ze voor eenzelfde productieniveau een vergelijkbaar of zelfs groter milieueffect kunnen hebben dan conventionele systemen. Samengevat is er nood aan betere inzichten in de ecologische, agronomische en economische implicaties van biologische landbouw om te kunnen beoordelen of het effectief leidt tot hogere duurzaamheid. In deze studie hebben we daarom een reeks ecologische, agronomische en economische indicatoren gekwantificeerd in zowel biologische appelboomgaarden als boomgaarden met geïntegreerde gewasbescherming (Engels: Integrated Pest Management, IPM), en onderzochten we hoe deze indicatoren werden beïnvloed door zowel lokaal beheer als de landschapscontext. Bovendien vergeleken we de ecologische prestaties van zowel

biologische als IPM boomgaarden met een halfnatuurlijke referentie, om zo het potentieel van de boomgaarden voor het behoud van biodiversiteit en ecosysteemdiensten te kunnen evalueren.

Eerst vergeleken we fysische, chemische en biologische bodemgezondheidsindicatoren tussen biologische boomgaarden, IPM-boomgaarden en halfnatuurlijke graslanden. Er werden geen significante verschillen in bodemgezondheid gevonden tussen de biologische en de IPM-boomgaarden, en geen van beide systemen had een verminderde bodemgezondheid in vergelijking met de halfnatuurlijke referentie, behalve een hogere strooiselafbraak in beide boomgaardtypes. Dit wijst erop dat zowel biologische als IPM-appelboomgaarden duurzaam kunnen worden beheerd wat bodemgezondheid betreft. De aanwezigheid van ruimtelijke variabiliteit in bodemgezondheid tussen gangpaden en gewasrijen binnen boomgaarden suggereert echter dat het bodembeheer nog kan worden verbeterd, en dan voornamelijk in de gewasrijen van IPM-boomgaarden.

Vervolgens onderzochten we de effecten van biologisch teelt en landschapscontext op biologische plaagbestrijding en bestuiving. Natuurlijke vijanden waren talrijker in biologische boomgaarden dan in IPM boomgaarden, wat een klein positief effect had op de biologische bestrijding, maar over het algemeen geen invloed had op de plaagdruk. Bovendien was de plaagdruk over het algemeen hoger in biologische percelen en in aanwezigheid van meer halfnatuurlijk habitat in het omringende landschap. Deze bevindingen geven aan dat factoren die natuurlijke vijanden ten goede komen, ook in het voordeel van plaagsoorten kunnen werken, wat belangrijke implicaties kan hebben voor het ontwerpen van milieuvriendelijke agrarische landschappen. In vergelijking met de halfnatuurlijke referentie vertoonden zowel biologische als IPM boomgaarden gedegradeerde gemeenschappen van natuurlijke vijanden en een lager potentieel voor biologische plaagbestrijding. Bestuivergemeenschappen, anderzijds, verschilden slechts minimaal tussen biologische en IPM boomgaarden, en deze verschillen hadden geen invloed op bestuivingsdiensten of gewasopbrengst. Opbrengsten waren echter wel direct en negatief geassocieerd met biologisch beheer. De bestuivergemeenschappen in de boomgaarden deden het over het algemeen beter in de perceelsranden, bij hoge landschapsdiversiteit en bij de aanwezigheid van halfnatuurlijk habitat in de directe omgeving, maar waren over het algemeen minder talrijk en divers dan gemeenschappen in de halfnatuurlijke gebieden. Verder werden de resultaten voor bodemgebonden ecosysteemdiensten, biologische plaagbestrijding en bestuiving ook gecombineerd met metingen van biodiversiteit, gewasopbrengst en het inkomen van de landbouwers om de algemene multifunctionaliteit van de boomgaarden te bepalen en mogelijke synergiën en

ruilfuncties tussen diensten te identificeren. Multifunctionaliteit verschilde niet tussen biologische en IPM boomgaarden, en in beide systemen werd een duidelijke ruilfunctie tussen biodiversiteit en gewasopbrengst gevonden.

Als conclusie kunnen we stellen dat de relatief beperkte voordelen van biologische landbouw op het gebied van biodiversiteitsbehoud en ecosysteemdiensten, in combinatie met het grote verschil in gewasopbrengst ten opzichte van IPM, erop wijst dat er verder moet worden gekeken dan louter biologische en conventionele teelt om de duurzaamheid van boomgaarden te verbeteren. De instandhouding en uitbreiding van perceelsranden, halfnatuurlijke habitats en complexe landschappen lijkt een meer doeltreffende strategie om biodiversiteit en ecosysteemdiensten te onderhouden. Deze conclusie wordt ook ondersteund door de aanwezigheid van een duidelijke ruilfunctie tussen biodiversiteit en gewasopbrengst in beide systemen en de veel hogere biodiversiteit in halfnatuurlijke gebieden. Daarom kan worden gesteld dat het beheer in appelboomgaarden moet focussen op het behouden of verbeteren van functionele agrobiodiversiteit om de levering van ecosysteemdiensten veilig te stellen, en dat meer aandacht moet worden besteed aan het behoud van halfnatuurlijke habitats vanwege hun rol in het behoud van regionale biodiversiteit. Ten slotte ondersteunt onze studie het standpunt dat de verbetering van de ecologische, agrarische en soco-economische duurzaamheid van de landbouw een nauwe samenwerking vereist tussen de verschillende belanghebbenden in het landbouwlandschap, en verder ondersteund moet worden door gepast beleid op regionaal, nationaal en internationaal niveau.

# LIST OF ABBREVIATIONS

| | |
|---|---|
| AECM | Agri-environment-climate measures |
| AIC | Akaike information criterion |
| ANB | Agentschap voor natuur en bos |
| CAP | Common agricultural policy |
| CAP SP | Common agricultural policy strategic plan |
| CICES | Common international classification of ecosystem services |
| dbMEM | Distance-based Moran's eigenvector maps |
| DSNH | Distance to nearest semi-natural habitat |
| EC | European commission |
| ED | Edge density |
| EFA | Ecological focus area |
| ES | Ecosystem service |
| EU | European union |
| FAO | Food and agriculture organization of the United Nations |
| GAECs | Good agricultural and environmental conditions |
| GLMM | Generalized linear mixed model |
| IPBES | Intergovernmental science-policy platform on biodiversity and ecosystem services |
| IPM | Integrated pest management |
| MEA | Millennium ecosystem assessment |
| MRL | Maximum residue level |
| NCP | Nature's contributions to people |
| NMDS | Non-metric multidimensional scaling |
| OTU | Operational taxonomic unit |
| PCA | Principal component analysis |
| PCoA | Principal coordinate analysis |
| PCR | Polymerase chain reaction |
| PES | Payment for ecosystem services |
| PSEM | Piecewise structural equation model |
| RDA | Redundancy analysis |
| SHDI | Shannon landscape diversity index |
| SMR | Statutory management requirements |
| SNH | Semi-natural habitat |
| TEEB | The economics of ecosystems and biodiversity |

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# Chapter 1

General introduction

## 1.1 Agriculture and the ecosystem

### 1.1.1 The concept of ecosystem services

The idea that natural ecosystems are invaluable to human society has long been recognized. In the late 19th and early 20th century, naturalists and scholars like George Perkins Marsh and Aldo Leopold already articulated the importance of preserving natural areas for ecological, cultural and aesthetic values (Mooney and Ehrlich, 1997). However, documentation traces back as far as Plato (c. 400 BC), who connected deforestation in his native province of Attica with increased soil erosion and reduced water availability ("the dying of springs") (Daily, 1997; Feen, 1996). Building on these earlier ideas and inspired by the emergence of global biodiversity crises, energy crises, and resource scarcity, Ehrlich and Ehrlich (1981) introduced the concept of ecosystem services (ES) to provide a more comprehensive framework for understanding how nature's capital benefits and sustains society. This concept was further developed by Daily et al. (1997), who described many ecosystem services in detail and defined them as the natural conditions and processes that sustain human life. Around the same time, Constanza et al. (1997) highlighted the economic importance of ES by providing the first estimation of the monetary value of the entire biosphere. Their publication in *Nature* provoked a great deal of discussion around the ecosystem service concept, as until that moment, ecosystems were solely valued based on the marked values of the products that they delivered. Together, these seminal works have led to an exponential increase in ecosystem service research, policy interest and possible applications over the last few decades (Constanza et al., 2017).

*"Ecosystem services are the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. They maintain biodiversity and the production of ecosystem goods, such as seafood, forage, timber, biomass fuels, natural fiber, and many pharmaceuticals, industrial products, and their precursors. The harvest and trade of these goods represent an important and familiar part of the human economy. In addition to the production of goods, ecosystem services are the actual life-support functions, such as cleansing, recycling, and renewal, and they confer many intangible aesthetic and cultural benefits as well." (Daily, 1997)*

*"Ecosystem functions refer variously to the habitat, biological or system properties or processes of ecosystems. Ecosystem goods (such as food) and services (such as waste assimilation) represent the benefits human populations derive, directly or indirectly, from ecosystem functions. For simplicity, we will refer to ecosystem goods and services together as ecosystem services." (Costanza et al., 1997)*

To make the ecosystem service framework better suited for the assessment, modelling, and valuation of natural capital and to facilitate translation into policy, several classification systems for ecosystem services have been introduced. A first classification was proposed in the Millennium Ecosystem Assessment (MEA, 2005), grouping ecosystem services into four different categories:

- **Supporting** ES: the ecosystem aspects that form the basis of all other ES. E.g. photosynthesis, soil formation, nutrient cycling, food-chain dynamics…
- **Provisioning** ES: the products or materials that are obtained from ecosystems. E.g. food, fodder, fresh water, medicines, fibers…
- **Regulating** ES: the benefits obtained from the regulating processes of ecosystems. E.g. pollination, biological control, carbon sequestration, flood control, climate regulation…
- **Cultural** ES: the non-product benefits that are obtained from ecosystems. E.g. recreation, aesthetic inspiration, spirituality, tourism, mental health…

Each of these categories is connected to elements of human well-being such as security from disasters, sufficient nutritious food, social cohesion and health (Fig. 1.1). The MEA's classification of ecosystem services has been adopted by many initiatives, but ongoing discussions have led to further development of the classification. While a consensus exists on the categorization into provisioning, regulating and cultural services, not all classifications support the potential fourth category of supporting services. The Economics of Ecosystems and Biodiversity (TEEB) project, for instance, added habitat services to the supporting ES category, shifting the focus from supporting processes to the ability of ecosystems to provide habitat and genetic diversity (TEEB, 2010). Other systems such as the Common International Classification of Ecosystem Services (CICES) (https://cices.eu/cices-structure/) exclude the supporting services category entirely because those services are considered part of the underlying structures and functions of ecosystems, and are thus indirectly accounted for in other ES (Masiero et al., 2019). A similar approach is used by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). Building on the ecosystem services concept, the IPBES framework introduced the term Nature's Contributions to People (NCP) and classified contributions (both positive and negative) into material, non-material and regulating groups (Diaz et al., 2015, IPBES, 2019). While these categories are similar as those in the CICES classification, the IPBES framework differs from earlier initiatives because it explicitly recognizes the role of cultural and social views in defining links between people and nature. This holistic and multidisciplinary approach takes into account the knowledge, views and interests of a wide range of

stakeholders, and may therefore lead to better incorporation of ecological and economic knowledge into policy and practice (Diaz et al., 2018).

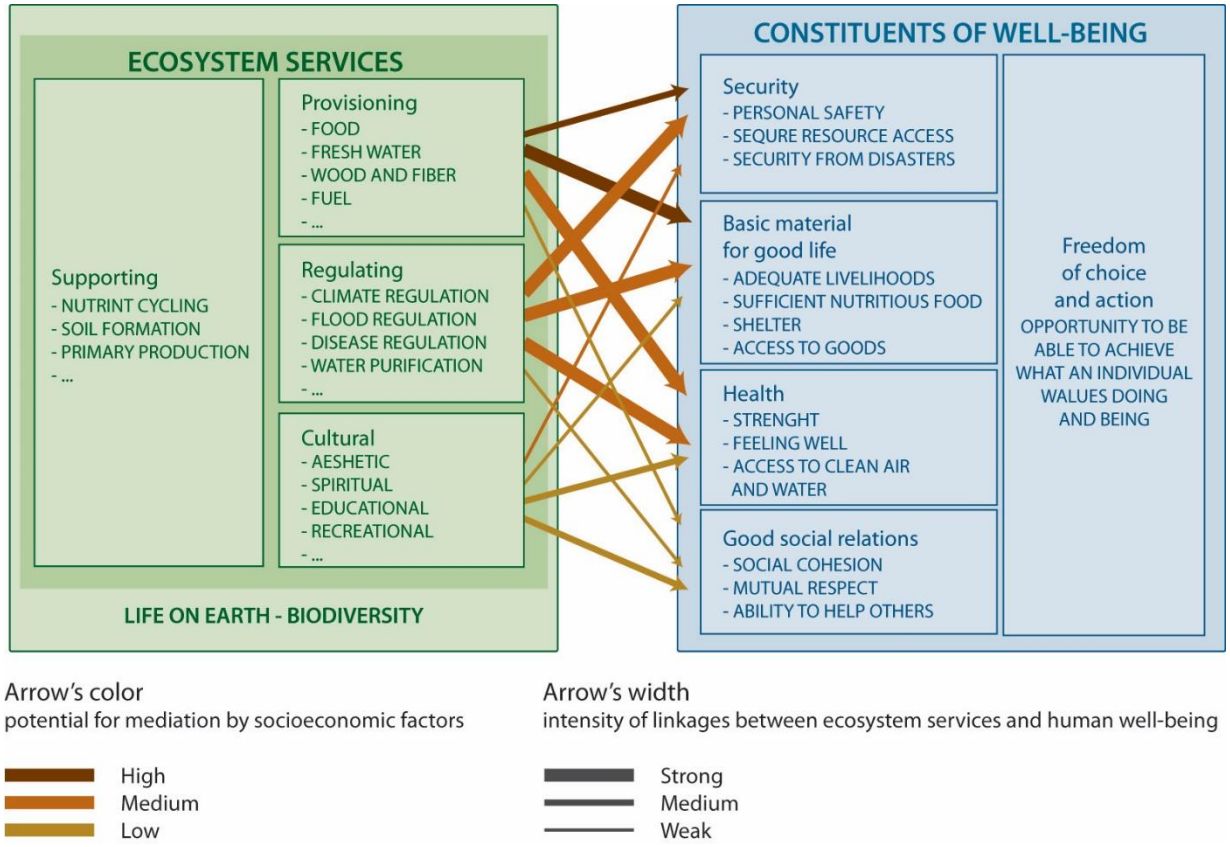



**Figure 1.1**. Relationships between categories of ecosystem services and components of human well-being (MEA, 2005).

While the assessment of ecosystem services has gained significant attention over the last few decades, the fact that some ecosystem processes or goods can also negatively affect human well-being has been largely overlooked. These negative impacts are referred to as ecosystem disservices and include for instance the harm caused by diseases, pests and pathogens, the spread of invasive species and the risk of natural hazards such as wildfires and droughts (Shackleton et al., 2016). Although the conceptual framework, classification and utility of ecosystem disservices is still highly debated, it is increasingly acknowledged that taking into account both services and disservices is essential to assess the net contribution of a specific ecosystem to human well-being (Blanco et al., 2019; Schaubroeck, 2017). Additionally, it is argued that in some cases, managing ecosystem disservices may require lower investments and yield higher benefits for human society, relative to managing ecosystem services (Shackleton et al. 2016). In this text, we define and classify ecosystem services and disservices following the structure of CICES.

### 1.1.2 Biodiversity and ecosystem services

A central topic in the classification and assessment of ecosystem services is the role and position of biodiversity. As biodiversity is a broad concept that includes the diversity within species, between species and of ecosystems, its role in the supply of ecosystem services is complex and multilayered (Mace et al., 2012). Biodiversity is mostly seen as an essential factor underpinning ecosystem functioning and service provisioning because it supports a variety of ecosystem processes, such as carbon sequestration, primary production, predation and decomposition. While taxonomic metrics such as species richness and abundance have been found to be positively correlated with ecosystem processes, it is mainly the diversity of functional traits of the species that are present within the ecosystem that drives overall ecosystem well-functioning (Bruelheide et al., 2018; Gagic et al., 2015) (Fig. 1.2). A high functional diversity increases ecosystem functioning due to a more efficient use of resources, for example due to increased specialization, resource partitioning or interspecific facilitation (Brun et al., 2019; Gagic et al., 2015; Tilman et al., 1997). This complementarity between species, together with spatial differentiation, can cause the entire community to deliver services at levels that exceed the cumulative contributions of the individual species, and is referred to as the *complementarity effect* (Balvanera et al., 2016; Loreau and Hector, 2001). Furthermore, a higher species diversity may also result in more species performing the same functions, leading to a higher functional redundancy within the system (Fetzer et al., 2015). This redundancy can be especially important when functionally similar species respond asynchronously to environmental pressure and disturbance, thus ensuring that ecosystem processes are sustained even if some species are lost. This effect is commonly referred to as the *insurance hypothesis* (Balvanera et al., 2016; Yachi and Loreau, 1999). Finally, a high diversity can also positively affect the provisioning of ecosystem services due to the presence of dominant species that provide exceptionally high levels of ecosystem services, also known as the *selection effect* (Balvanera et al., 2016; Loreau and Hector, 2001).

Although it is often argued that the magnitude of many ecosystem functions and services only depends on a limited number of species or functional groups (Luck et al., 2009), the increased ecosystem stability and service provisioning that is expected with higher biodiversity advocates for the conservation of biodiversity in general, rather than protecting specific species or functional groups. Additionally, due to the great uncertainty of the role of many species and the complex interrelation between species, also the precautionary principle is often quoted as an argument to conserve as many species as possible (Ridder, 2008).

Secondly, besides its role in underlying the delivery of other ES, biodiversity can also be considered as a final ES itself. For example, crop wild relatives can provide genetic diversity that can be used to improve the productivity and quality of cultivated crops. Furthermore, a high diversity of organisms with specific secondary compounds can also be of great value for commercial exploitation, or for the development of novel pharmaceuticals. Biodiversity in itself can also be valued and appreciated for inspirational, educational, spiritual and recreational reasons. Therefore, both genetic diversity and species diversity are valued as ecosystem services or ecosystem goods that directly contribute to human well-being (Mace et al., 2012). This is also reflected in ecosystem management, which often targets the conservation of specific species, species groups or habitat types. In this context, considering biodiversity as a separate ES also stimulates its inclusion in policy and provides extra opportunities for its conservation (e.g., the European habitat and bird directive). Finally, the integration of biodiversity into ES evaluations also helps to better study trade-offs that might exist between biodiversity and other ES.

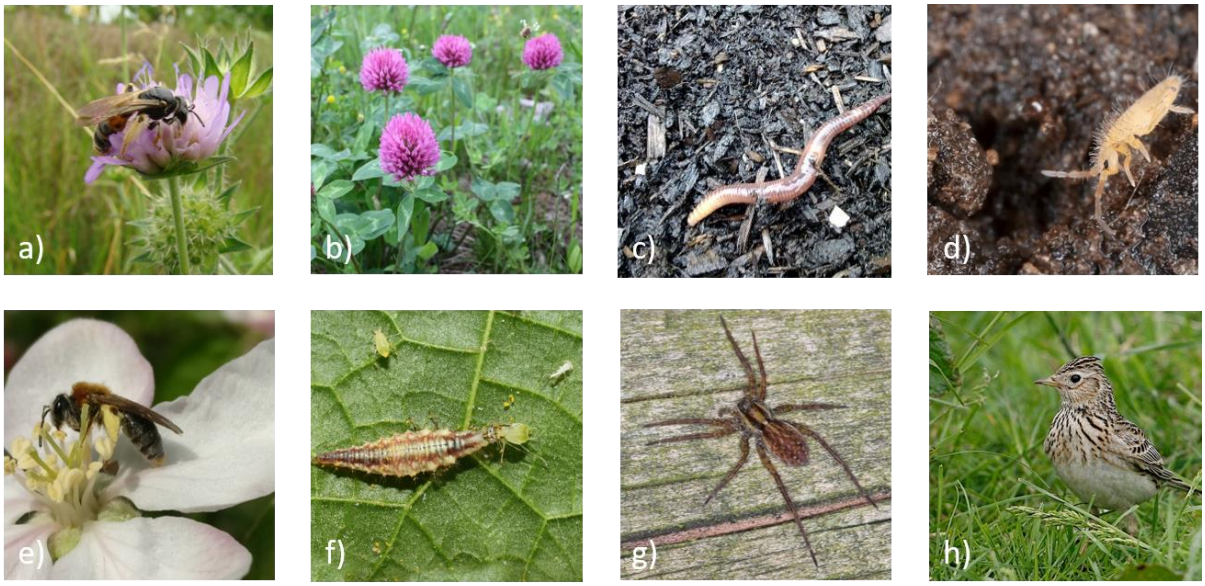



**Figure 1.2**. Ecosystem functioning is driven by the combined effect of the environmental conditions and the functional diversity of the organisms that are present in the ecosystem. Each of these organisms contributes to specific ecological processes due to their species-specific functional traits and biological activity. For example, (a, b) flowering plants provide resources for a variety of organisms, including wild bees, (c) earthworms and (d) springtails contribute to organic matter decomposition, (e) wild bees help pollinate flowering plants and (f) lacewing larvae, (g) spiders and (h) birds all contribute to the control of crop pests.

### 1.1.3 Ecosystem services and agriculture

Agricultural ecosystems are essential to human well-being as they provide society with food, forage, pharmaceuticals and bioenergy. To do so, they strongly rely on a variety of ecosystem services such as pollination, biological pest control, nutrient cycling, soil formation and structure, soil fertility and water provisioning (Power, 2010). Animal pollination, for instance, contributes to the production of 75% of the world's leading food crops and accounts for 9.5% of the value of the global agricultural output (Ollerton et al., 2011). As most of the essential ecosystem services in agricultural landscapes are dependent on biodiversity, local species assemblages will greatly determine the quality and quantity of service provisioning. Many recent studies have shown that within-field biodiversity, as well as the resulting ecosystem services, are in turn strongly affected by the landscape context and the local agricultural management (Couthouis et al., 2022; Karp et al., 2018; Martin et al., 2019; Metzger et al., 2021). Both local and landscape factors act as environmental filters that constrain species based on their biological traits, such as diet breadth and dispersal ability (Weiher et al., 2011) (Fig. 1.3). The landscape context, defined as the configuration and composition of the habitats within a certain perimeter around the agricultural fields, mainly influences the local species pool by controlling the influx of organisms from the surrounding habitat (Martin et al., 2019). Landscapes with a high complexity and a large proportion of semi-natural habitat (SNH) generally facilitate the spillover of dispersal-limited species into the agricultural fields, increasing the diversity of within-field communities (Tscharntke et al., 2005). For example, both landscape edge density and the presence and proximity of SNH have been found to enhance the diversity of pollinators and natural enemies of crop pests, resulting in higher pollination and biological control services, respectively (Dainese et al., 2019; Kennedy et al., 2013; Schoch et al., 2022). However, the net effect of the landscape context on ecosystem services is not always straightforward. Higher landscape complexity, for instance, has also been found to benefit pest species and to delay the colonization of agricultural fields by beneficial arthropods (Chaplin-Kramer et al., 2011; Karp et al., 2018; Wamsera et al., 2011).

At a smaller spatial scale, also the presence of agroecological infrastructures within or around fields is known to enhance the influx of organisms. Just like the wider landscape, elements such as flower strips, grass strips and hedgerows can greatly enhance ecosystem services like biological pest control and pollination (Feltham et al., 2015; Van Vooren et al., 2017), but conversely can also act as refugia for pest and reduce or delay the influx of beneficial organisms (Blitzer et al., 2012; Gontijo, 2019; Metcalfe et al., 2019). Once spillover from surrounding habitat has occurred, the local biotic and abiotic conditions will further determine if species can survive and establish within the

agricultural field. These filters are strongly linked with the agricultural management, as disturbances like soil tillage, fertilizer and pesticide applications are detrimental to many species (Bourgeois et al., 2019; McLaughlin and Mineau, 1995; Ryan et al., 2010). As a result, local species assemblages will consist of species that can either cope with these disturbances (resident species), or move between the agricultural land and its surroundings (transient species) (Metcalfe et al., 2019). In conclusion, the combined effects of both natural and management-induced filters will determine the within-field communities that drive ecological functions and processes, and therefore determine the provisioning of ecosystem services (or disservices) within the agricultural land.

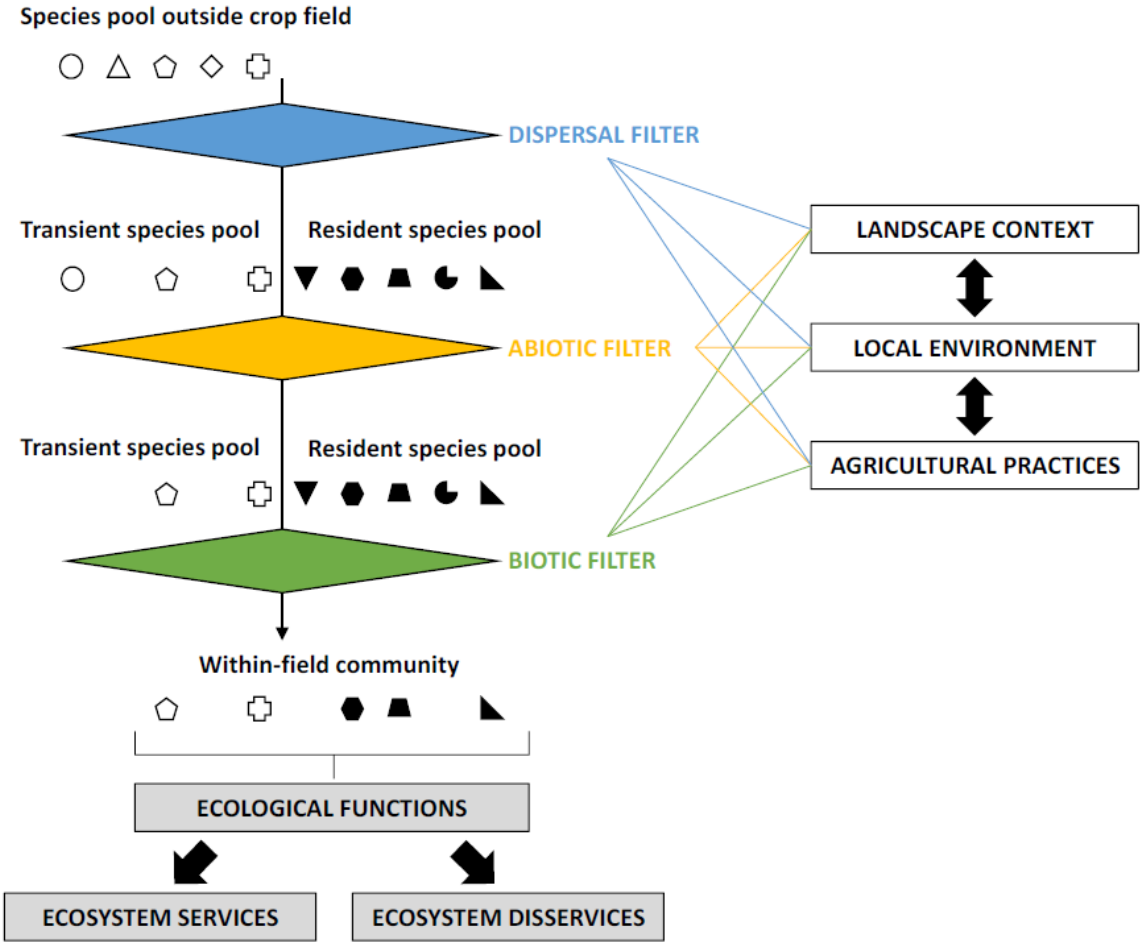



**Figure 1.3.** Schematic overview of the environmental filters that determine the composition of within-field communities. In accordance to the community assembly theory, species from the regional species pool are filtered based on functional traits such as dispersal ability, competitiveness, diet breadth or tolerance to disturbance (Weiher et al., 2011). The combined effect of landscape context, local environment and agricultural practices determines the strength of each filter. The resulting within-field communities perform ecological functions and processes that regulate the provisioning of ecosystem (dis)services. Figure adapted from © S. Boinot, with permission.

## 1.2 Agricultural expansion and intensification

### 1.2.1 Agricultural intensification and environmental impact

Since the second World War, the development of new technologies and farming practices has tremendously changed modern agriculture. Increased mechanization, high-yielding crop varieties and the replacement of biological functions and processes by high inputs of synthetic agrochemicals have all greatly boosted agricultural production, food security, food quality and economic development (Bommarco et al., 2013; Tilman et al., 2017). However, as the growing population is expected to further increase global food demand by an additional 50% by 2050, safeguarding food security will also remain a major challenge in the next decades (FAO, 2022; van Dijk et al., 2021). While this growing demand for agricultural products might be partially compensated by measures such as shifting towards plant-based diets and reducing food loss and waste, it is predicted that agricultural productivity still needs to increase by at least 43% to feed the global population in 2050 (European Commission, 2017; World Resources Institute, 2019). At the same time, it has become clear that agricultural intensification has given rise to severe environmental problems. The high use of pesticides and fertilizers has caused water pollution and degradation of habitats, large scale monocultures have simplified the landscape and led to a decline in resources and habitat for wild species, and up to 40% of agricultural fields experience problems with erosion and soil degradation (Beckmann et al., 2019; Clough et al., 2020; Tilman et al., 2017). Together with further agricultural expansions at the detriment of natural habitats, these factors have severely degraded biodiversity as well as biodiversity-based ecosystem services that support agricultural productivity (Bommarco et al., 2013; Ramankutty et al., 2018). To achieve both long-term food security and environmental sustainability, it is therefore necessary to develop farming systems that can reconcile high productivity with minimal environmental impacts.

### 1.2.2 Policy responses for sustainable agriculture

The recognition of the need to decrease the environmental footprint of agriculture has led to the development of various initiatives aimed at promoting environmentally friendly farming. In the European Union, the Common Agricultural Policy (CAP) is the main policy instrument for supporting sustainable farming practices (European Union, 2012). The CAP was originally established in 1962 with the aim of reviving the agricultural sector and food markets following the second world war. However, over time, the policy underwent several reforms that led to its increased support for agricultural activities that align with the environmental and climate goals of the

European Union (Hill, 2012). Currently, the CAP consists of two pillars, with the first pillar covering direct income support and marked measures, and the second pillar addressing rural development. Several measures that stimulate sustainable farming and enforce compliance with EU environmental law have a central position within both these pillars (European Commission, 2019).

Within the first pillar, there is the principle of 'cross-compliance', which entails that farmers need to comply with EU law relating to animal health and welfare, food safety and public health, land management, and environmental protection in order to receive direct income support. Rules that farmers need to comply with include on the one hand the Good Agricultural and Environmental Conditions (GAECs), which define requirements and standards for water, soil, carbon stocks and landscape that apply to all farmers receiving support, and on the other hand the Statutory Management Requirements (SMRs), which apply to all farmers whether or not they receive income support. The SMRs include compliance with several directives, such as the Directive on the use of nitrates (Council Directive 91/676/EEC), which is one of key instruments to protect surface water and groundwater from nitrate pollution resulting from agricultural practices. In Flanders, this directive is formalized in the 'Mestdecreet' (Mest Actie Plan, MAP), which regulates for instance the fertilization intensity, the allowed fertilizer types and the storage of manure (VLM, 2018). New requirements in the most recent MAP (MAP 7, which will likely come into effect starting from January 1, 2024) include a cultivation-free zone of six meters along all watercourses, a reduction of fertilization standards by 15% and, from 2024, a complete ban on fertilization from the 1st of August (Minaraad, 2022). Other environmental directives that farmers need to comply with include the Birds an Habitat Directives, as part of the Natura 2000 network. The Natura 2000 network consists of areas that all have specific conservation prescriptions for animals, plants or habitats (European Commission, 2008). In Flanders, 12% of the land area is included in the Natura 2000 network, of which one third is under agricultural management. The requirements for farmers in relation to the Natura 2000 network are mostly focused on the prevention of excessive nutrient use as to not jeopardize the quality of nature within the Natura 2000 sites (ANB, 2017). Within the Natura 2000 sites, there is a complete ban on the use of fertilizers. In addition to the cross-compliance conditions, there are also three mandatory greening measures included in the first pillar of the CAP. These measures include i) diversifying crops, ii) maintaining permanent grasslands and iii) dedicating 5% of arable land to ecological focus areas (EFAs). While the GAECs and SMRs are passive measures following the "Polluter-Pays Principle", the greening measures follow the "Provider-Gets Principle" and compensate the income loss following implementation.

The second pillar of the CAP concerns the rural development policy, which strengthens the first pillar of direct income support and marked regulations by stimulating investments and farming activities that contribute to the environmental sustainability of rural areas. The second pillar supports for instance initiatives such as the Agri-Environment-Climate Measures (AECMs), which provide farmers with compensations when they voluntarily implement environmentally friendly practices such as the management and protection of (semi-)natural elements in the landscape, or the implementation of grass strips for erosion control. Furthermore, other measures within the second pillar include subsidies for organic farming, payments related to the Natura 2000 network and Water Framework Directive, and payments for areas that face natural or other specific constraints (European Commission, 2019).

In the newest reform of the CAP (2023-2027), some changes were implemented that should lead towards a fairer, greener and more performance-based CAP (European Commission, 2022). Within the first pillar, the cross-compliance and greening measures are now aggregated in the New Enhanced Conditionality, which entails that farmers have to comply to a stronger set of mandatory requirements to receive direct income support. Additionally, the reform also included the introduction of voluntary eco-schemes within the first pillar, which are direct payment schemes from the EU to reward farmers that take actions to protect the climate, environment, water quality and biodiversity (Lampkin et al., 2020). Furthermore, the New Delivery Model of the CAP also requires all member states to draw up a CAP Strategic Plan (CAP SP). Each plan should address the coordination and implementation of CAP interventions (GAECs, SMRs, AECMs and eco-schemes) according to the specific needs of the member state, and should deliver substantial results in relation to the objectives of the CAP (European Commission, 2023). With this new approach, the CAP shifts from income support based on 'compliance' towards a greater performance- and results-based policy, with higher flexibility for the member states to implement measures according to their own needs.

The CAP's environmental goals are furthermore also reflected in the European Green Deal (European Commission, 2020a). This initiative was launched by the European Commission in 2019 and aims at reaching climate neutrality by 2050. Central elements within the Green Deal with a strong link to agriculture are the Biodiversity Strategy and the Farm to Fork Strategy, both of which heavily rely on the CAP to deliver on their goals (European Commission, 2020b). The Biodiversity strategy mainly aims at conserving nature and reversing the degradation of ecosystems. Its targets for 2030 include for instance that 30% of EU's land needs to be legally protected, with 10% under strict protection, and that at least 10% of agricultural land is under high-diversity

landscape features. The Farm to Fork strategy mainly intends to make the EU food system more sustainable, and includes targets such as reducing pesticide use by 50%, reducing fertilizer use by 20% and increasing organic farming to reach 25% of the EU's agricultural land by 2030.

## 1.3 Integrated pest management (IPM) and organic farming

### 1.3.1 Integrated pest management

As part of the European Commission's strategy to promote sustainable farming within the EU, all professional farmers are obliged since 2014 to apply Integrated Pest Management (IPM) practices in accordance with the 2009/128/EC directive on the sustainable use of pesticides (EU, 2009). IPM entails a more sustainable approach to pest control that focuses on minimizing the use of pesticides and maximizing the use of more environmentally friendly strategies. The first principle of IPM concerns the prevention and/or suppression of pests to prevent them from becoming a threat, for instance through crop rotation, the use of resistant cultivars or implementation of adequate cultivation techniques such as under-sowing or adjusting sowing dates and densities (EU, 2009; DLV, 2019). Furthermore, IPM also involves the establishment of action thresholds, which are pest population sizes or environmental conditions at which the implementation of pest control measures is necessary to prevent economic damage. To make appropriate pest control decisions in association with these action thresholds, IPM requires careful identification and monitoring of pest species. This identification and monitoring should prevent that the wrong kind of pesticides are used, or that they are used when they are not really necessary. When monitoring, identification, and action thresholds indicate the need for pest control, and preventive strategies prove ineffective or unviable, IPM programs proceed to decide on suitable control methods based on their effectiveness and risk (DLV, 2019). Initially, less risky options are chosen, including for instance highly target-specific chemicals such as pheromones or mechanical weeding. In cases where less risky control measures prove inadequate based on further monitoring, additional measures such as targeted pesticide spraying are allowed. The application of broad, non-specific pesticides is used as a final recourse. When pesticide applications are unavoidable, crop protection products should be selected based on the following criteria: (i) pose the least harm to humans, (ii) exhibit high selectivity, (iii) do not harm natural enemies, (iv) have low persistence, (v) carry minimal risk of surface or groundwater contamination, and (vi) have been thoroughly evaluated for potential side effects (DLV, 2019).

However, the extent to which the European Commission's approach to lower the harmful effects of pesticides has been effective, remains largely unknown. While the use of some dangerous pesticides has been banned, the total sales of pesticides in the EU has remained stable at around 360 million kilograms per year between 2011 and 2021 (Eurostat, 2023). While many studies have described the environmental effects of specific IPM practices, an overall estimation of the environmental impact of IPM policy in comparison with previous conventional management (before 2014) is lacking (Deguine et al., 2021). A common critique on the IPM system concerns the high inconsistency between IPM concepts, practices, and policies between and within EU member states (Deguine et al., 2021; Helepciuc and Todor, 2021). Moreover, farmers are often not adequately involved in the development of IPM technologies, and as a results, the integration of IPM practices often deviates from its fundamental principles, leading to ineffective outcomes. It has for instance been show that, in the majority of cases, chemical control still remains the basis of plant protection programs, despite continuous policy efforts to promote IPM (Deguine et al., 2021).

### 1.3.2 Organic farming in Europe and Flanders

The growing awareness of the imperative to reduce the environmental impact of agriculture has also led to the development of new farming systems that prioritize sustainability. In this context, organic farming is often put forward as a more sustainable alternative to conventional farming, and has gained significant traction in recent years due to promotion of the Farm to Fork strategy and financial support by the CAP. Organic farming strongly builds on the idea of ecological intensification, which is to achieve environmental sustainability by implementing nature-oriented measures such as the incorporation of semi-natural elements in the agricultural landscape and the application of ecological principles in agricultural practices (Bommarco et al., 2013; Tittonell, 2014). While the concept was already developed in the early 20$^{th}$ century, its popularity increased sharply from the 1990s due to increasing public concerns about the health risks of pesticides, antibiotics and hormones used in food production (Seufert et al., 2017). Today, unlike other alternative forms of agriculture (e.g. agroecological farming, agroforestry, permaculture and biodynamic farming) organic farming is recognized worldwide, has a clear system of control and certification and has an own specific label to identify its produce (Migliorini and Wezel, 2017). The regulations and restrictions of organic farming include for instance the prohibition of synthetic fertilizers, synthetic pesticides, genetically modified organisms and processing additives, and violation of these rules can cause farmers to lose certification and access to markets. In Europe, organic production and labeling are legally governed by

Regulation (EU) 2018/848 of the European Parliament and the Council of 30 May 2018, repealing and replacing the former EU Council Regulation (EC 2007) No 834/2007 of June 2007 (EU, 2018).

Organic farming constitutes only 1.5% of global agricultural land area, but is one of the fastest growing agricultural sectors (Willer et al., 2021). The share of agricultural land under organic farming in Europe increases by 5.7% annually, and has more than doubled in the period between 2012 and 2020 (Eurostat, 2022). In 2020, 9.1% of the total EU farmed area was under organic management, mainly consisting of permanent grassland (40%), green fodder (17%), cereals (16%) and perennial crops such as fruit orchards and vineyard (11%). In Belgium, the share of agricultural land under organic farming is close to the European average (7.2% in 2020), but is very unevenly distributed between the northern part (Flanders) and the southern part (Wallonia) (De Cock et al., 2016). Only 1.7% of the total agricultural area in Flanders is under organic management, although this has been steadily increasing (Fig. 1.4) (Eurostat, 2022; Timmermans and Van Bellegem, 2022). Furthermore, this positive trend is expected to continue in the next years, as both the consumer demand and policy support for organic farming are still increasing (EU, 2020; Willer et al., 2021). Compared to the previous CAP period (2013-2022), the revised 'green architecture' of the CAP (2023-2027) entails some additional benefits for Flemish organic farmers. Under to previous CAP, farmers received a fixed yearly compensation during conversion (depending on the sector, e.g. €860 $ha^{-1}$ for permanent fruit farms) and €210 $ha^{-1}$ for the continuation of organic farming afterwards. Under the new agricultural policy, compensations during conversion have increased to €1700 $ha^{-1}$ across all sectors. The subsidies for continuation are now dependent on the farms size, with €200 $ha^{-1}$ for the first 5 ha, €100 $ha^{-1}$ for up to 70 ha additional to the first 5 ha, and €50 $ha^{-1}$ for any area above 75 ha. Furthermore, the newly introduced eco-schemes now also allow organic farmers to apply for additional compensation when they apply certain environmental measures, which was not possible under the previous CAP. For mechanical weeding, for instance, which most organic farmers already apply, they can request a compensation of €310 $ha^{-1}$. In total, the subsidies available for organic farmers under the current CAP are thus higher than those available during the previous CAP period.

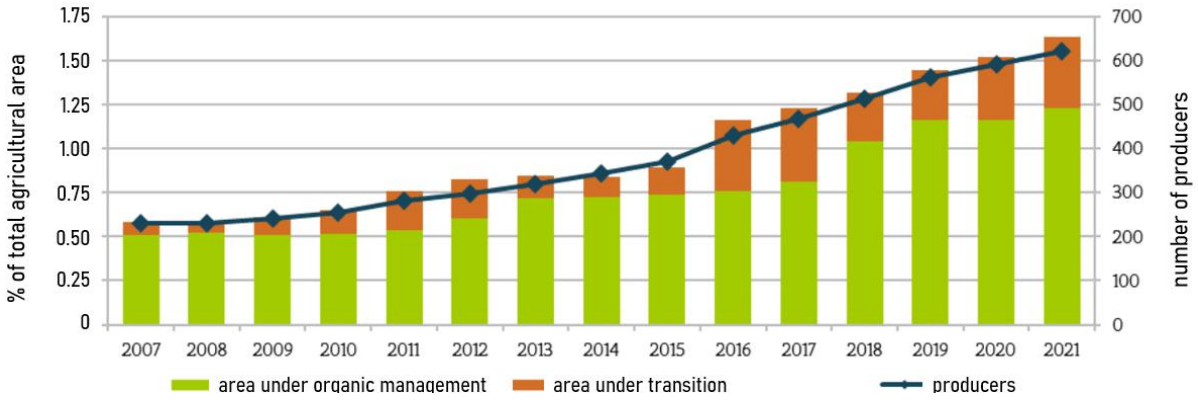



**Figure 1.4.** Evolution of the share of organic farming in the total agricultural land area (left axis) and the number of organic producers (right axis) in Flanders, Belgium. Figure adapted from Timmermans & Van Bellegem (2022).

### 1.3.3 Ecological, agronomical and economic performance of organic farming

Although the organic sector is steadily growing due to increasing consumer demand and policy support, the effects of organic farming on environmental and agricultural sustainability still remain debated. Several meta-analyses have shown that organic farming generally increases farmland biodiversity, reporting on average 30% higher species richness and 50% higher species abundance in organic farms relative to conventional farms (Bengtsson et al., 2005; Tuck et al., 2014). However, these effects are found to differ between taxonomic groups, functional groups and crop types (Fig. 1.5). Additionally, higher biodiversity in organic farms does not necessarily entail that these systems also support higher levels of agroecosystem functions and services. Due to the lower effectiveness of organic pesticides, for instance, both natural enemies and pest species can benefit from organic farming, leading to inconsistent outcomes for biological pest control services (Muneret et al., 2018a). Pollination services, on the other hand, are mostly reported to benefit from higher pollinator diversity in organic farms, although results seem to depend strongly on crop type. While most studies on annual crops for instance report higher pollinator richness, abundance and diversity as well as higher pollination services under organic management, studies in perennial crops are scarce and yield inconsistent results (Andersson et al., 2014; Pardo et al., 2020; Porcel et al., 2018). Furthermore, the effects of organic farming on biodiversity and ecosystem services are also found to strongly dependent on the landscape context. The intermediate landscape-complexity hypothesis states that the effectiveness of local management practices aimed at increasing biodiversity and associated ecosystem functions and services will be highest in relatively simple landscapes with intermediate

complexity (Tscharntke et al., 2012). In landscapes with high complexity and a high proportion of semi-natural habitat, biodiversity and biodiversity-based services are expected to reach high levels throughout the entire landscape, so that the effects of local agricultural management will be negligible. In very simple landscapes, on the other hand, the regional species pool is expected to be too small or isolated for management practices to effectively enhance local biodiversity and service provisioning. While several studies support this hypothesis, these effects are also found to depend greatly on the study region and the identity and mobility of the studied taxa (Batáry et al., 2011; Tscharntke et al., 2012). For example, some studies found higher beneficial effects of organic farming in complex landscapes (Martin et al., 2019; Ricci et al., 2019), while others showed that organic farming more effectively enhances biodiversity and ecosystem services when applied in simple landscapes (Flohre et al., 2011a; Lichtenberg et al., 2017; Tuck et al., 2014). To assess how organic farming affects local biodiversity and ecosystem services, it is thus essential to simultaneously take into account the landscape context. Finally, to fully understand how different agricultural management systems affect biodiversity and ecosystem services, it is also useful to evaluate them against a reference where no agricultural management is applied (Forrest et al., 2015; Katayama et al.., 2019). A comparison with a (semi-) natural benchmark is seldom implemented, but provides valuable insights into the extent to which biodiversity and service provisioning have been degraded due to agricultural management, as well as an idea about the potential biodiversity that can be reached within the agricultural fields.

Despite the potential environmental benefits of organic farming, its lower productivity compared with conventional farming systems has raised concerns about its actual sustainability. Meta-analyses have shown that the yields of organic farming systems are on average 19-25% lower than those of conventional systems (De Ponti et al., 2012; Ponisio et al., 2015; Seufert, 2019; Seufert et al., 2012). These lower yields are mainly attributed to the lower efficiency of organic fertilizers, pesticides, and herbicides compared to synthetic products, leading to lower soil fertility and higher levels of pest infestation in organic systems (Büchi et al., 2019; Ponisio et al., 2015; Seufert et al., 2012). Additionally, organic systems are also found to have, on average a, 15% lower yield stability than conventional agriculture (Knapp and van der Heijden, 2018). As a result, organic systems require more land per unit of food, meaning that for similar production levels, organic systems might have a similar or even greater environmental impact compared to conventional systems (Clark and Tilman, 2017; Seufert and Ramankutty, 2017). However, lower yield levels in organic farming do not necessarily lead to lower profitability. Despite higher production costs, the economic benefits of

organic farming are on average 22-35% higher than those of conventional farming because of higher product valuation and subsidies (Crowder and Reganold, 2015; Shennan et al., 2017; Smith et al., 2020). Overall, many questions remain regarding the real environmental, agronomical, and economic performance of organic farming, and it is especially unclear what the long-term effect will be if the increase in organic farming continues (Seufert and Ramankutty, 2017).

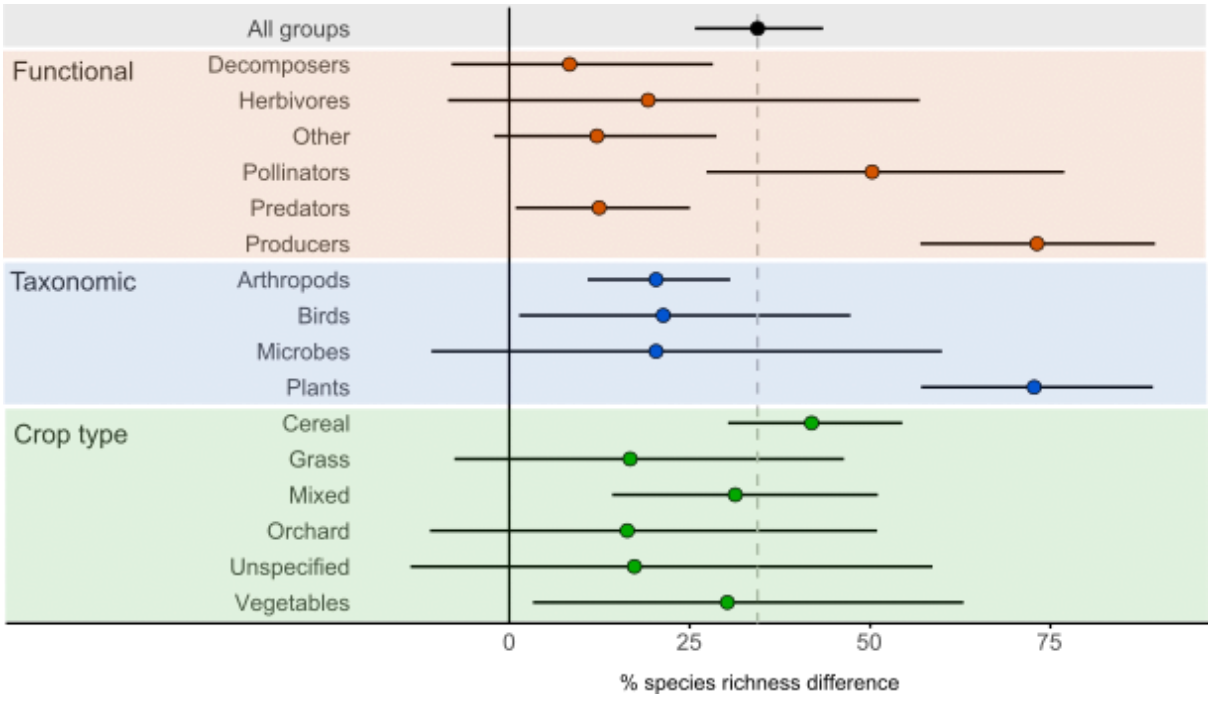



**Figure 1.5.** The difference in species richness (%) in organic farms as compared to conventional farms for different functional groups, taxonomic groups and crop types, as well as the overall mean difference across all groups of organisms (dotted line). Figure adapted from Tuck et al. (2014).

### 1.3.4 Agroecosystem multifunctionality

In recent years, there has been a growing recognition of the importance of agroecosystem multifunctionality in sustainable agriculture (Manning et al., 2018). While traditional approaches have focused on individual services, such as maximizing yields and economic returns, agroecosystem multifunctionality takes a more holistic approach that recognizes the various functions and services provided by agricultural ecosystems. As many ecosystem functions and services are interconnected, it is argued that multifunctional landscapes are more resilient to disturbances and thus increase agricultural sustainability and food security (DeClerck et al., 2016; Seppelt et al., 2020; Winkler et al., 2017). Within agroecosystem multifunctionality research, two different fields can be distinguished; one at the level of ecosystem functions and one at the level

of ecosystem services. The former addresses more fundamental questions about the provisioning of multiple functions, without referring to a specific spatial scale, type of land use of human benefit (Huang et al., 2015; Manning et al., 2018). This area mainly concerns the links between biodiversity and ecosystem functioning, such as the crucial role of biodiversity in supporting the three main axes of ecosystem functioning: the maximum productivity, water use efficiency and carbon use efficiency (Yan et al., 2023). The second area addresses more applied questions by focusing on the simultaneous provisioning of multiple ecosystem services that are relevant for human-wellbeing. Unlike the ecosystem functioning approach, it also takes into account spatial and socio-economic aspects, and is often used to evaluate how land use strategies relate to different stakeholder objectives (Manning et al., 2018). For the purpose of this text, the term 'multifunctionality' will refer to this second area of research, concerning the simultaneous provisioning of multiple ecosystem services.

As it is not feasible to take into account all possible ecosystem services, the calculation of agroecosystem multifunctionality requires selecting the services that are relevant for the specific study case. This selection can be based on, for instance, specific ecological situations, different stakeholder interests or relevant policy objectives. A priori knowledge of possible interaction between services can also be used to select relevant bundles of ES, as the existence of synergies and trade-offs can greatly determine management outcomes. For the actual quantification of multifunctionality, two main approaches exist: the averaging approach and the threshold approach. In the averaging approach, multifunctionality is calculated as the average of the standardized values of all separate ecosystem service measures (Byrnes et al., 2014; Manning et al., 2018). The threshold approach, on the other hand, counts the number of services that exceed a certain threshold. The threshold for each separate service can be preset, or can be expressed as a certain percentage of the highest observed level of service provisioning within the study (Byrnes et al., 2014; Manning et al., 2018; Perkins et al., 2015; Soliveres et al., 2016; Van Der Plas et al., 2016). A relevant threshold for an agroecosystem can for instance be a yield target for agricultural production, below which farming is not profitable and thus entails no benefit for the farmer. Additionally, as a stakeholder might attach different value to different ecosystem services (e.g. agricultural production is the main objective for a farmer), the weight of a certain service in the overall multifunctionality measure might also vary. Therefore, several calculations of multifunctionality can be made for the same system when there are multiple stakeholders involved, as each stakeholder or stakeholder group might value ecosystem services differently (Manning et al., 2018). While there is still some discussion about the conceptualization and calculation of agroecosystem

multifunctionality, it is considered a good starting point to better understand the impact of different types of land use on multiple service provisioning (Hölting et al., 2019). In the context of organic farming, few studies so far have investigated how organic management affects agroecosystem service multifunctionality in terms of its ecological, agronomical and socio-economic performance, and the results remain largely inconclusive. While Wittwer et al. (2021) found higher overall multifunctionality under organic management, this was not confirmed by the studies of Couthouis et al. (2022) and Ostandie et al. (2022), although they did found higher ecological performance and lower trade-offs between ecosystem services under organic management. Furthermore, the effects of local management on multifunctionality might also interact with the landscape context. Characteristics of the surrounding landscape have been shown to affect the simultaneously provisioning of multiple services, but the effects on overall agroecosystem multifunctionality remain unknown (Botzas-Coluni et al., 2021; Martin 2019; Le Provost et al., 2022). Overall, the simultaneous effects of local agricultural management and the landscape context on agroecosystem multifunctionality need to be further investigated.

## 1.4 Research overview

### 1.4.1 Study system and selection of ecosystem services

In this study, we focus on the impact of organic management on ecosystem service provisioning in apple orchards. This system is particularly interesting due to the current trend towards an increasing proportion of organic apple orchards, as well as the relative lack of knowledge regarding the impacts of organic management on ecosystem service provisioning in perennial crops. As perennial crops are less commonly grown than annual crops and make up a relatively small part of the total global area under organic farming, much is still to learn about their ecological, agronomical and socio-economic performance under different management systems (Eurostat, 2022; FAO, 2017). They differ from annual systems due to their longer lifespan, as they typically produce crops for multiple years. This allows them to have deeper root systems that can access water and nutrients from deeper soil layers, making them more resilient to environmental stresses such as droughts and soil erosion (Chapman et al., 2022). Due to the lower soil disturbance, they also have greater potential to achieve sustainable soil use compared to annual crops (Crews et al., 2018; Kreitzman et al., 2020). Additionally, perennial crops have permanent structural elements such as understory vegetation and the crops themselves, which can provide habitat and food sources for a wide range of wildlife year-round. This for instance includes pollinators and natural enemies of pest species,

which can provide important ecosystem services such as pollination and biological pest control. On the other hand, the long lifespan and permanent availability of habitat and resources may also allow pests and diseases to build up over time, counteracting ecosystem service provisioning and increasing the need for pest control measures (Annaert et al., 2017; Muneret et al., 2018b). As a consequence, the effects of organic management on ecosystem services and agroecosystem multifunctionality in perennial crops are not always straightforward, which is reflected in the inconsistent results of the few studies that address these topics (Muneret et al., 2018b; Ostandie et al., 2022; Pardo et al., 2020; Porcel et al., 2018; Samnegård et al., 2018). Here, we specifically selected apple cultivation as a study system as apples are the second most commonly grown perennial crop in Flanders, after pears (DLV, 2023a). A substantial part of apple cultivation is organic (approximately 5% of the total area in 2021, which is the highest proportion of all perennial crops), and this proportion is steadily increasing due to increasing consumer demands and policy support (DLV, 2022; European Commission, 2020b; Timmermans and Van Bellegem, 2022; Willer and Leroud, 2020). Furthermore, apple orchards are known to highly depend on a variety of ecosystem services (Demestihas et al., 2017; Garratt et al., 2014), and both conventional and organic production have a substantial economic relevance within the region (Avermaete et al., 2018). However, both the number of apple producers and the total apple production in Flanders have been steadily decreasing over the last few decades (Avermaete et al., 2018). Compared to 2005, the number of apple producers in Flanders decreased by 42% (1081 in 2005 vs. 625 in 2021, respectively) and the total apple production by approximately 24% (331 635 tons in 2005 vs. 249 742 tons in 2021, respectively) (DLV, 2022). These decreases can be attributed to several factors, such as the increasing market competition due to the Russian ban on European fruits since 2014, and unfavorable weather conditions due to climate change (Avermaete et al., 2018). Nevertheless, within the intensively managed agricultural landscape in Flanders, apple orchards are a representative study system for investigating how organic farming can contribute to the reconciliation of food production, economic viability, and environmental sustainability.

While apple cultivation systems are dependent on, and contribute to, a wide variety of ecosystem services, this study focuses on a comprehensive subset of ecosystem services that are both important for apple cultivation and are expected to be influenced by organic management. As organic farming refrains from using synthetic fertilizers, herbicides and pesticides and aims to promote natural ecosystem functions and processes to grow and protect crops, the greatest impacts of organic farming are likely related to biodiversity-based services. More specifically, pollination, biological pest

control and soil health were retained as ecological performance indicators. While several studies have investigated the effects of organic farming on these individual services, this approach has also been criticized because it ignores potential trade-offs between services. (Howe et al., 2014; Reiss et al., 2009). Specifically, there is a need to investigate the simultaneous response of multiple ecosystem services to organic agriculture, as well as the possible synergies and trade-offs that might exist among services. At the same time, the yield costs that are typically associated with organic farming emphasize the need to also include measures of agricultural production and farmer livelihood. This is especially important for the development of agricultural policy, as economic feasibility will greatly determine farmers' adoption of organic practices (Bommarco et al., 2013). To this end, also apple production and farmer income were included in this study. Cultural services, on the other hand, were not taken into account. The reason for this mainly lies in the focus on field-scale quantification of ES, while cultural services are generally appreciated and determined at larger spatial scales (Milcu et al., 2013; Plieninger et al., 2013). Although a truly multidisciplinary evaluation of organic farming would require the assessment of a wider range of ecosystem services and stakeholders at a larger spatial scale, this lies outside the scope of this study. Moreover, our assessment of agroecosystem multifunctionality at the field scale can be seen as an essential step towards a full assessment of ecosystem service provisioning within the entire agricultural landscape, concerning multiple crop types, stakeholders and policy scenarios.

Ideally, the impact of organic farming at the field scale would be assessed by comparing ecosystem services and economic measures before and after adoption of organic farming within the same sites. However, the practicality and reliability of this approach is limited by the three-year conversion period from conventional to organic farming, and the high environmental variability that might exist between years. Therefore, we compare fully converted organic apple orchards with conventional orchards within the same region, and during the same years. In all professional farms in the EU, the implementation of Integrated Pest Management (IPM) became mandatory in 2014, following the 2009/128/EC directive on the sustainable use of pesticides (EU, 2009). More specifically, this means that the use of pest control measures and their application is restricted to levels that are ecologically and economically justified and limit potentially detrimental effects for human health and the environment. To clarify the difference between 'traditional' conventional management and current conventional management with IPM practices, we further refer to the conventional farms as 'IPM orchards' in this text. In addition to the organic and IPM orchards, biodiversity and biodiversity-based services were also determined in semi-natural reference sites within

the study region. These sites are free of agricultural management and therefore provide a valuable benchmark for the ecological performance of both the organic and IPM orchards.

### 1.4.2 Thesis objectives and outline

The main goal of this thesis is to enhance the understanding of the impact of organic farming on the delivery of multiple ecosystem services in a perennial crop. To this end, we quantify a comprehensive set of indicators for ecological, agronomical an economic performance in organic and IPM apple orchards. To provide a benchmark for the impact of both organic and IPM management on biodiversity and biodiversity-based services, we also assess ecological performance indicators in semi-natural reference habitats. Furthermore, as the performance of organic agriculture has been found to depend on characteristics of the surrounding landscape, we investigate how the effects of local management on multiple ecosystem service provisioning are modulated by the landscape context. Finally, we aim to advise farmers, policymakers and other stakeholders on the most optimal strategies to lower the environmental impact of apple cultivation, while maintaining sufficient yield levels and a viable income for farmers. More specifically, our objectives are to:

1. Investigate how organic orchard management performs in terms of maintaining soil health as compared to conventional management and a semi-natural reference.
2. Quantify how communities of natural enemies, the pest control services they provide, and ultimately pest-induced crop damage are influenced by local orchard management and characteristics of the surrounding landscape.
3. Quantify how local management and the landscape context affect pollinator communities, pollination services, and apple yield.
4. Evaluate the ecological performance of both organic and IPM apple orchards by comparing biodiversity and biodiversity-based ES with those in a semi-natural reference.
5. Explore the relative importance of local and landscape drivers in shaping biodiversity, biodiversity-based services, yield and farmer income in apple orchards, and investigate how these drivers might underpin synergies and trade-offs between service indicators.
6. Calculate overall agroecosystem multifunctionality based on the indicators for biodiversity, biodiversity-based ecosystem services, yield and farmer income.

Additionally, compare multifunctionality measures between organic and IPM orchards and for different scenarios of stakeholder preference.

7. Formulate recommendations for farmers, policymakers, and other stakeholders to promote sustainable apple production systems based on the findings of our research.

Following the introductory chapter, the first three chapters of this thesis focus on the effects of local management and landscape context on biodiversity-based ES (Fig. 1.6). In **chapter 2**, we assess how orchard management affects soil health by quantifying a series of soil health indicators in 12 organic and 12 IPM apple orchards, as well as in 12 semi-natural reference sites. Additionally, we also investigate the role of the local biotic and abiotic environment in shaping soil functions and processes, and examine whether different management of drive rows and crop rows in the orchards leads to within-orchard spatial variability in soil health indicators. In **chapters 3 and 4**, we shift our focus to aboveground ecosystem services provided by arthropods, and use Piecewise Structural Equation Modelling (PSEM) to test the direct and indirect effects of landscape composition, landscape configuration and local management on biological pest control (chapter 3) and pollination services (chapter 4). We investigate how local management and landscape characteristics are shaping both the taxonomic and functional diversity of natural enemies and pollinators, and examine how this eventually affects crop damage and crop yield in the organic and IPM orchards, respectively. In **chapter 5**, we combine the data from the previous chapters with measures of biodiversity, yield and farmer income to calculate overall orchard multifunctionality, and compare this between organic and IPM orchards under different hypothetical scenarios of stakeholder interest. In addition, we provide an overview of the different drivers of all ecosystem service indicators quantified in this thesis, and discuss how these drivers might explain synergies and trade-offs between services. While in chapters 2-4 biodiversity is mainly assessed as an underlying driver of other ES, in this chapter we also address biodiversity as a separate ES due to its intrinsic an political importance (e.g. the European Biodiversity Strategy), and to better investigate potential trade-offs between biodiversity and other ES. In **chapter 6**, an overview of the main results presented in the previous chapters is given. Based on this synthesis, we formulate some recommendations on how to reconcile the agronomical and economic performance of apple farming with environmental sustainability. Finally, we discuss the shortcomings and drawbacks of this study and suggest several future research topics that could further improve the understanding of agroecosystem multifunctionality and lead to more environmentally-friendly management of intensive farming landscapes.

While this thesis specifically examines the influence of organic farming on the provisioning of ecosystem services, it is important to note that this research is part of a larger project that also investigates the effects on biodiversity and the socio-economic context of the apple farms. Finally, the combined results of this project will be used to identify optimal land use strategies to reconcile biodiversity conservation, ecosystem service provisioning, agricultural production and a sustainable livelihood for farmers.

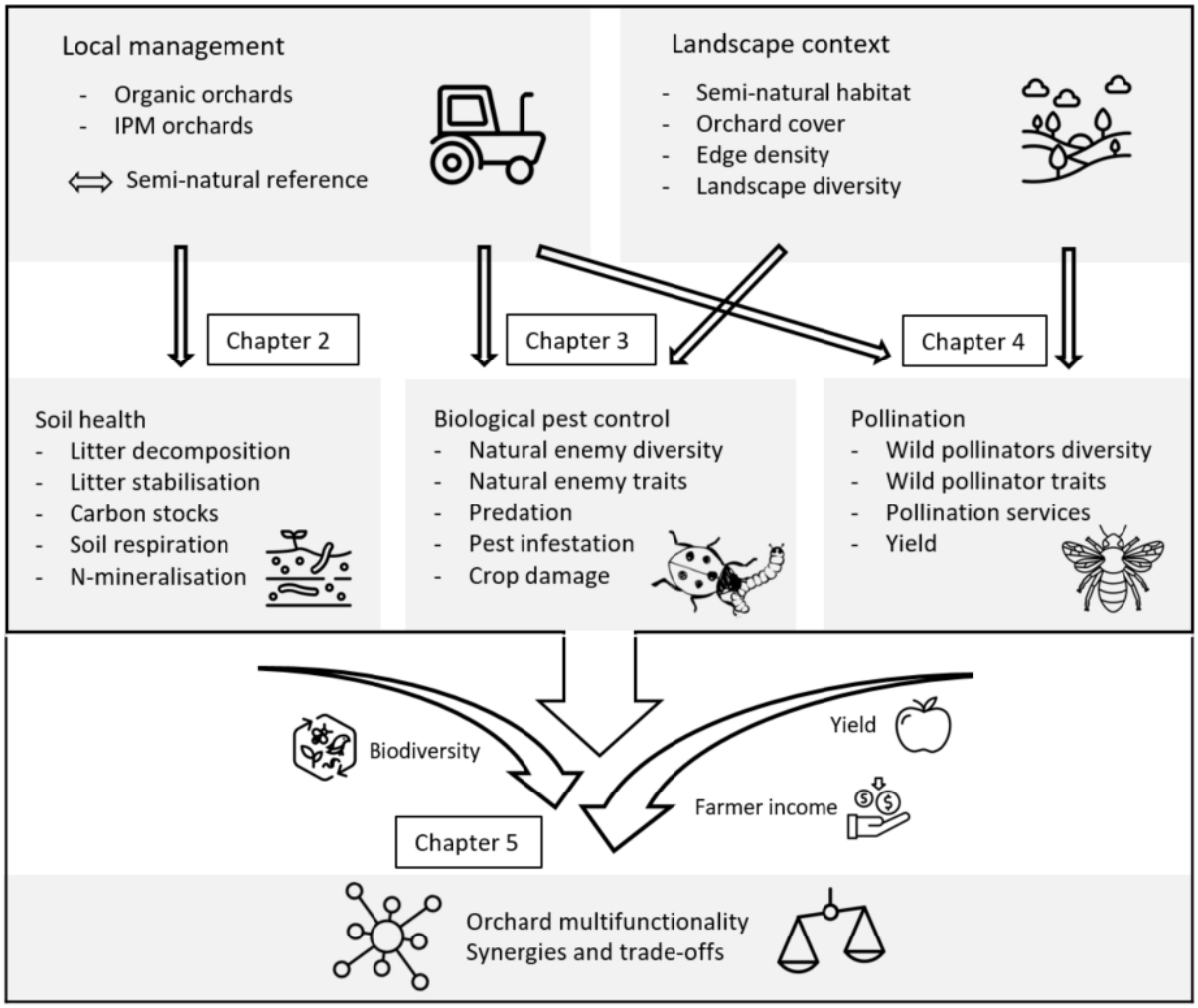



**Figure 1.6**. Schematic overview of the research topics and chapters of this PhD dissertation. The first three chapters discuss the impact of local agricultural management and landscape characteristics on soil health, biological pest control and pollination in apple orchards, and compare the ecological performance of the orchards with a semi-natural benchmark. These chapters are integrated and combined with data on biodiversity, yield and farmer income to assess overall agroecosystem multifunctionality, as well as synergies and trade-offs between ecosystem services in chapter 5.

## 1.4.3 Description of the study system

The study was conducted in and around the Hageland-Haspengouw region in the southeast of Flanders, Belgium (Fig. 1.7). The region has a temperate oceanic climate with an average temperature of 9.8 °C and an average annual precipitation of 925 mm (data obtained from the Royal Meteorological Institute of Belgium, KMI). The soil texture varies from sandy loam in the Hageland to loamy soils in the Haspengouw region. The Hageland-Haspengouw region is generally known as the center of fruit cultivation in Flanders, which mainly takes place on the fertile soils in the transition regions between Dry Haspengouw (in the south) and Hageland and Humid Haspengouw (in the northwest and northeast of the region, respectively). While the region represents only 10% of the Flemish land area, it contains almost 90% (4736 ha) of the total Flemish area dedicated to apple cultivation (De Saeger et al., 2017; LV, 2020). Fruit cultivation in the region is typically characterized by a high degree of intensification and specialization, and is of great economic importance (DLV, 2023a). The landscape can be described as complex and pluri-active, and consists of a mosaic of agricultural fields (47% of the total land area), urban area's and fragmented patches of (semi-) natural habitat (De Saeger et al., 2017; Pinto-Correia et al., 2016). Due to the highly intensive agricultural land use and the relatively low cover of (fragmented) semi-natural areas, most of the regions' land area is of poor ecological quality (De Saeger et al., 2017).

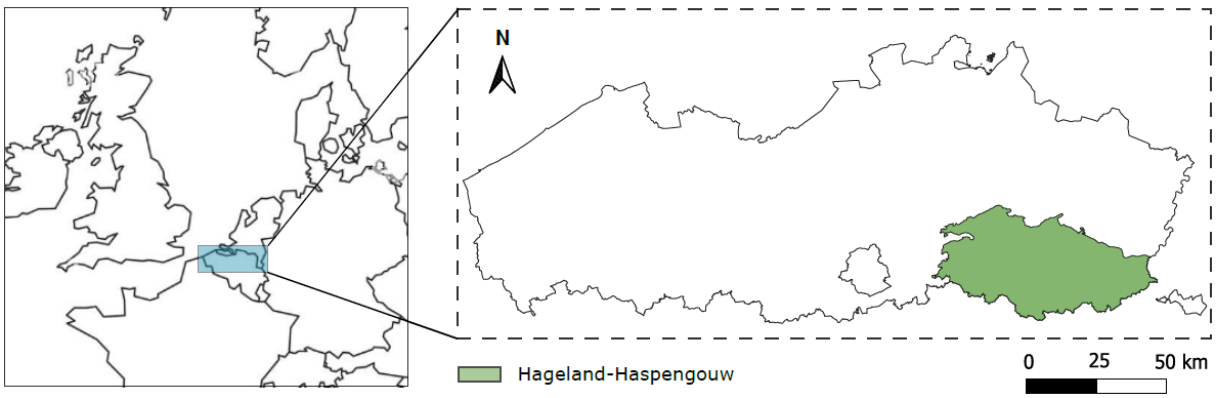



**Figure 1.7.** Location of the Hageland-Haspengouw region within Flanders, Belgium.

Within this landscape, we selected 24 apple orchards (12 organic and 12 IPM) and 12 semi-natural reference sites with similar soil type, hydrology and slope (Fig. 1.8). The average size of the study sites was 1.4 ha (min. 0.4 ha and max. 3.9 ha), with an average distance of 5.2 km between sites (min. 0.5 km and max. 34.2 km). Organic and IPM orchards were all planted with Jonagold apple trees (*Malus domestica*) that reached production age, and were managed in accordance to European and Flemish legislation.

In the IPM orchards, principles concerning the sustainable use of pesticides were applied, meaning that mechanical, physical and biological practices are prioritized over chemical methods, and that the application of chemicals is limited to a level that is economically and ecologically justified. Synthetic fertilizers are commonly used within IPM orchards, and crop row weeds are typically removed by the application of herbicides (Fig. 1.8, Table S1.1). The management of the organic orchards also complies with IPM practices, but organic certification additionally requires the abolishment of synthetic fertilizers and pesticides. Only when all other methods have been exhausted, the use of organically certified pesticides is allowed in organic farming (Table S1.2). These organic pesticides are typically derived from naturally occurring substances, meaning that they are from plant, animal, microbial or mineral origin, except when products of these sources are not available in sufficient quantities or qualities, in which case synthetic products are allowed as well (e.g. pheromones, copper sulfate, soaps…) (EC Council Regulation No834/2007). Crops row weeds in organic orchards are typically removed mechanically, and drive rows in both organic and IPM orchards are regularly mown.

The semi-natural reference sites that were used as a benchmark for the ecological performance of both orchard types consisted of semi-natural grasslands that were managed extensively for nature conservation purposes. Management included either mowing or grazing, and no pesticides or fertilizers were used. There are several reasons why we specifically chose semi-natural grasslands as a reference for biodiversity and biodiversity-based ecosystem services in our study. First, semi-natural grasslands are important biodiversity hotspots within the study region and are considered essential for biodiversity conservation and ecosystem functioning in agroecosystems (Tamburini et al., 2022). Second, semi-natural grasslands within the study region can be found on similar soils as the apple orchards, which is for instance not the case for other habitats that are important biodiversity hotspots, such as forests. Within the study region, forests are typically located on soils that are less suited for agriculture, for instance in riparian areas that are too wet for agriculture, and therefore less suited as a reference habitat. Third, semi-natural grasslands represent a situation where management (mowing or grazing) is aimed at the maintenance of ecosystem functions and properties, rather than at agricultural production. Indeed, when the apple trees would be removed and the agricultural management would be stopped, the orchards would develop to become very similar to the studied semi-natural grasslands in terms of structure and vegetation composition. The semi-natural grasslands thus represent a comparable habitat to the orchards, but without agricultural production. In each of the orchards and semi-natural grasslands, six sampling plots were randomly established; three in the center of each

site and three in the edge. The edge plots were located at the inner edge of the administrative field border, containing the outer crop row and the grass strip between the outer crop row and the field border in the orchards. Center plots, on the other hand, were located in the center of the fields at a distance of at least 10 m from the field border (semi-natural grasslands) or from the outer crop rows (orchards) (Fig. S1.1).

Although the same study system is used throughout the entire thesis, some minor differences exist between the exact study sites used in each chapter (Fig. 1.9). During the period in which the research took place (2018-2022) some study sites were replaced because they were unexpectedly taken out of production, or because the growers involved no longer wished to participate in research. Additionally, some adjustments in the selection of semi-natural reference sites were made as not all sites met the required environmental conditions of each research topic. The assessment of natural enemies and biological control services, for instance, required the presence of woodland patches and hedgerows, which were not present in each of the originally selected semi-natural grasslands. However, in 29 out of 36 sites (9 semi-natural grasslands, 10 organic orchards and 10 IPM orchards), the full set of ecosystem service indicators could be determined. These sites were therefore used to calculate synergies and trade-offs between services and to assess overall agroecosystem multifunctionality in chapter 5 (Fig. 1.9d).




**Figure 1.8.** Image of (a) an apple orchard with Integrated Pest Management, (b) an apple orchard with organic management and (c) a semi-natural grassland reference within the study region in Flanders, Belgium. Pictures by author © Robin Daelemans 2020-2021.

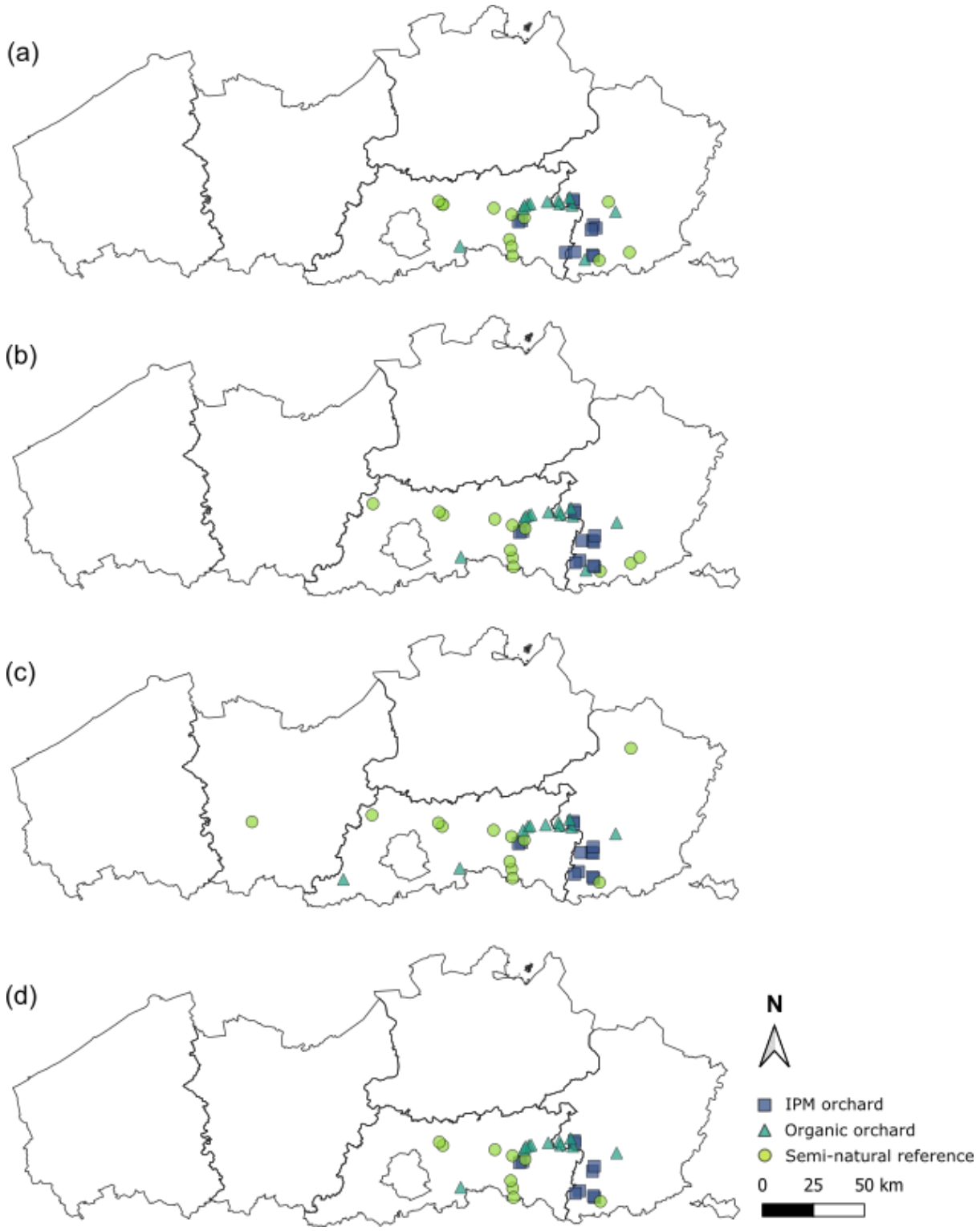



**Figure 1.9.** Locations of the sampling sites used in (a) chapter 2 on soil-based ecosystem services, (b) chapter 3 on biological pest control, (c) chapter 4 on pollination and (d) chapter 5 for the calculation of agroecosystem multifunctionality and trade-offs between all ecosystem services (including biodiversity), yield and farmer income.

### 1.4.4 Landscape analysis

To investigate how the effects of local management on multiple ecosystem services were modulated by the landscape context, the landscape surrounding each of the sampling plots was characterized. More specifically, the surrounding land use was categorized into seven land use classes based on data from the Biological Valuation Map (De Saeger et al., 2017) and the map of Flemish agricultural land-use parcels (LV, 2020): arable land, agricultural grassland, orchards, herbaceous and wooded semi-natural habitat, urban areas and other land uses (Fig. 1.10, see Table S1.3 for a detail description of each category). The proportional cover of each of these land use classes, as well as the land use Shannon-Weiner diversity, landscape edge density and distance to the nearest semi-natural habitat were determined at seven spatial scales (50, 100, 250, 500, 1000, 1500 and 2000 m) using QGIS v.3.16.10 (QGIS Development Team, 2021) and R package landscapemetrics (Hesselbarth et al., 2019). The landscape variables were further used in this thesis as predictors in the different models describing ecosystem service indicators.

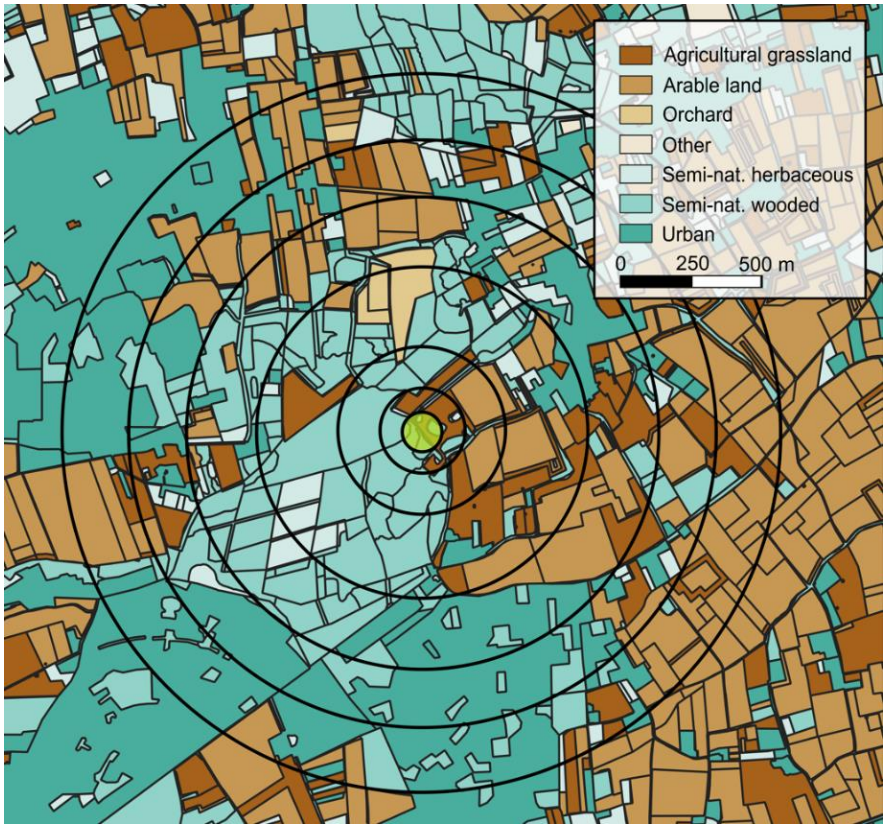



**Figure 1.10.** Categorization of land use classes surrounding a sampling plot. Within buffers with increasing radius (concentric circles) the proportion of each land use class was calculated, as well as the landscape Shannon-Weiner diversity, landscape edge density and the distance to the nearest semi-natural habitat (either wooded or herbaceous).

# Chapter 2

## Both organic and integrated pest management of apple orchards maintain soil health as compared to a semi-natural reference system

Adapted from:

Daelemans, R., Hulsmans, E., Honnay, O., 2022. Both organic and integrated pest management of apple orchards maintain soil health as compared to a semi-natural reference system. J. Environ. Manage. 303, 11

## 2.1 Summary

Growing concerns about the negative environmental impacts of agriculture have resulted in the increasing adoption of farming systems that try to reconcile crop production with environmental sustainability, such as organic farming. As organic farming refrains from using synthetic inputs, it heavily relies on maintaining soil health. However, it is still poorly understood how organic management performs in terms of maintaining soil health in real commercial and heterogeneous farm settings as compared to conventional management, and especially as compared to a natural reference system. Here, we compared a set of soil health indicators among 24 commercial apple orchards that were either managed organically or conventionally using Integrated Pest Management (IPM) practices. In addition, we quantified the same indicators in 12 semi-natural grasslands as a benchmark to assess to what extent soil processes and functions have been degraded due to agricultural practices. As soil heath indicators, we quantified soil bulk density, organic matter content, organic carbon content, organic carbon stock, total nitrogen (N), potential heterotrophic respiration, potential net N mineralization, litter decomposition and litter stabilization, and we added the diversity of the herbaceous vegetation and the soil microbiome as covariates in our models. We found no differences between organic and IPM orchards, and neither of the farming systems showed evidence of impaired soil health compared to the semi-natural benchmark, with the exception of higher decomposition rates measured in both orchard types. We observed, however, high spatial variation in soil health between drive and crop rows within the orchards. Especially in the IPM orchards, crop rows showed impaired soil health compared to the adjacent drive rows, indicating that there is still opportunity to improve soil management in the IPM system. In addition, our results show that a considerable part of the variation in soil characteristics can be attributed to the study site, suggesting that both natural heterogeneity and personal management preferences by individual farmers are more important than the management system. Overall, and at least in terms of the soil variables measured in this study, our results suggest that perennial crop systems can be managed in a sustainable way, without jeopardizing soil health.

## 2.2 Introduction

Since the 1950s, agricultural productivity has greatly increased due to the use of agrochemicals and high-yielding crop varieties in combination with increased irrigation and mechanization. At the same time, land use conversions have further expanded agricultural lands, mostly at the expense of natural habitats (Tilman et al., 2017). These practices have allowed agricultural output to keep ahead of the increasing global food demand, but have come at a high cost for biodiversity and the delivery of ecosystem services (ES) (Foley et al., 2011; Tilman et al., 2017). With a projected further increase in food demand of 50% by 2050 (FAO, 2017), it is crucial to mitigate these negative environmental impacts of agriculture and yet at the same time maintain or even enhance yield levels.

Over the last decades, a variety of solutions has been put forward to achieve this goal, such as sustainably increasing agricultural productivity, reducing food waste or shifting to more sustainable, plant-based diets (Foley et al., 2011; Williams et al., 2020a). At the same time, there has been an increasing interest in the adoption of farming systems that aim at minimizing environmental degradation and improving the efficiency of internal resource use, such as organic farming (Barrios, 2007; Tuomisto et al., 2012). As organic farming refrains from using synthetic fertilizers and pesticides, it relies on natural ecosystem processes such as nutrient cycling and food web dynamics to grow and protect crops (Boone et al., 2019; Reganold and Wachter, 2016). Literature reviews and meta-analysis show that organic farming practices, at least on a per area basis, generally perform better than conventional practices in terms of environmental impacts (Boone et al., 2019; Gomiero et al., 2011; Lynch et al., 2012; Tuomisto et al., 2012, but see Clark & Tilman, 2017). For example, organic farms are often found to sustain a higher floral and faunal diversity, as well as related ecosystem services such as pollination and natural pest control (Crowder et al., 2010; Tuck et al., 2014). Whereas the greatest beneficial impacts of organic farming are likely to be expected in the soil environment, as organic farming practices are frequently reported to lead to higher soil organic matter contents, more efficient nutrient cycling, and better soil quality in general (Bai et al., 2018; Gattinger et al., 2012; Lynch et al., 2012), these impacts often highly depend on the specific farming practices, the crop type and soil texture (Bai et al., 2018).

Awareness of the importance of soil multifunctionality has recently increased, both in the scientific and the farming community (Bünemann et al., 2018; Hou et al., 2020). In this context, the concept of soil health is commonly used, not only in terms of agricultural production and the delivery of ecosystem services, but also as an essential

component of meeting the United Nations' Sustainable Development Goals (SDGs) (Hou et al., 2020; Lehmann et al., 2020). Yet much remains to be learned about how soil health is influenced by different agricultural practices. Most research so far has used controlled field plot experiments to assess how soil health metrics are impacted by specific soil management practices, such as (no-)tillage or the application of certain amendments (e.g. Keel et al., 2019; Montanaro et al., 2017a; Nazaries et al., 2021). Although providing useful insights in the functioning of agroecological processes, the highly controlled and simplified nature of these experiments makes it difficult to extrapolate results to real and intrinsically heterogeneous farm settings. An alternative approach is the use of on-farm studies, which are more realistic in terms of scale and heterogeneity, and which are generally conducted in well-established and stabilized systems (Drinkwater, 2002). Furthermore, farming systems can consist of a multitude of different practices within the boundaries that are set by (inter)national legislation. As a result, farming systems are often very heterogeneous, making on-farm studies in commercial farms much needed to assess the effectiveness of these systems in meeting agricultural and environmental goals. Finally, few studies so far have included natural references when comparing soil health among farming systems (but see Williams et al., 2020b). Such a natural reference system can be used as a benchmark to assess to what extent soil processes and functions have been degraded due to agricultural practices, thus providing an additional perspective to the comparison between farming systems. Including a reference allows to assess the potential soil health that can be reached on agricultural soils, if the impact of agricultural practices is minimized. A natural reference system should preferentially consist of unmanaged land or land that is managed with the purpose of ecosystem conservation.

Much of the current research on the impact of conventional and organic farming practices on soil health is centered around annual cropping systems (Bai et al., 2018; Lee et al., 2015). Perennial crops, such as fruit trees, have received less attention, most likely because of their relatively low share in the total global area under organic farming (FAO, 2017; Montanaro et al., 2017b). Yet, recent studies suggest that perennial cropping systems might have greater potential to accomplish sustainable soil use compared to annual systems (Crews et al., 2018; Kreitzman et al. 2020). In addition, policy support and the increasing consumer demand for organic fruits have led to a rapid increase in organic fruit production in recent years (Willer and Lernoud, 2019). In the European Union, 3.4 million hectares are dedicated to fruit cultivation of which approximately 25% is being managed organically (Eurostat, 2021). With an increase in the total area under organic management of approximately 7% each year, fruit crops are the third fastest growing organic crop after dry pulses and oilseeds (Eurostat, 2021). In

this context, it is important to know how organic fruit cultivation impacts soils, not only compared to conventional cultivation, but also compared to natural reference systems. Most relevant research to date has focused on soil carbon sequestration, for which fruit crops hold great potential due to low soil disturbance and the presence of ground cover vegetation (Midwood et al., 2020; Montanaro et al., 2017a; Zanotelli et al., 2015). Several studies have shown that carbon stocks are generally greater in organic systems compared to conventional systems (Canali et al., 2009; Montanaro et al., 2017a). This difference is mostly attributed to the higher input of organic fertilizers and higher retention of pruning debris, leaf litter and understory vegetation in organic fruit systems compared to conventional systems (Montanaro et al., 2017a). For other soil health metrics, differences among organic and conventional fruit cultivation systems remain less clear and seem to be highly context dependent. Several studies report that organic practices are associated with improved levels of soil organic matter, lower soil bulk densities, higher availability of N and P and improved biological soil properties in general (Carey et al., 2009; Di Prima et al., 2018; Reganold et al., 2001; Sanchez et al., 2003). However, other studies have found no significant difference between organic and conventional fruit farms (Glover et al., 2000; Orpet et al., 2020).

Here, we aimed to compare soil health among commercial apple orchards that are either managed organically or conventionally. As the implementation of Integrated Pest Management (IPM) became mandatory in the EU in 2014 (EU, 2009), we further refer to the conventional study sites as 'IPM orchards' in this text to clarify the difference between 'traditional' conventional management and current management with IPM practices. We also aimed to quantify to what extent soil health has been degraded due to agricultural practices, and therefore included a semi-natural reference system as benchmark in our sampling. More specifically, during our sampling in March 2020 we covered 12 organic orchards, 12 IPM orchards and 12 reference semi-natural grasslands in the main fruit cultivation region in Flanders, Belgium. In the orchards, we separately sampled the drive rows and the crop rows. Since the interpretation of a "healthy" soil is highly context-specific (Baveye, 2021; Fierer et al., 2021; Lehmann et al., 2020), we refrained from using an overall soil health index but instead selected a set of physical, chemical and biological soil characteristics that were relevant for our specific study system.

## 2.3 Materials and methods

### 2.3.1 Study sites and sampling

Soil samples were collected in 24 orchards and 12 semi-natural grasslands in March 2020, right before the start of the growing season. Six 2 $m^2$ sampling plots were established in each orchard at a distance of at least 10 m from the borders; three in the drive rows and three in the adjacent crop rows. We distinguished between drive and crop rows because they are managed differently, possibly affecting soil properties such as organic carbon an total nitrogen content (Carey et al., 2009; Midwood et al., 2020). Drive rows have a vegetation cover mainly consisting of grasses and are left unmanaged, except for mowing and the disposal of pruning debris, whereas in the crop rows all herbaceous vegetation is removed and fertilizers are applied. In the reference semi-natural grasslands, only three plots were established because there were no drive and crop rows. In each plot, five different soil cores were taken with a 2-cm diameter auger at three different depths (0-10 cm, 10-30 cm and 30-50 cm) and the cores were pooled into one aggregate sample per depth per plot. In total, 540 soil samples from 180 plots were obtained across all study sites. Samples were stored at 4 °C until further analysis.

### 2.3.2 Soil physical analysis

From each sample (n=540), 10 g of fresh soil was oven-dried at 105 °C to obtain the soil gravimetric water content (% moisture). Bulk density was measured in a subset of 60 plots; one drive row plot and one crop row plot in each orchard, and one plot in each semi-natural grassland. In each depth layer (0-10 cm, 10-30 cm and 30-50 cm), an undisturbed sample was obtained using Kopecky rings, totaling 180 samples for bulk density measurement. Samples were first air-dried for two weeks, then crushed and oven-dried for 24 h at 105 °C before weighing. Bulk density (Mg $m^{-3}$) was calculated using the volume of the ring and the sample weight, correcting for the presence of stones when necessary.

### 2.3.3 Soil chemical analysis

For chemical analysis, aliquot samples (n=540) were air dried and sieved through a 2-mm sieve before further processing. Weight loss of dry soil after combustion at 650 °C was used to determine soil organic matter (SOM) content. Soil organic carbon (SOC) and total nitrogen (N) concentrations were determined using an EA1108 Elemental Analyzer (CARLO ERBA Reagents, Milan, Italy) after powdering the dried soil and

removal of carbonates by 2 M HCl. Soil organic carbon stocks (Mg $ha^{-1}$) were calculated for each depth layer in both the crop and drive rows (n=180), based on SOC concentrations, bulk densities and the thickness of the respective soil layer. We accounted for differences in soil mass using the equivalent soil mass approach described by Poeplau and Don (2013). This was necessary because in the organic orchards, weeds in the crop row are controlled mechanically by tillage of the topsoil, possibly affecting soil bulk density. Soil pH was quantified for all samples from the top layer (n=180) using a pH probe in a 1:10 soil/distilled water solution.

### 2.3.4 Soil biological analysis

Potential heterotrophic respiration rate, a measure of the metabolic activity of the soil microbiota, was determined with an *ex situ* respiration experiment following the protocol of Aerts et al. (2017). Soil samples from the top layer (0-10 cm) were combined across plots, resulting in two samples per orchard (crop row and drive row) and one sample for each semi-natural grassland. From each sample (n=60), 40 g air-dried soil was transferred into air-tight glass jars (287 mL), compacted to a bulk density of 1.5 g $cm^{-3}$ and set to 60% of water filled pore space by adding demineralized water. The jars were placed at 25 °C in a dark incubation room and, after an incubation period of 8 days, sealed air-tight. $CO_2$-concentrations in the headspace of the jars were measured periodically using a LI-820 $CO_2$ infrared gas analyzer (LI-COR Biosciences, Lincoln, Nebraska USA). Three blank jars ware included to correct for atmospheric background concentrations of $CO_2$. In total, 11 measurements spread over a period of 24 days were used to calculate an average respiration rate (mg $CO_2$ $kg^{-1}$ $h^{-1}$) for each sample, using the method described by Aerts et. al. (2017). Simultaneously, aliquot samples (n=60) were used to determine potential net nitrogen (N) mineralization rates. Two 10-g dry soil weight equivalent duplicates per sample were weighed into 50 mL Falcon tubes and brought to 60% of water filled pore space. One sample was analyzed immediately for $NO_3^-$ and $NH_4^+$ concentrations using an automated colorimetric analysis system, while the other sample was incubated at 22 °C in a dark room for 25 days before analysis. Potential net N mineralization rate (mg $kg^{-1}$ $d^{-1}$) was calculated as the difference in N content before and after incubation, divided by the number of incubation days.

In addition, we quantified *in situ* litter decomposition using the standardized 'Tea Bag Index' (TBI) developed by Keuskamp et al. (2013). At each sampling plot, 3 pairs of Lipton green tea and Lipton rooibos tea bags were buried at a depth of 8 cm, totaling 36 tea bags per orchard and 18 tea bags per semi-natural grassland site. The tea bags were retrieved after approximately 80 days and mass loss was calculated after drying

the bags for 48 h at 70 °C. Due to their different composition, the labile fraction of the green tea is completely decomposed after the incubation period but part of the labile fraction of the rooibos tea remains. This difference in decomposition rate allows for the simultaneous calculation of the decomposition rate constant k and the stabilization factor S, following the guidelines by Keuskamp et al. (2013). Both parameters play an important role in carbon cycling, k relating to short-term carbon dynamics and S being indicative for long-term carbon storage (Górecki et al., 2021; Keuskamp et al., 2013). A total of 897 tea bags (83%) was retrieved undamaged, resulting in litter decomposition data for 33 out of 36 study sites. For two semi-natural grasslands and one organic orchard, no data could be calculated due to lost and damaged bags.

### 2.3.5 Data analysis and statistics

To assess the effect of soil management on the different soil health indicators, linear mixed-effects models (LMMs) were used with management type (organic vs. IPM vs. semi-natural), location (drive row vs. crop row) and sampling depth as fixed factors. Separate models were constructed for soil organic matter, bulk density, total N, soil organic carbon, soil organic carbon stock, soil respiration, N mineralization, litter decomposition rate k and litter stabilization factor S. Whenever sampling depth was a significant factor in the full model, additional models were constructed for each depth layer separately. Because of different depth layer thickness, also SOC stocks were analyzed using separate models for each depth layer, as well as a model for the summed SOC stock up to a depth of 50 cm. Depending on the response variable, several fixed covariates were included in the models. Diversity indices for the plant species from the vegetation cover and for the soil microbiome were calculated based on data from a parallel project (see Supplementary material, Methods S2.1 for details and methodology). Diversity indices included plant species richness (S_Plant), Shannon diversity (H_Plant) and Inverse Simpson index (IS_Plant). For the biological soil characteristics, several covariates relating to the soil microbiome were included: OTU richness fungi (S_Fun), OTU richness bacteria (S_Bac), Shannon diversity fungi (H_Fun), Shannon diversity bacteria (H_Bac), Inverse Simpson index fungi (IS_Fun) and Inverse Simpson index bacteria (IS_Bac) (see Supplementary material, Methods S2.2). In addition, a set of spatial predictors (distance-based Moran's eigenvector maps, dbMEMs) were added as explanatory variables to the models to account for trends resulting from the spatial structure of the study system (Dray et al., 2006). dbMEMs were calculated based on the geographical coordinates of the study sites using the function ‘dbmem’ from R package adespatial (Dray et al., 2021). First-order interaction terms between management, location and depth and all other relevant fixed factors and

covariates were also included. Before inclusion in the models, variance inflation factors (VIF) were calculated for all predictor variables to test for multicollinearity. Variables with a VIF higher than 3 were dropped.

All LMMs were simplified using a backwards-stepwise selection based on Akaike's Information Criterion (AIC) using the 'buildlme' function from the R package buildmer (Voeten, 2021). Location nested in sampling plot nested in study site was fitted as a random effects term to account for the non-independent spatial structure of the study design. If samples were pooled, as was for instance the case for the biological soil characteristics, the random effect structure was adjusted accordingly. F- and p-values were calculated using ANOVA tables and marginal and conditional $R^2$-values were obtained for all models, representing respectively the variance explained by the fixed factors and the variance explained by the fixed and random factors combined, using the function 'r.squaredGLMM' in R package MuMIn (Bartoń, 2020). Semi-partial $R^2_\beta$ coefficients were calculated using the method of Edwards et al. (2008) to assess the percentage of variation in the response variable that can be explained by the respective explanatory variables (function 'r2beta' from R package r2glmm; Jaeger, 2017). When necessary, variables were transformed to meet the assumptions of normal distribution and independence of residuals.

## 2.4 Results

### 2.4.1 Soil physical variables

Overall, soil bulk density was not significantly different between the three management systems (Table 2.1). Most of the variation in bulk density was explained by sampling location (drive row vs. crop row) and sampling depth, with bulk density increasing with depth and generally being lower in the crop rows compared to the drive rows (Table 2.2, Fig. 2.1). Multiple comparison tests, however, showed that lower bulk density in the crop rows, compared to the drive rows, was only significant in the organic orchards, and only in the two uppermost soil layers ($1.21 \pm 0.05$ g $cm^{-3}$ vs. $1.35 \pm 0.04$ g $cm^{-3}$ for the 0-10 cm layer and $1.37 \pm 0.02$ g $cm^{-3}$ vs. $1.50 \pm 0.03$ g $cm^{-3}$ for the 10-30 cm layer, respectively). Compared to the semi-natural reference system, no differences in bulk density were found except for the 10-30 cm depth layer under the crop rows from both orchard types, which had lower bulk densities than the semi-natural grasslands ($1.37 \pm 0.02$ g $cm^{-3}$ for organic and $1.43 \pm 0.02$ g $cm^{-3}$ for IPM, compared to $1.52 \pm 0.03$ g $cm^{-3}$ for semi-natural grasslands). As expected, soil bulk density decreased with increasing soil organic matter content, this relationship was present in all management systems and all depth layers (Table 2.1, Fig. S2.1).

**Table 2.1.** Results of the final linear mixed-effects models for all physical and chemical soil health indicators, showing marginal ($R_m^2$) and conditional ($R_c^2$) $R^2$-values for all models. For each indicator, a full model as well as separate models for each depth layer are shown. Test statistic (F) and semi-partial $R_\beta^2$ are given for each retained explanatory variable after model reduction. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Bulk density (BD) | Full model $R_m^2$= 0.526 ; $R_c^2$ = 0.636 | | Depth 0-10 cm $R_m^2$= 0.248 ; $R_c^2$ = 0.641 | | Depth 10-30 cm $R_m^2$= 0.418 ; $R_c^2$ = 0.630 | | Depth 30-50 cm $R_m^2$= 0.151 ; $R_c^2$ = 0.554 | |
|---|---|---|---|---|---|---|---|---|
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 2.0 | 0.029 | 1.8 | 0.096 | 2.4 | 0.118 | 0.8 | 0.042 |
| Location | 23.2*** | 0.339 | 11.7** | 0.297 | 16.6*** | 0.401 | 2.4 | 0.086 |
| Depth | 13.6*** | 0.251 | - | - | - | - | - | - |
| SOM | 23.8*** | 0.119 | 8.1** | 0.129 | 12.6*** | 0.183 | 7.2** | 0.118 |
| Management x Location | 9.5** | 0.240 | 6.1* | 0.121 | 7.2* | 0.222 | 2.8 | 0.102 |
| Management x SOM | 5.8** | 0.063 | - | - | - | - | - | - |
| **Soil organic matter (SOM)** | **Full model $R_m^2$= 0.366 ; $R_c^2$ = 0.782** | | **Depth 0-10 cm $R_m^2$= 0.144 ; $R_c^2$ = 0.662** | | **Depth 10-30 cm $R_m^2$= 0.024 ; $R_c^2$ = 0.779** | | **Depth 30-50 cm $R_m^2$= 0.058 ; $R_c^2$ = 0.850** | |
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 1.3 | 0.031 | 1.1 | 0.024 | 0.4 | 0.010 | 2.1 | 0.040 |
| Location | 5.0* | 0.059 | 6.5* | 0.071 | 0.4 | 0.006 | 4.1 | 0.043 |
| Depth | 230.7*** | 0.609 | - | - | - | - | - | - |
| IS_Plant | 3.0 | 0.026 | 3.4 | 0.026 | 0.3 | 0.000 | 1.8 | 0.004 |
| Open | 0.2 | 0.001 | 2.1 | 0.016 | - | - | - | - |
| MEM10 | 1.6 | 0.014 | 3.9 | 0.031 | 0.7 | 0.005 | 0.1 | 0.001 |
| Management x Location | 7.2** | 0.083 | 16.8*** | 0.184 | 5.7 | 0.071 | 2.2 | 0.034 |
| Management x IS_Plant | 1.7 | 0.027 | 1.3 | 0.019 | 0.6 | 0.010 | 1.2 | 0.022 |
| Management x Open | 1.3 | 0.011 | - | - | - | - | - | - |
| **Soil organic carbon (SOC)** | **Full model $R_m^2$= 0.543 ; $R_c^2$ = 0.764** | | **Depth 0-10 cm $R_m^2$= 0.162; $R_c^2$ = 0.505** | | **Depth 10-30 cm $R_m^2$= 0.453 ; $R_c^2$ = 0.944** | | **Depth 30-50 cm $R_m^2$= 0.137 ; $R_c^2$ = 0.940** | |
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 2.9 | 0.145 | 0.1 | 0.009 | 2.7 | 0.140 | 0.6 | 0.032 |
| Location | 4.5* | 0.162 | 7.1* | 0.199 | 0.9 | 0.040 | 3.5 | 0.148 |
| Depth | 113.7*** | 0.699 | - | - | - | - | - | - |
| S_Plant | 0.4 | 0.010 | - | - | 2.2 | 0.054 | 2.3 | 0.065 |
| Open | - | - | 0.0 | 0.000 | - | - | - | - |
| MEM6 | 5.8* | 0.195 | - | - | 12.7** | 0.347 | - | - |
| MEM10 | 6.0* | 0.193 | - | - | 3.3 | 0.115 | 5.1* | 0.154 |
| Management x Location | 5.6* | 0.195 | 5.5* | 0.175 | 3.1 | 0.125 | 2.3 | 0.094 |
| Management x S_Plant | 3.1 | 0.153 | - | - | 3.5* | 0.202 | - | - |
| **Total nitrogen (N)** | **Full model $R_m^2$= 0.579 ; $R_c^2$ = 0.824** | | **Depth 0-10 cm $R_m^2$= 0.174 ; $R_c^2$ = 0.524** | | **Depth 10-30 cm $R_m^2$= 0.031 ; $R_c^2$ = 0.919** | | **Depth 30-50 cm $R_m^2$= 0.026 ; $R_c^2$ = 0.937** | |
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 3.0 | 0.143 | 0.2 | 0.012 | 0.4 | 0.026 | 0.2 | 0.013 |
| Location | 1.8 | 0.099 | 11.0** | 0.303 | 1.0 | 0.046 | 2.8 | 0.120 |
| Depth | 189.8*** | 0.795 | - | - | - | - | - | - |
| S_Plant | 0.2 | 0.005 | - | - | - | - | - | - |
| MEM1 | 6.2* | 0.198 | - | - | - | - | - | - |
| Management x Location | 4.0 | 0.165 | 7.7* | 0.234 | 3.4 | 0.131 | 4.6* | 0.173 |
| Management x S_Plant | 2.9 | 0.137 | - | - | - | - | - | - |
| Location x S_Plant | 0.4 | 0.021 | - | - | - | - | - | - |
| **SOC stock** | **Depth 0-50 cm $R_m^2$= 0.032 ; $R_c^2$ = 0.911** | | **Depth 0-10 cm $R_m^2$= 0.129 ; $R_c^2$ = 0.650** | | **Depth 10-30 cm $R_m^2$= 0.034 ; $R_c^2$ = 0.870** | | **Depth 30-50 cm $R_m^2$= 0.029 ; $R_c^2$ = 0.855** | |
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 0.1 | 0.005 | 0.3 | 0.020 | 0.0 | 0.001 | 0.0 | 0.002 |
| Location | 1.2 | 0.058 | 8.7** | 0.271 | 0.0 | 0.000 | 0.1 | 0.004 |
| S_Plant | 0.1 | 0.004 | - | - | 1.2 | 0.036 | 0.5 | 0.015 |
| Open | - | - | 0.3 | 0.007 | - | - | - | - |
| Management x Location | 2.6 | 0.113 | 4.2* | 0.182 | 0.2 | 0.011 | 0.4 | 0.017 |

### 2.4.2 Soil chemical variables

Soil organic matter content varied with sampling depth, with higher concentrations closer to the soil surface (Table 2.1, Table 2.2, Fig. 2.1). Sampling location had a significant effect in the full model, and this effect differed between management systems as indicated by the significant interaction term (management x location). However, separate models for each depth layer revealed that there was a location effect only in the top layer of the IPM orchards. For the 0-10 cm depth layer, soil organic matter content was higher in the drive rows of the IPM orchards compared to the crop rows (6.80 ± 0.39% vs. 4.79 ± 0.15%, respectively) (Table 2.2, Fig. 2.1). Furthermore, no differences in soil organic matter content were found between IPM orchards, organic orchards or semi-natural grasslands.

Both soil organic C and total N as measured by elemental analysis were most strongly effected by sampling depth, with higher concentrations closer to the soil surface (Table 2.1, Table 2.2, Fig. 2.1). In the models for the 0-10 cm depth layer, also location had a significant effect on both organic C and total N, with concentrations generally being lower in the crop rows relative to the drive rows. However, pairwise comparison tests revealed that lower values in the crop rows compared to the drive rows were only significant in the IPM orchards (0.13 ± 0.01% vs. 0.21 ± 0.02% for total N and 1.37 ± 0.09% vs. 2.19 ± 0.18% for organic C, respectively). For total N, lower concentrations in the drive rows of the IPM orchards were also found in the 30-50 cm layer (0.06 ± 0.01% for the drive rows vs. 0.07 ± 0.01% for the crop rows).

SOC stocks were highest in the semi-natural grasslands and lowest in the crop rows of the IPM orchards. This applied to all depth layers, as well as to the summed SOC stock up to a depth of 50 cm (Table 2.2, Fig. 2.2). However, differences in SOC stock between management types and locations were not significant, except for the higher SOC stock in the drive rows compared to the crop rows of the IPM orchards in the 0-10 cm layer (3.29 ± 0.26 Mg $ha^{-1}$ vs. 2.20 ± 0.14 Mg $ha^{-1}$, respectively). None of the other fixed factors were significant, and all had very low explanatory power as reflected by the low semi-partial $R^2_\beta$ coefficients and low marginal $R^2$-values (Table 2.1). Conditional $R^2$-values, however, were very high, indicating that most of the variation in SOC stock is explained at the random factor level, more specific by study site ID (> 90% of random effect variance).

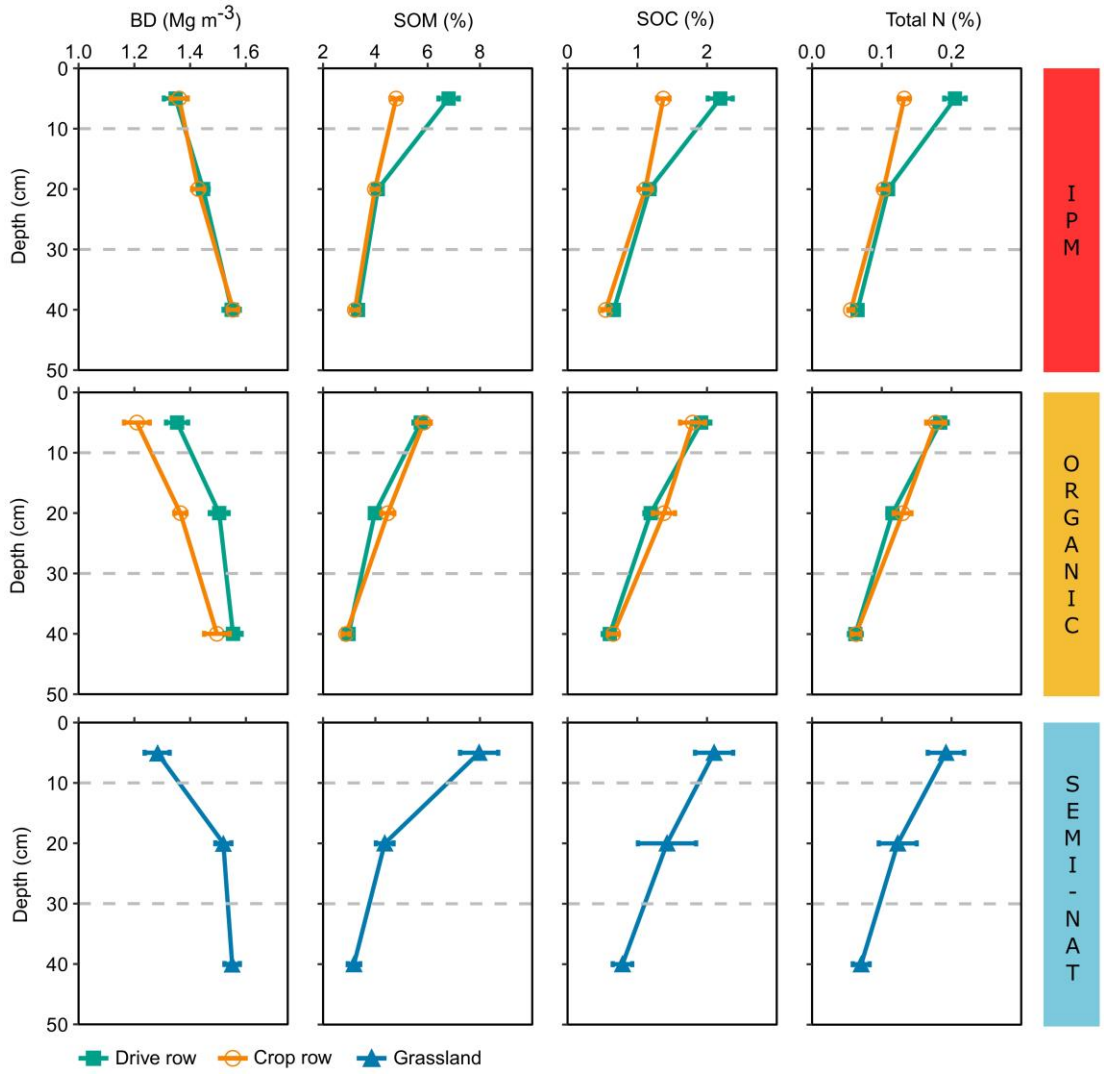



**Figure 2.1.** Variation in bulk density (BD), soil organic matter (SOM), soil organic carbon (SOC) and total nitrogen (N) with depth for the different management systems and locations. Mean values ± 1SE error bars are displayed.

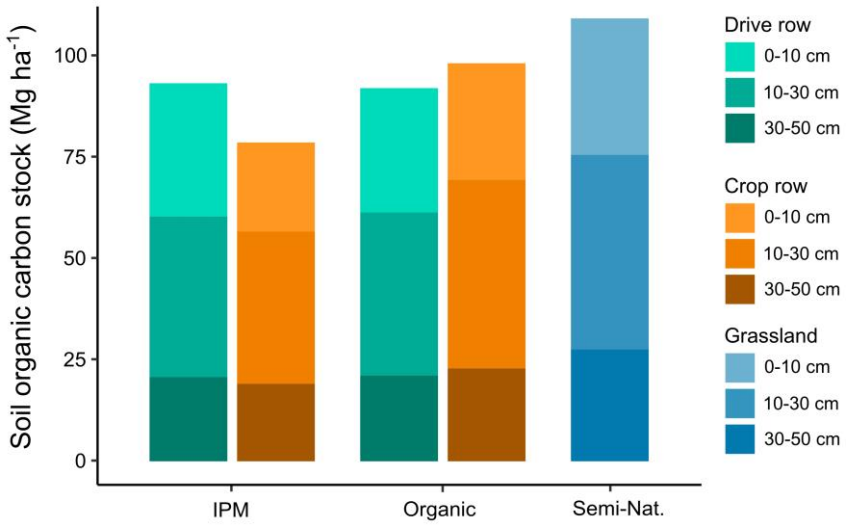



**Figure 2.2.** Soil organic carbon (SOC) stocks under different management systems, locations and at different depths. Stacked bars represent the total organic carbon stock summed to a depth of 50 cm.

### 2.4.3 Soil biological variables

Potential heterotrophic respiration rate differed significantly between management systems, with lowest average respiration rates measured for soils from the IPM orchards (1.11 ± 0.11 mg $CO_2$ $kg^{-1}$ $h^{-1}$), intermediate respiration rates for soils from the organic orchards (1.28 ± 0.07 mg $CO_2$ $kg^{-1}$ $h^{-1}$) and highest respiration rates for soils from the semi-natural grasslands (1.78 ± 0.17 mg $CO_2$ $kg^{-1}$ $h^{-1}$). In both orchard types, heterotrophic respiration was higher for samples taken from the drive rows compared to the crop rows (Table 2.2, Fig. 2.3a). However, this difference was only significant for IPM orchards (1.54 ± 0.10 mg $CO_2$ $kg^{-1}$ $h^{-1}$ for the drive rows vs. 0.69 ± 0.07 mg $CO_2$ $kg^{-1}$ $h^{-1}$ for the crop rows). Soils samples from the semi-natural grasslands showed significantly higher respiration rates than samples from the crop rows in both orchard types, but were not different from respiration rates measured on samples from the drive rows. In addition, respiration rates significantly increased with species richness of the fungal microbiome and decreased with the soil C:N ratio (Table 2.3, Fig. S2.2.). When potential respiration rates were calculated relative to the organic carbon content of the soils, management system and fungal microbiome richness did not longer have a significant effect in the linear mixed effects model, and most of the variation was explained by the C:N ratio (Table S2.1, Fig. S2.3).

Potential net N mineralization rates were significantly higher in soil samples taken from the crop rows of the organic orchards compared to the drive rows (0.63 ± 0.20 mg $kg^{-1}$ $d^{-1}$ vs. 0.37 ± 0.18 mg $kg^{-1}$ $d^{-1}$, respectively). For the IPM orchards a similar trend was found, though not significant (Table 2.2, Fig. 2.3b). Soil samples from the semi-natural grasslands showed similar net N mineralization rates as samples from the orchards, only being lower than those from the crop rows of the organic orchards (which were highest overall, Fig. 2.3b). In addition, potential net N mineralization rates and soil organic carbon content were positively correlated in the crop rows, but negatively correlated in the drive rows (Fig. S2.4).

The decomposition rate constants (k) that were obtained with the tea bag technique were significantly lower in the semi-natural grasslands (0.01 ± 0.01) compared to the organic and IPM orchards (0.02 ± 0.01 and 0.02 ± 0.01, respectively). Also the location within the orchards had a significant effect, with higher decomposition rates in the crop rows of the IMP orchards compared to the drive rows. In the organic orchards, this effect was opposite but not significant (Fig. 2.3c). Decomposition rates also increased with increasing soil C:N ratio (Table 2.3, Fig. S2.5). Litter stabilization factor (S) did not differ between any of the management systems or locations (Fig. 2.3d), but was strongly positively correlated with pH (Table 2.3, Fig. S2.6).

**Table 2.2.** Mean values ± 1SE for bulk density (BD), soil organic matter (SOM), total nitrogen (N), soil organic carbon (SOC), soil organic carbon stock, potential heterotrophic respiration (Pot. RH), potential net nitrogen (N) mineralization (Pot. Nmin), litter decomposition constant (k) and litter stabilization factor (S). Separate values by depth layer are shown for the drive and crop rows of both orchard types, as well as for the semi-natural grasslands. Significant differences ($P < 0.05$) between values within the same row are indicated by letters and were calculated using a Tukey's test for pairwise comparisons.

| | | Organic orchard | | IPM orchard | | Semi-nat. grassland |
|---|---|---|---|---|---|---|
| Variable | Depth (cm) | Crop row | Drive row | Crop row | Drive row | Grassland |
| BD (Mg $m^{-3}$) | 0-10 | 1.209 (0.046)$^{a}$ | 1.353 (0.039)$^{b}$ | 1.361 (0.031)$^{ab}$ | 1.348 (0.042)$^{b}$ | 1.282 (0.045)$^{ab}$ |
| | 10-30 | 1.365 (0.022)$^{a}$ | 1.504 (0.034)$^{bc}$ | 1.429 (0.022)$^{ab}$ | 1.447 (0.020)$^{ac}$ | 1.519 (0.029)$^{c}$ |
| | 30-50 | 1.496 (0.046) | 1.554 (0.031) | 1.554 (0.019) | 1.549 (0.029) | 1.551 (0.028) |
| SOM (%) | 0-10 | 5.851 (0.265)$^{ab}$ | 5.707 (0.273)$^{ab}$ | 4.792 (0.152)$^{a}$ | 6.800 (0.388)$^{b}$ | 7.967 (0.729)$^{ab}$ |
| | 10-30 | 4.476 (0.247) | 3.962 (0.146) | 3.981 (0.132) | 4.092 (0.145) | 4.358 (0.337) |
| | 30-50 | 2.878 (0.135) | 2.976 (0.101) | 3.215 (0.148) | 3.337 (0.144) | 3.181 (0.237) |
| Total N (%) | 0-10 | 0,177 (0.014)$^{ab}$ | 0,184 (0.011)$^{ab}$ | 0,132 (0.007)$^{a}$ | 0,205 (0.015)$^{b}$ | 0,192 (0.026)$^{ab}$ |
| | 10-30 | 0,130 (0.013) | 0,115 (0.007) | 0,103 (0.007) | 0,109 (0.006) | 0,123 (0.027) |
| | 30-50 | 0,063 (0.006)$^{ab}$ | 0,062 (0.009)$^{ab}$ | 0,056 (0.005)$^{a}$ | 0,065 (0.005)$^{b}$ | 0,070 (0.012)$^{ab}$ |
| SOC (%) | 0-10 | 1.794 (0.180)$^{ab}$ | 1.916 (0.120)$^{ab}$ | 1.373 (0.089)$^{a}$ | 2.190 (0.179)$^{b}$ | 2.101 (0.274)$^{ab}$ |
| | 10-30 | 1.382 (0.160) | 1.192 (0.096) | 1.114 (0.096) | 1.175 (0.078) | 1.426 (0.417) |
| | 30-50 | 0.655 (0.076) | 0.606 (0.101) | 0.546 (0.054) | 0.664 (0.073) | 0.787 (0.140) |
| SOC stock (Mg $ha^{-1}$) | 0-10 | 2.872 (0.289)$^{ab}$ | 3.068 (0.209)$^{ab}$ | 2.199 (0.142)$^{a}$ | 3.288 (0.264)$^{b}$ | 3.364 (0.438)$^{ab}$ |
| | 10-30 | 4.657 (0.538) | 4.018 (0.303) | 3.756 (0.324) | 3.959 (0.269) | 4.807 (1.406) |
| | 30-50 | 2.294 (0.266) | 2.123 (0.355) | 1.914 (0.188) | 2.083 (0.248) | 2.760 (0.489) |
| | Sum 0-50 | 9.823 (0.900) | 9.209 (0.785) | 7.868 (0.589) | 9.330 (0.646) | 10.650 (2.113) |
| Pot. RH (mg $kg^{-1}$ $hr^{-1}$) | 0-10 | 1.144 (0.116)$^{ab}$ | 1.421 (0.113)$^{bc}$ | 0.687 (0.067)$^{a}$ | 1.537 (0.101)$^{bc}$ | 1.777 (0.167)$^{c}$ |
| Pot. RH/SOC | 0-10 | 0.680 (0.075)$^{ab}$ | 0.776 (0.079)$^{bc}$ | 0.541 (0.077)$^{a}$ | 0.751 (0.071)$^{bc}$ | 0.911 (0.131)$^{c}$ |
| Pot. $N_{min}$ (mg $kg^{-1}$ $d^{-1}$) | 0-10 | 0.370 (0.184)$^{a}$ | 0.628 (0.196)$^{b}$ | 0.161 (0.053)$^{a}$ | 0.238 (0.075)$^{a}$ | 0.260 (0.096)$^{a}$ |
| k | 0-10 | 0.017 (0.001)$^{bc}$ | 0.020 (0.001)$^{bc}$ | 0.020 (0.001)$^{b}$ | 0.016 (0.001)$^{ac}$ | 0.014 (0.001)$^{a}$ |
| S | 0-10 | 0.177 (0.005) | 0.219 (0.007) | 0.187 (0.005) | 0.205 (0.004) | 0.158 (0.008) |

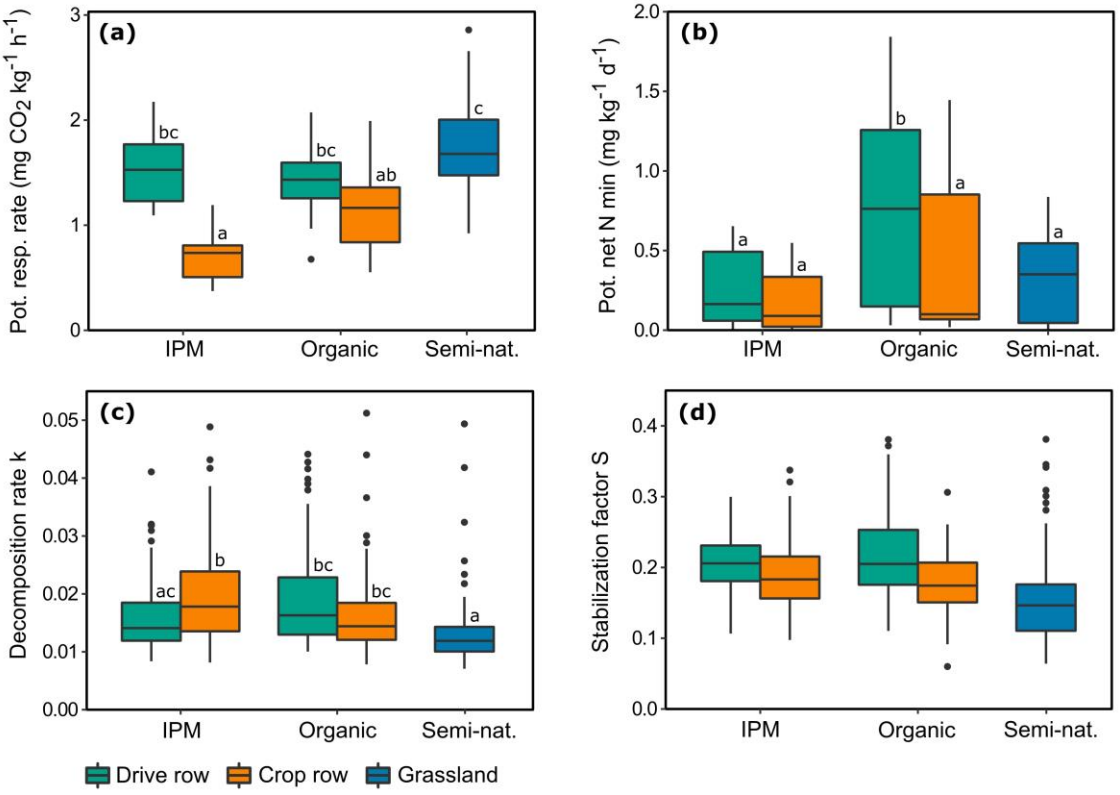



**Figure 2.3.** Box plots of a) potential heterotrophic respiration rate, b) potential net nitrogen (N) mineralization rate, c) decomposition rate constant k and d) stabilization factor S of the different management systems and locations. Significant differences ($P < 0.05$) between boxes are indicated by letters and were calculated using a Tukey's test for pairwise comparisons.

**Table 2.3.** Results of the final linear mixed-effects models for all biological soil health indicators, showing marginal ($R_m^2$) and conditional ($R_c^2$) $R^2$-values for all models. Test statistic (F) and semi-partial $R_\beta^2$ are given for each retained explanatory variable after model reduction. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Soil biological indicators | Pot. heterotrophic resp. $R_m^2$= 0.643 ; $R_c^2$ = 0.729 | | Pot. net N mineralization $R_m^2$= 0.249 ; $R_c^2$ = 0.615 | | Litter decomposition k $R_m^2$= 0.358 ; $R_c^2$ = 0.512 | | Litter stabilization S $R_m^2$= 0.333 ; $R_c^2$ = 0.700 | |
|---|---|---|---|---|---|---|---|---|
| | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ | *F* | $R_\beta^2$ |
| Management | 3.6* | 0.178 | 1.3 | 0.075 | 6.2** | 0.235 | 1.3 | 0.032 |
| Location | 15.2*** | 0.318 | 10.4* | 0.250 | 10.0** | 0.087 | 4.4 | 0.062 |
| pH | 0.8 | 0.011 | - | - | - | - | 14.1*** | 0.217 |
| SOC | - | - | 1.8 | 0.040 | - | | - | - |
| C:N | 5.1* | 0.156 | - | - | 6.8* | 0.142 | 2.0 | 0.035 |
| S_Fun | 5.9* | 0.142 | - | - | - | - | 1.8 | 0.030 |
| IS_Fun | - | - | - | - | - | - | 2.3 | 0.027 |
| IS_Bac | - | - | 0.2 | 0.005 | - | - | - | - |
| IS_Plant | - | - | - | - | 0.3 | 0.003 | 2.7 | 0.047 |
| Management x Location | 2.2 | 0.064 | 5.2* | 0.210 | 6.4* | 0.084 | 3.6 | 0.058 |
| Management x S_Fun | - | - | - | - | - | - | 1.6 | 0.047 |
| Management x pH | 3.3 | 0.092 | - | - | - | - | - | - |
| Location x C | - | - | 6.8* | 0.174 | - | - | 1.6 | 0.048 |

## 2.5 Discussion

### 2.5.1 Soil health indicators

In this study, we compared a set of physical, chemical and biological soil health indicators among commercial apple orchards that were either managed organically or conventionally using IPM practices, both in relation to a semi-natural reference system. Our results show that none of the physical or chemical soil health indicators were significantly different between any of the three systems, not in the full models nor in the separate models for each depth layer. For the biological indicators, we did find differences in potential heterotrophic respiration and decomposition rate among management systems. Potential respiration rates were lowest in the IPM orchards and highest in the semi-natural grasslands. However, this is most likely caused by similar patterns of variation in SOC content between the management systems. Since SOC plays an key role in supplying carbon and energy to the microbial community, higher SOC content is expected to increase microbial activity, resulting in higher respiration rates (Awale et al., 2017; Luján Soto et al., 2021; Montanaro et al., 2017b). Indeed, when respiration rates were calculated relative to the soil organic carbon content, differences between management systems were no longer present. For the decomposition rates calculated by the tea bag method, differences between management systems only existed between the both orchard types on the one hand, and the semi-natural reference on the other hand. However, the lower decomposition rates in the semi-natural grasslands were most likely caused by extremely warm and dry weather during the final weeks of field incubation. Although all tea bags were buried in soils with similar temperature and moisture content, lack of shade trees made the soils in the semi-natural grasslands dry out before the end of the incubation period, possibly interrupting litter decomposition (Parton et al., 2007). In summary, we can conclude that none of the soil health indicators differed between the organic and the IPM system, and only the decomposition rates slightly deviated from those measured in the semi-natural reference system.

### 2.5.2 Comparison between organic and IPM apple cultivation systems

The lack of contrast in soil health between organic and IPM apple cultivation systems is in line with results from other studies (Glover et al., 2000; Orpet et al., 2020; Reganold et al., 2001). This might be due to the fact that those studies, like ours, were designed to evaluate the management systems in their entirety, rather than evaluating specific management practices. Although specific organic practices, such as the application of certain organic amendments, are often associated with increased soil

health (Nazaries et al., 2021; Nunes et al., 2018; Sanchez et al., 2003), this does not always imply similar results for real organic farm settings, where a variety of soil management practices can be used within the boundaries of organic certification (Orpet et al., 2020). While some organic farmers, for instance, choose to maximize the reliance on natural ecosystem processes, other might lean more towards adopting the features of conventional farming systems in a process that is often referred to as organic "conventionalization" (Goldberger, 2011; Rover et al., 2020). Examples of this conventionalization are an increased prevalence of large-scale monocultures, increased mechanization, and the replacement of synthetic pesticides and fertilizers with certified organic alternatives (Best, 2008; Buck et al., 1997; Goldberger, 2011). At the same time, conventional farms in Europe are obliged to apply IPM practices following the 2009/128/EC directive on the sustainable use of pesticides (EU, 2009), causing them to shift towards practices with a lower environmental impact. Both factors may have contributed to a convergence in management practices between management systems in our study, resulting in the absence of large differences in soil characteristics. At the same time, we observed that a considerable part of the variation in soil health can be attributed to the study site, suggesting that both natural heterogeneity and personal management preferences by individual farmers are more important than management system.

### 2.5.3 Comparison with a semi-natural reference system

Importantly, and with the exception of small differences in decomposition rate, our results show no differences in soil health indicators between both farming systems on the one side and the semi-natural reference system on the other side. This is in contrast to the few other studies that used a reference to quantify potential soil health, which reported lower soil health under agricultural management (Wander and Bollero, 1999; Williams et al., 2020b). However, these two studies considered annual crops and used unmanaged field margins as a benchmark, whereas our study focused on a perennial crop and a reference system that is managed for biodiversity and ecosystem conservation. Consequently, and at least for the soil variables measured in this study, our results suggest that agricultural practices in both organic and IPM orchards do not cause strongly impaired soil properties and that both systems seem close to having their potential soil health. It could be argued that even the semi-natural grasslands are to a certain extent degraded regarding soil properties and functions, since they do not represent real pristine habitats. However, primary, non-managed grasslands do not occur in Flanders. An alternative would have been to use forest as a reference system, which could possibly have indicated that both organic and IPM agricultural systems are,

in fact, not reaching full soil health potential. This was for instance the case in Gonzaga et al. (2016) and Ortiz et al. (2017), where soils under perennial sugarcane crops and coconut orchards in Brazil were found to be of less quality compared to soils under native Atlantic forest.

### 2.5.4 Spatial variability within the orchards

Unlike management system, location (drive row vs. crop row) did have an effect on most soil health indicators. This impact often differed between the organic and IPM systems, as indicated by the presence of a significant interaction between management system and location in most of the linear mixed models. For the IPM orchards, the drive rows had higher levels of SOM, total N, SOC, SOC stock, potential RH and potential net $N_{min}$ than the adjacent crop rows. Only decomposition rates were higher in the crop rows. For the organic orchards, only bulk density and potential net $N_{min}$ differed between the drive and crop rows, with both indicators showing lower average values in the crop rows. Differences between drive and crop rows were exclusively present in the top soil layer (0-10 cm), with exception of bulk density for which the effect of location was also present in the 10-30 cm layer. These findings indicate that there is a high level of spatial variability within the orchards, and that this variability is more pronounced in the IPM orchards. Higher soil health in the drive rows of the IPM orchards compared to the adjacent crop rows is probably the result of a combination of management factors. In the drive rows, the permanent vegetation cover together with the regular addition of mulched prunings and leaf litter all contribute to higher organic inputs, which are known to increase soil organic carbon content, total N and mineralisable N content (Carey et al., 2009; Marquez-Garcia et al., 2013; Midwood et al., 2020; Palese et al., 2014). Similar organic inputs are likely absent in the crop rows of the IPM orchards, where herbicides prevent the development of a vegetation cover. For organic orchards, where herbicides are replaced with mechanical weeding, we expected similar results since tillage is also associated with lower organic inputs and generally impaired soil properties (Di Prima et al., 2018; Houben et al., 2018; Nunes et al., 2018). However, only minor differences were found between the drive and crop rows of the organic orchards, possibly due to the addition of organic amendments in the crop rows, or the fact that some farmers only apply mechanical weeding when weeds are growing too tall, allowing for the temporal development of a vegetation cover in the crop rows. Finally, pairwise comparison revealed that only the crop rows of the IPM orchards slightly differed from our semi-natural reference system, with lower bulk density in the 10-30 cm soil layer and lower potential heterotrophic respiration. This result, together with the high discrepancy between crop and drive rows in the IPM orchards, suggests

that some improvement concerning sustainable soil management is still possible in the crop rows of the IPM orchards.

### 2.5.5 Implications and future prospects

The results from our on-farm study show that, with the exception of slightly higher decomposition rates measured in the orchards, both organic and IPM farming systems can maintain soil health as compared to a semi-natural reference system. Because of the high variety of applied practices within both farming systems, these results suggest that there is no single best solution to maintain soil health in apple cultivation, but rather a variety of different practices can be used to achieve this result. Future research should address whether the IPM and organic systems, as applied in our study region, are also effective in maintaining soil health in other regions. For example in the dryland regions in China, where fruit cultivation typically depends on conventional methods with high input of synthetic fertilizers and pesticides, and is often associated with severe soil degradation (Gao et al. 2021a). On-farm studies that investigate the potential of IPM or organic management practices in these regions can be set up to develop farming systems that can better meet environmental standards. Finally, comparing soil health with a local (semi-)natural benchmark can allow the quantification of the degree of soil degradation and the assessment of the potential soil health that can be reached under local conditions.

## 2.6 Conclusions

Overall, and at least in terms of the soil variables measured in this particular study, our results suggest that perennial crop systems can be managed in a sustainable way, without jeopardizing soil health. Although there was some spatial variability in soil characteristics between the drive and crop rows within the orchards, both the IPM and organic farming system in our study were generally able to maintain soil health as compared to our semi-natural benchmark. Exploring the potential of both farming systems for the maintenance or improvement of soil quality can be of great interest in other regions where fruit cultivation heavily depends on conventional farming methods, and where agricultural intensification is associated with severe soil degradation. Finally, as some perennial crops have recently been suggested to be a worthy alternative to annual staples in terms of their contribution to global food supply (Kreitzman et al., 2020), this study further highlights the potential of perennial crops to accomplish food production while at the same time minimizing soil degradation.

# Chapter 3

## Direct and indirect effects of management and landscape on biological pest control and crop pest infestation in apple orchards

Adapted from:

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## 3.1 Summary

Biological pest control, relying on naturally occurring predator-prey dynamics, is considered a key element to achieve more sustainable farming systems. However, the combined effects of local management and landscape factors on communities of natural enemies as well as the cascading effects on pest infestations are rarely addressed, especially in perennial crops. Here, we used Piecewise Structural Equation Modelling (PSEM) to test direct and indirect effects of landscape composition, landscape configuration and local management practices on natural enemy communities, the pest control services they provide and ultimately on pest infestation and pest-related yield damage in apple crops. To this end, we surveyed 12 organic and 12 Integrated Pest Management (IPM) orchards during three consecutive years, and we also established a semi-natural benchmark to quantify the extent to which predator communities in the orchards were degraded. Natural enemies had a different community composition and were more abundant in organic orchards compared to IPM orchards. This had a small and positive effect on sentinel egg predation rates in organic orchards, but overall had very little impact on actual apple pest infestation. On the contrary, apple pest infestation levels were directly and positively affected by organic management practices and by increasing semi-natural habitat cover and landscape edge density. Compared to a semi-natural benchmark, both agricultural management systems showed degraded predator communities, which translated into an impaired delivery of biological control services. Our results indicate that organic management and habitat conservation can enhance natural enemies and stimulate pest control, but also show that these factors can enhance pest infestations and can even lead to an overall increase in pest-related crop damage. Our study thus highlights the complex interplay of ecosystem services and disservices provided by biodiversity, which should be taken into account when advising farmers, policy makers and land managers on effective and sustainable strategies to control pest species and safeguard crop production.

## 3.2 Introduction

Over the past decades, agricultural intensification has strongly contributed to the rapid decline of farmland biodiversity (Flohre et al., 2011b). Larger field sizes, decreased crop species diversity and removal of non-productive landscape elements such as hedgerows, trees and ponds all contributed to the simplification of the agricultural landscape, resulting in a decline in food resources, nesting sites and overwintering habitat for wild species (Clough et al., 2020; Rusch et al., 2016). Together with a high input of agrochemicals such as synthetic fertilizers and pesticides, these practices have not only affected farmland biodiversity, but also jeopardized the delivery of biodiversity-based ecosystem services that support agricultural production (Bommarco et al., 2013). In this context, there is a clear need for more sustainable farming systems that can better reconcile biodiversity conservation, ecosystem services provisioning and long-term food security. Organic farming is often considered a key approach to meet these requirements, as it refrains from using synthetic inputs and seeks to employ natural ecosystem functions and services for the production and protection of crops (Boone et al., 2019).

One of the key ecosystem services that organic agriculture aims to promote is natural pest control, because it can substantially reduce the need for pesticides while at the same time maintaining yield levels by decreasing crop infestation (Muneret et al., 2018a). However, the success of organic agriculture in utilizing and enhancing biological pest control services remains a point of discussion. While there is strong evidence that organic farming increases both the diversity and abundance of natural enemies (Muneret et al., 2018a; Tuck et al., 2014), positive effects on pest control services are less pronounced and do not necessarily translate into lower levels of pest infestation and yield loss (Muneret et al., 2018a, but see Török et al., 2021). Moreover, meta-analyses have shown that fields under organic management generally have higher levels of pest infestation, which can be attributed to the lower efficiency of biological pest control compared to the use of synthetic pesticides (Bianchi et al., 2013; Muneret et al., 2018a). Furthermore, also characteristics of the landscapes surrounding crop fields have been found to be key factors affecting the abundance and richness of natural enemies and the provided pest control services (Haan et al., 2019; Karp et al., 2018). Both the proportion of semi-natural habitat (SNH) and edge density (ED), as commonly used measures of landscape composition and landscape configurational complexity, are generally thought to benefit natural enemies and the pest control service they provide (Martin et al., 2019). The effects of the landscape on pest species, however, remain largely inconclusive as pests on crops have been reported to both increase and decrease with more SNH cover

and higher ED (Chaplin-Kramer et al., 2011; Karp et al., 2018). Overall, responses of both natural enemies and pests to the landscape context seem to be highly dependent on the study taxa, the crop type and the specific habitat types in the landscape (Haan et al., 2019; Karp et al., 2018). It has furthermore been hypothesized that the potential benefits of local management on biodiversity and ecosystem services are greatest in landscapes with intermediate complexity (Tscharntke et al., 2012). In contrast, very simple or complex landscapes will have such low or high biodiversity, respectively, that local management practices hardly affect the presence of ecosystem service providers. To better understand how landscape factors and local management drive the presence of natural enemies in the agricultural land, it is therefore informative to quantify the regional diversity of natural enemies. The presence of natural enemies in semi-natural habitats within the landscape can also provide a benchmark to assess the potential abundance and richness of natural enemies that can be obtained in the agricultural land. Although natural enemy diversity in source habitats has often been determined to assess the effectiveness of agri-environmental schemes (AES) such as flower strips or beetle banks (Boetzl et al., 2020), the role of true (semi-) natural references is rarely considered.

Whereas the literature on both local and landscape effects on natural enemies and pest control is extensive, only few studies have explored the simultaneous effects and possible interactions between local and landscape scales (Karp et al., 2018; Muneret et al., 2018a). Even fewer studies have quantified how local and landscape factors affect the entire trophic cascade of biological pest control, starting from natural enemies and the herbivore pest species they predate on, and all the way down to the crop damage inflicted by these herbivores (Chaplin-Kramer et al., 2011; Haan et al., 2019). Especially the quantification of crop damage and the resulting crop yield loss have been often lacking in landscape-scale studies, despite their importance in driving farmers' decisions on the adoption and application of specific management practices. One of the reasons for this may be the methodological difficulty of disentangling direct and indirect effects between variables and distinguishing between associative and causal relationships. Recently developed statistical tools such as Piecewise Structural Equation Modelling (PSEM), however, can tackle these issues and have been increasingly used to investigate the effects of local and landscape variables on communities of natural enemies and the cascading effects they have on pest infestations and crop damage (Flores-Gutierrez et al., 2020; González et al., 2020; Lefcheck, 2016; Lu et al., 2021; Samnegård et al., 2019). Studies employing this methodology found evidence of direct effects of both local management and landscape variables on pest abundance and crop damage (Flores-Gutierrez et al., 2020; Samnegård et al., 2019) as well as indirect,

predator-mediated effects (Lu et al., 2021), or combinations of both (Flores-Gutierrez et al., 2020; González et al., 2020).

Most studies that investigate the simultaneous effects of agricultural management and landscape on biological pest control focus on annual cropping systems, and little is known about perennial systems (but see Flores-Gutierrez et al., 2020; Rusch et al., 2017). Compared to annual crops, community dynamics of both pests and natural enemies are expected to be different in perennial systems because the more permanent availability of resources, lower soil disturbance and lack of crop rotation can provide both pests and natural enemies with additional opportunities to establish and develop on the agricultural land itself (Rusch et al., 2017). On the other hand, perennial crops, even when under organic agriculture, are often associated with more intensive (organically certified) pesticide use compared to annual crops, possibly counteracting these effects (Annaert et al., 2017; Muneret et al., 2018b). Overall, more studies are needed that disentangle the relative effects of farm management and landscape characteristics on biological pest control in perennial systems, especially since the share of perennial crops under organic management has been rapidly increasing in recent years. In the European Union, for instance, organic management of perennial fruit crops is increasing with approximately 7% each year, making it the fastest growing organic crop after dry pulses and oilseeds (Eurostat, 2021). Furthermore, it is likely that this trend will continue in the next years due to the increasing consumer demand for organic fruits together with policy decisions such as the European Farm to Fork strategy, which targets 25% of EU farmland to be farmed organically by 2030 (European Commission, 2020; Willer and Lernoud, 2019).

In this study, our goal was to explore the direct and indirect effects of organic farm management versus conventional management on pest control services in apple orchards, while simultaneous taking into account influences of the surrounding landscape. As the implementation of Integrated Pest Management (IPM) became mandatory in the EU in 2014 (EU, 2009), we further refer to the conventional study sites as ‘IPM orchards’ in this text to clarify the difference between ‘traditional’ conventional management and current management with IPM practices. As a study system we focused on the codling moth (*Cydia pomonella*), which is a major pest species of pome fruits worldwide that causes severe yield loss and economical damage (Knight et al. 2019), and is expected to become an even greater threat in the future due to the development of resistance against a variety of commonly used insecticides (Ju et al., 2021). Furthermore, codling moth also has a generalist and diverse community of natural enemies (Glen, 1975), making *C. pomonella* infestation in apple orchards a

suitable study system to explore the potential of biological pest control under different management regimes in a perennial crop. More specifically, we sampled natural enemies and performed a sentinel egg predation experiment with eggs from codling moths in 12 certified organic apple orchards and 12 conventional orchards with IPM practices. We then used this data to assess the effects of local management (organic vs. IPM) and landscape (composition and complexity) on (i) natural enemy community composition, (ii) natural enemy abundance, richness and functional traits and (iii) predation on sentinel eggs as a measure of biological pest control. In addition, we determined the same variables in 12 semi-natural habitats free of disturbance and pesticides to provide a benchmark to assess the extent to which the predator communities in the orchards are deteriorated, and subsequently how this affects their potential to suppress pest species. Furthermore, we measured pest infestation and yield damage in the orchards and applied PSEM to identify (iv) the relative importance, (v) the direct and indirect, biodiversity-mediated effects and (vi) the cascading, causal influences of local and landscape factors on pests and pest-related yield loss.

## 3.3 Materials and methods

### 3.3.1 Study sites and landscape characteristics

A total of 36 study sites were selected, consisting of 24 orchards and 12 semi-natural reference sites that were all situated in similar landscapes (Tables S3.1-3). In each orchard, six sampling plots were randomly established; three in the edge of the orchard and three in the center at a distance of at least 10 m from the edge. The reference sites that were used as a benchmark for the predator communities consisted of patches of woodland or hedgerows located in semi-natural grasslands. In each semi-natural reference site, three sampling plots were randomly established on the edge of the woodland patches or hedgerows, resulting in a total of 180 sampling plots over all orchards and reference sites combined.

The landscape surrounding each sampling plot was classified into seven land use classes based on data from the Biological Valuation Map (De Saeger et al. 2017) and the map of Flemish agricultural land use parcels (LV 2020): orchards, arable land, agricultural grasslands, wooded semi-natural habitat, herbaceous semi-natural habitat and urban areas. The proportional cover of each of these land use classes as well as a series of additional variables relating to landscape composition and configuration were calculated at seven spatial scales (50 m, 100 m, 250 m, 500 m, 1000 m, 1500 m and 2000 m) using QGIS v.3.16.10 (QGIS Development Team 2021). To reduce collinearity

between landscape variables, a Pearson correlation matrix was constructed and five variables with $r < 0.3$ were retained for further analysis (Table 3.1).

**Table 3.1**. Landscape variables retained after correlation analysis.

| Landscape variable | Abbreviation | Details |
|---|---|---|
| Proportion of orchards (%) | OR | Includes fruit and nut trees; related to landscape composition |
| Proportion of semi-natural habitat (%) | SNH | Summed proportions of herbaceous and wooded semi-natural habitat; related to landscape composition |
| Shannon landscape diversity index | SHDI | Integrates both the number and abundance of landscape classes; related to landscape composition |
| Distance to the nearest semi-natural habitat (m) | DSNH | Related to landscape configuration |
| Edge density (m $ha^{-1}$) | ED | Related to landscape configurational complexity |

## 3.3.2 Sampling of predatory arthropods

Predator communities were sampled in 2020 and 2021 during the second week of August, coinciding with the second annual egg-laying period of *C. pomonella* (Monteiro et al., 2013). This period is of specific interest as the second annual generation of *C. pomonella* is becoming increasingly prevalent, causes high crop damage and might be more susceptible to biological control relative to the first generation due to a high overlap with the phenology of most natural enemies (Horton et al., 2012; Juszczak et al., 2013). At each sampling plot, three branches of three adjacent trees were beaten over a collecting tray at a height of approximately 1.5 m. Collected arthropods were stored in 70% ethanol and both adults and juvenile live stages were later sorted into 14 different taxonomic families that were identified as predators of codling moth eggs in previous studies, or were likely predators based on their feeding behavior (Table S3.4) (Glen, 1975; Glen, 1977; Unruh et al., 2016). In addition to predator abundance and richness, we also calculated the energy use of the predator communities as a trait-based proxy of their predation potential. Predator energy use integrates the abundance, body mass and metabolic rate of the predators and is increasingly used as a predictor of pest suppression in agricultural landscapes (Perović et al., 2018; see Supplementary material, Methods S1 for details and calculation). As predator energy use is partly confounded by predator abundance and richness, we standardized energy use in each sampling plot with null values generated with an

independent swap null model for functional alpha diversity using package "picante" in R (Kembel et al., 2010). More specifically, this model randomizes trait values by reshuffling predator families in the family-trait matrix, while keeping the observed abundance and richness constant. After 999 randomizations of the null model, we calculated the standardized effect size of predator energy use (SES energy use = [observed energy use – mean of simulated energy use] / standard deviation of simulated energy use) and used this metric in all subsequent analyses.

### 3.3.3 Assessment of egg predation rates and pest infestation

Right before predator community sampling, sentinel prey cards with eggs of codling moth were exposed to the predators during four consecutive days to assess pest control levels (Lövei & Ferrante, 2017; see Supplementary material, Methods S2 for details). Per sampling plot, three sentinel prey cards were placed on the outer branches of the trees at a height of 1.5 m, totaling 18 egg cards for each orchard and 9 egg cards for each semi-natural reference site. After retrieval of the cards, the proportion of predated eggs was determined for each card based on the predation patterns described by Glen (1975). Subsequently, the egg cards were kept at 20 °C for two weeks to check for the development of parasitoids. As the number of parasitized eggs and hatched parasitoids was very low (seven individuals from eleven eggs), and because all were found in the semi-natural reference sites, parasitoids were not included in the study and the contribution of egg parasitism to the biological control of *C. pomonella* was not further investigated. Finally, pest infestation was determined just before harvest by examining 100 randomly selected apples per sampling plot for the presence of codling moth larvae. The infestation rate was calculated as the proportion of infected apples and served as a measure of yield damage.

### 3.3.4 Data analysis and statistics

The effect of local management and landscape context on the predator community composition was assessed using partial Redundancy Analysis (pRDA) on Hellinger-transformed predator abundance data (Legendre & Gallagher, 2001). Management type (Organic vs IPM vs Semi-natural), Location (center vs edge) and the five landscape variables (cover of semi-natural habitat, distance to nearest semi-natural habitat, cover of orchards, Shannon landscape diversity and landscape edge density) were used as fixed variables, whereas sampling year and study site ID were included as random factors. In this and all subsequent analyses, we determined the most predictive scale for each landscape variable based on ΔAICc ranking (Jackson & Fahrig, 2015, Table S3.5). To account for trends in predator community composition resulting from the spatial

structure of the study system, distance-based Moran's eigenvector maps (dbMEMs) were calculated based on the geographical coordinates of the study sites with the function 'dbMEM' in R package adespatial (Dray et al., 2021) and added to the RDA model to partial out spatial variation. Subsequently, a forward stepwise selection was performed using the function 'ordiR2step' in R package vegan to avoid model over-parameterization (Oksanen et al., 2018). Significance of all axes and variables in the final model were tested using permutations (n = 999), and variation partitioning based on adjusted $R^2$ values was conducted using the 'varpart' function from the package vegan to determine the unique and shared part of variation explained by the local and landscape variables in the final model.

Next, (generalized) linear mixed-effect models ((G)LMMs) were constructed to assess the effects of local and landscape factors on predator community abundance and richness (Poisson distribution) and predator energy use (normal distribution after log-transformation). To allow log-transformation, sampling plots for which predator energy use equaled zero were assigned a value corresponding to half the energy use of the plot with the smallest value. Models all included management, plot location and the five landscape variables as fixed effects, as well as first-order interaction terms between management and all other fixed factors and covariates. Similar to the RDA model, sampling year and study site ID were included as random factors and dbMEMs were incorporated to account for spatial autocorrelation. To further assess the robustness of our results in the presence of spatial autocorrelation, a sensitivity analysis was performed on a subset of eight organic, eight IPM and eight semi-natural reference sites for which no spatial autocorrelation was detected, which confirmed that spatial patterns did not affect any of our main results or conclusions. To avoid multicollinearity, predictor variables with a Variance Inflation Factor (VIF) higher than 3 were excluded prior to model building. Starting from the full models, all (G)LMMs were simplified using model selection based on AIC value using the 'dredge' function in the R package MuMIn (Bartoń, 2020). The same modelling strategy was used to assess the influence of local management, landscape factors and predator community characteristics on sentinel egg predation and codling moth infestation, which were both fitted with a binomial error distribution. Both egg predation and pest infestation were determined over three years (2019, 2020 and 2021), which allowed to calculate coefficients of variation (CV) to study the variability of these metrics over time. CVs for egg predation and pest infestation were modelled using LMMs with management and landscape factors as explanatory variables. All GLMMs were systematically checked for data overdispersion and an observation-level random factor was added when overdispersion was detected. Residuals of all LMMs were checked for normality and heteroscedasticity

and when necessary, variables were transformed to meet these assumptions. To better understand the differences between organic orchards, IPM orchards and the semi-natural benchmark, we calculated effect sizes based on differences in marginal means between the management types using the package emmeans (Lenth et al. 2018).

Finally, we used PSEM to test direct and indirect, predator-mediated effects of local management and landscape factors on pest infestation in the orchards. To this end, the mixed-effects models for predator abundance, predator richness, predator energy use, sentinel egg predation and pest infestation were first refitted to a subset of the data excluding all semi-natural reference sites, then reduced by retaining only significant predictors and finally combined into a structural equation model using the package piecewiseSEM (Lefcheck, 2016). Missing pathways in the initial PSEM were detected by the D-separation test and overall model fit was assessed using Fisher's C statistic. Three correlated errors between predator abundance, predator richness and predator energy use were included because these factors are presumably driven by similar underlying factors. Finally, the relative importance of pathways was determined using standardized path coefficients. All statistical analysis were done in R v.4.0.0 (R Core Team, 2021).

## 3.4 Results

### 3.4.1 Predator communities and predation rates in the orchards as compared to a semi-natural benchmark

We collected 7361 foliar arthropods in total, of which 2673 or 37% were identified as possible natural enemies of codling moth. Overall, Philodromidae (running crab spiders) were the most common predators (19%), followed by Coccinellidae (ladybugs, 13%) and Miridae (mirid bugs, 11%) (Fig. S3.1). Partial RDA revealed that the composition of the predator community was significantly affected by management type, ED, SHDI, SNH and DSNH (Fig. 3.1, Table S3.6). Additional post-hoc tests indicated that the predator community composition significantly differed between all three management types (Table S3.6). Overall, local management and landscape variables explained 15% and 9% of total variation in predator community composition, respectively (Table S3.6).

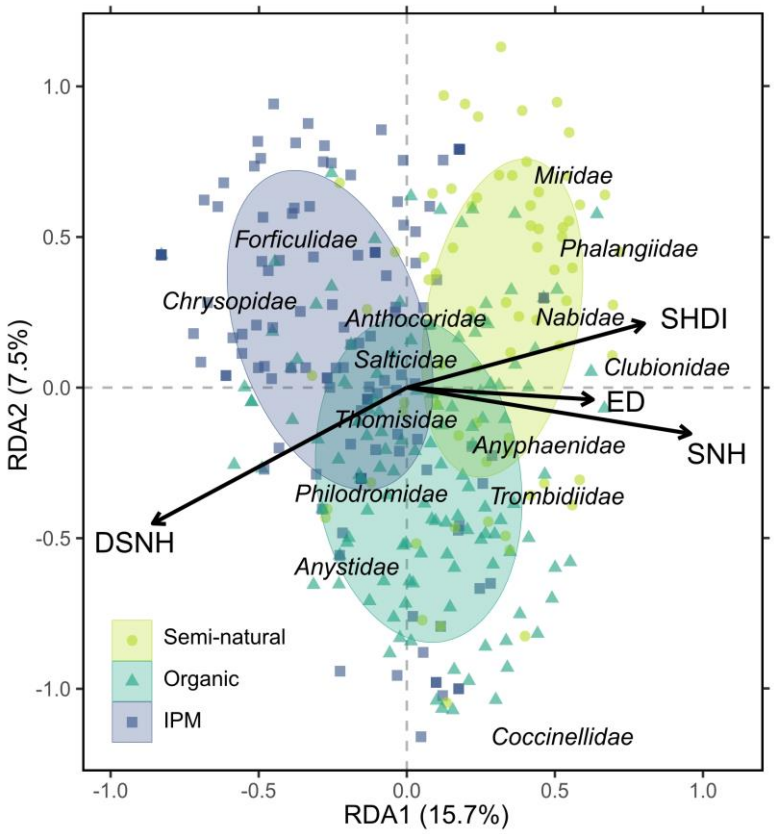



**Figure 3.1.** Partial redundancy analysis (pRDA) triplot visualizing predator community composition with management type and four landscape factors (arrows) as explanatory variables. DSNH: distance to nearest semi-natural habitat, SHDI: Shannon landscape diversity index, ED: edge density, SNH: semi-natural habitat. Ellipses depict the standard deviation from the centroid for each management type.

Mean predator abundance and family richness per sampling plot were highest in the semi-natural reference sites (14 ± 8 individuals from 6 ± 2 families) followed by the organic orchards (7 ± 3 individuals from 4 ± 2 families) and the IPM orchards (5 ± 3 individuals from 2 ± 2 families) (Fig. 3.2, Table S3.7a-b). Both abundance and family richness decreased with higher proportions of orchards in the landscape, and predator abundance was negatively affected by higher DSNH and higher ED (Fig. 3.3a-c, Fig. S3.2-3.3, Table S3.7a-b). Higher SNH cover in the surrounding landscape increased predator abundance, but had no significant effect on family richness. The response of both predator abundance and family richness to SHDI differed between management types, with abundance and richness both increasing with higher SHDI in the semi-natural reference sites, but showing no significant correlation in the organic and IPM orchards (Fig. S3.2-3.3, Table S3.8). Predator energy use was higher in the organic and IPM orchards relative to the semi-natural reference sites (Fig. 3.2, Table S3.7a-b), increased with higher SNH cover and decreased with higher ED (Fig. S3.4, Table S3.7a-b).

Sentinel egg predation rates were higher in the semi-natural reference sites (0.65 ± 0.28) compared to the organic and IPM orchards (0.51 ± 0.31 and 0.52 ± 0.33, respectively) (Fig. 3.2, Table S3.9a-b). Higher SNH cover, SHDI, predator abundance and predator energy use all increased predation rates, and in the orchards predation was higher in the edge plots relative to the center plots (Fig. S3.5, Table S3.9a-b). Over a three-year period, predation rates showed highest variability in the IPM orchards (CV = 0.92 ± 0.40), intermediate variability in the organic orchards (CV = 0.68 ± 0.32) and were most stable in the semi-natural reference sites (CV = 0.42 ± 0.21) (Fig. 3.2, Table S3.9a-b). Predation variability increased with orchard cover in the landscape and was higher in the center plots of the orchards compared to the edge plots (Fig. S3.6, Table S3.9a-b).

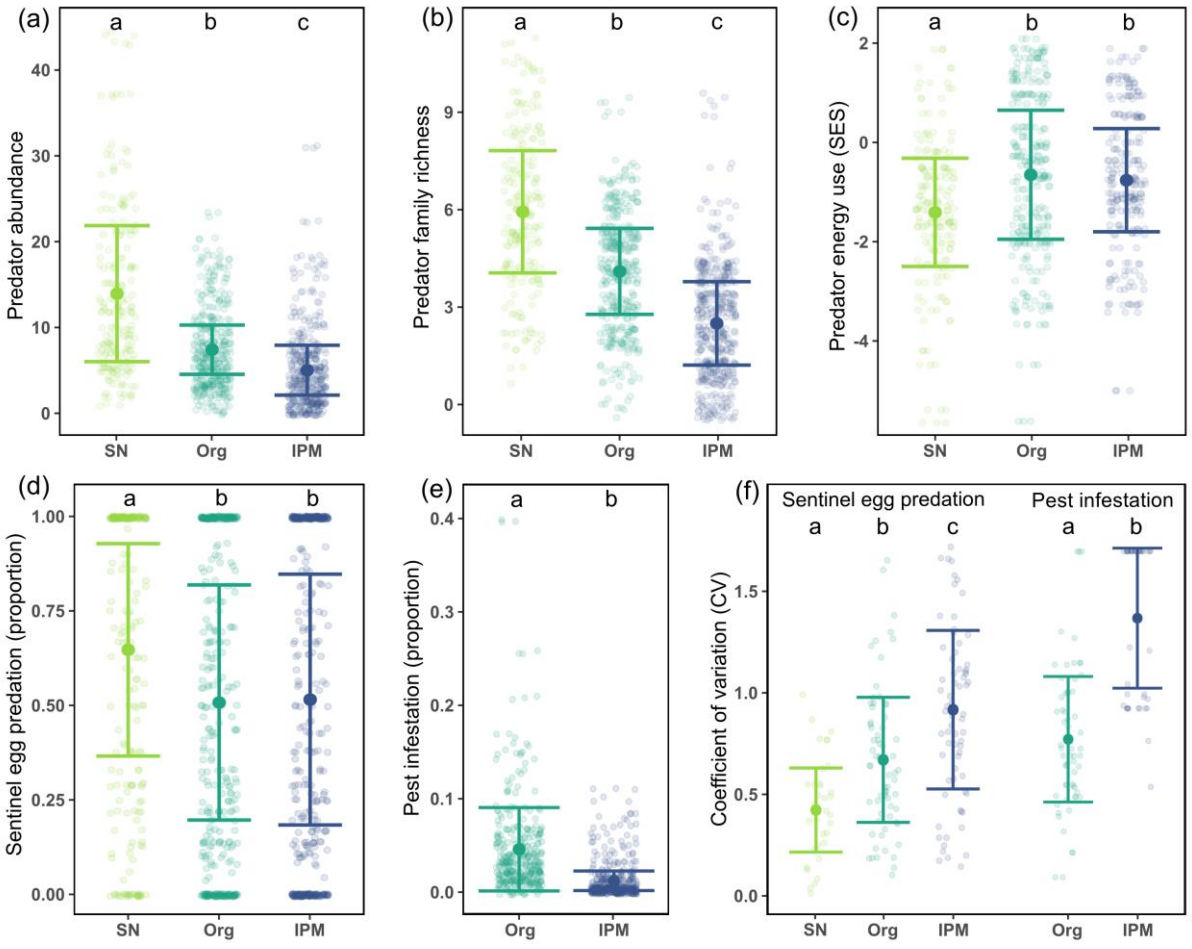



**Figure 3.2.** Mean ± 1SE per sampling plot of (a) predator abundance, (b) predator family richness, (c) standardized effect sizes (SES) of predator energy use, (d) sentinel egg predation, (e) pest infestation and (f) coefficients of variation for sentinel egg predation and pest infestation in semi-natural reference sites (SN), organic orchards (Org) and orchards with integrated pest management (IPM). Letters indicate significant differences between management types. Summary statistics for the corresponding (G)LMM models can be found in Tables S3.7-3.9.

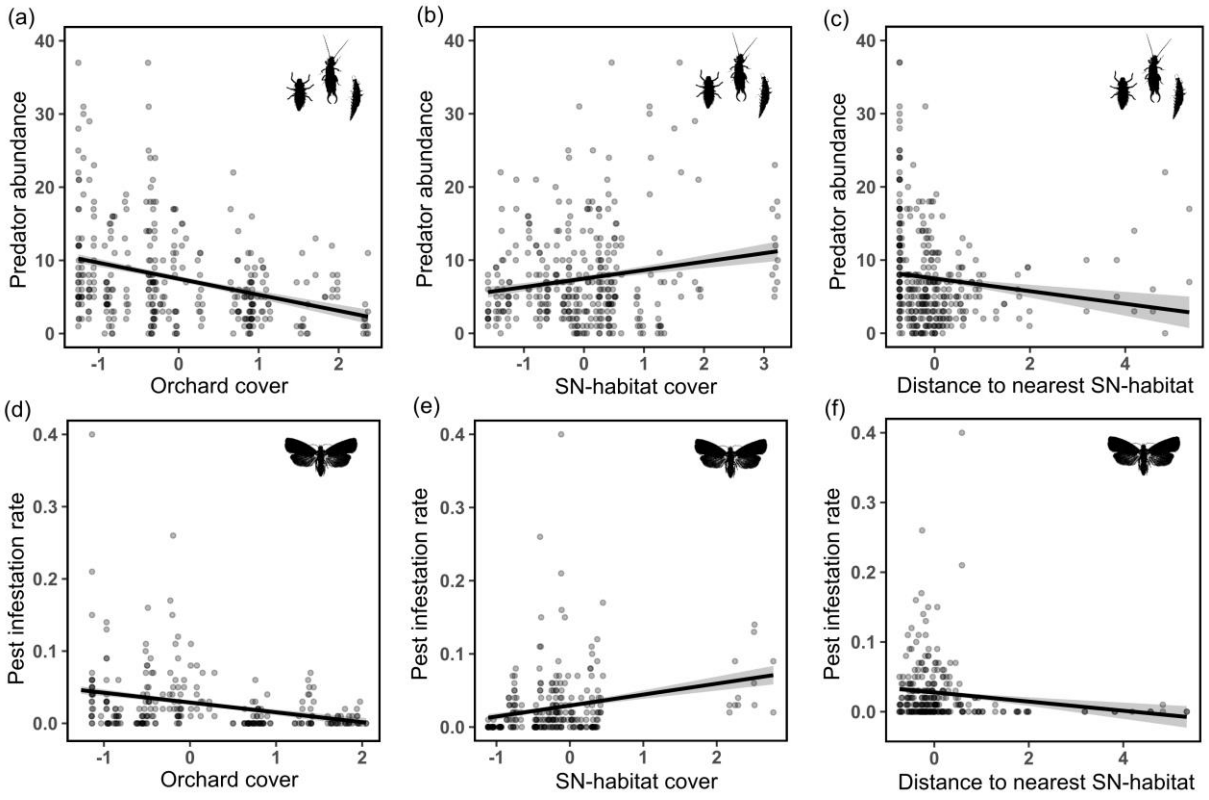



**Figure 3.3.** Relationships between predator abundance (a-c) and pest infestation (d-f) and a selection of landscape variables including orchard cover, semi-natural habitat cover and distance to nearest semi-natural habitat. Fitted lines with 95% confidence intervals are based on GLMMs and are plotted together with raw data points. The x-axes show standardized values of landscape predictors, as were used in the GLMMs (Tables S3.7-3.9).

Compared to the semi-natural benchmark, the overall effects of orchard management on predator energy use and (CV of) sentinel egg predation were greater than the effects on predator abundance and richness (Fig. 3.4).

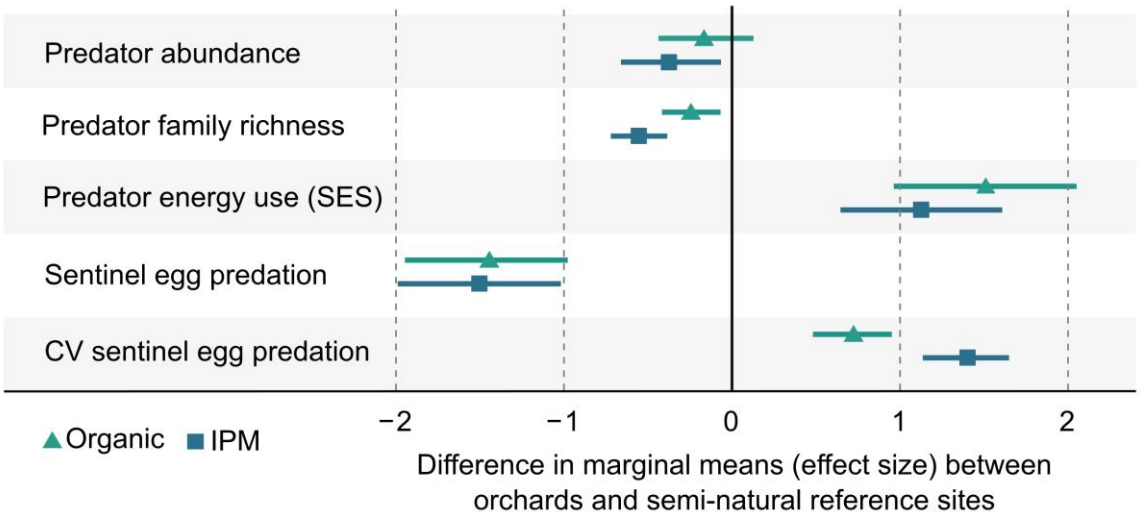



**Figure 3.4.** Effect sizes (mean ± 95% CI) for predator community metrics, sentinel egg predation and the coefficient of variation (CV) of sentinel egg predation based on differences in marginal means between organic orchards, IPM orchard and the semi-natural benchmark. Positive effect sizes indicate a higher mean than the semi-natural benchmark while negative values indicate a lower mean. (G)LMM statistics that were used to estimate effect sizes and confidence intervals can be found in Tables S3.7-3.9.

### 3.4.2 Cascading effects on pest infestation

Pest infestation levels, measured by the proportion of codling moth infected apples, were higher in the organic orchards (0.05 ± 0.04) compared to the IPM orchards (0.01 ± 0.01) (Fig. 3.2, Table S3.9a-b). Infestation levels increased with higher SNH cover and ED, lower DSNH, and were positively correlated with predator richness and energy use (Fig. 3.3d-f, Fig. S3.7, Table S3.9a-b). Over a three-year period, infestation levels were more stable in the organic orchards (CV = 0.76 ± 0.38) compared to the IPM orchards (CV = 1.36 ± 0.44) (Fig. 3.2, Table S3.9a-b).

The piecewise structural equation model indicated that pest infestation levels were predominantly shaped by strong positive, direct effects of organic orchard management, SNH cover and ED (Fig. 3.5, Tables S3.10-3.11). To a lesser extent, these variables also indirectly stimulated infestation by increasing predator richness and energy use, which were both positively associated with pest infestation. Direct negative effects on pest infestation were relatively small and were found for location (orchard edge) and orchard cover in the landscape, the latter of which also indirectly affected infestation through predator richness. Several direct and indirect, mostly positive effects of local and landscape variables on sentinel egg predation were identified, but predation in turn had no significant effect on pest infestation.

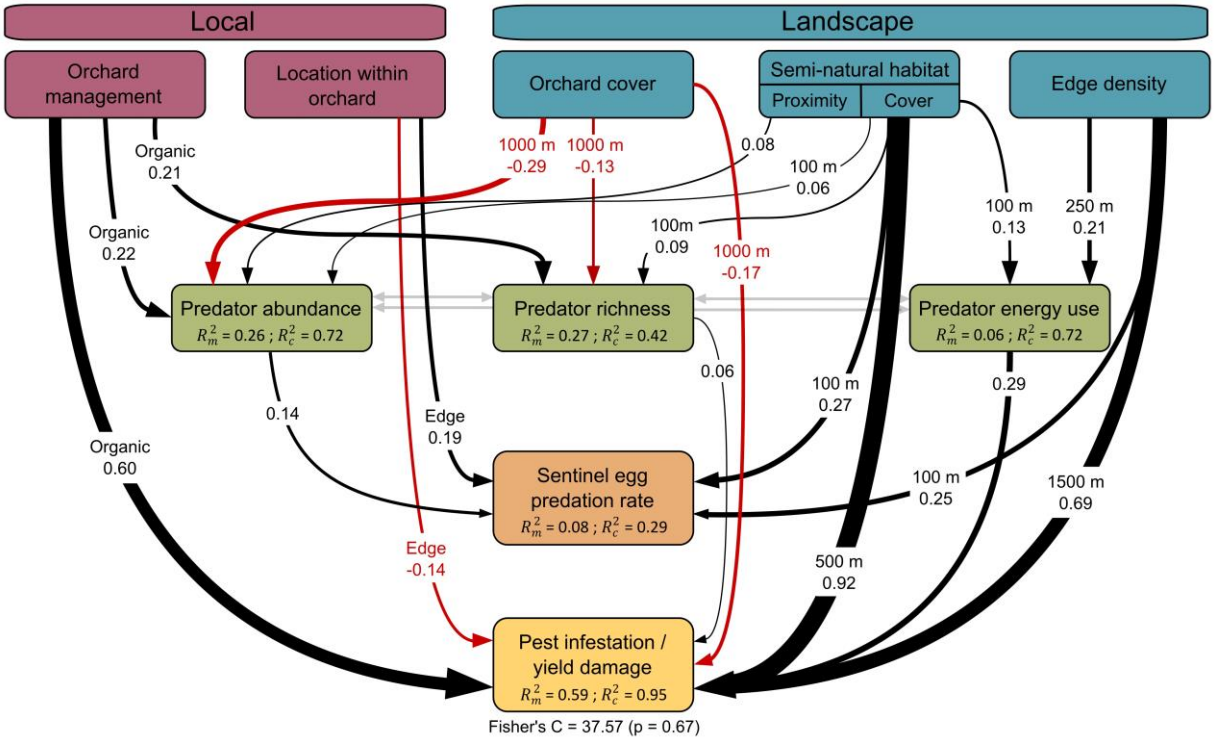



**Figure 3.5**. Final PSEM showing significant direct and indirect, predator-mediated effects of local and landscape variables on pest infestation. Black and red arrows represent significant positive and negative pathways, respectively, with arrow thickness corresponding to the value of the standardized path coefficients. Grey double-headed arrows illustrate correlated errors. Relevant spatial scales for landscape predictors are indicated together with the path coefficients. Marginal and conditional $R^2$ values are shown for all response variables and overall model fit is indicated by Fisher's C statistic. Summary statistics for the PSEM model are shown in Table S3.11.

## 3.5 Discussion

Here, we explored direct and indirect, predator-mediated effects of local management and landscape context on pest control services provided by natural enemies in a perennial fruit crop. We showed that natural enemies had a different community composition and were more abundant in organic orchards compared to IPM orchards, which had a small positive effect on sentinel egg predation rates but overall had very little impact on apple pest infestation. Instead, apple pest infestation levels were directly and positively impacted by organic management practices, semi-natural habitat cover and landscape edge density.

### 3.5.1 Predator communities and sentinel egg predation

Organic management was positively associated with predator abundance and family richness, which is in line with results from previous studies (Muneret et al., 2018a, Tuck et al., 2014), and likely due to a higher resource availability compared to the IPM orchards, for example by differences in weed management, or lower impact of organically certified pesticides on non-target organisms. Predator energy use, however, did not differ between organic and IPM orchards, indicating that orchard management did not affect traits related to body size and metabolic rate. Besides local management, also landscape is known to shape predator communities, with natural enemies benefitting from the presence and proximity of semi-natural habitat structures such as mixed hedgerows, and generally increasing with higher landscape complexity and heterogeneity (Beliën et al., 2021; Haan et al., 2019). This was confirmed by our study, which showed increased predator abundance and family richness with higher SNH cover and, in the case of abundance, also when SNH was closer to the orchards. Higher SNH cover and ED also increased predator energy use, indicating that higher resource availability and landscape complexity support arthropods with higher energy requirements.

Linking natural enemies with the potential services they provide, we found that sentinel egg predation increased with predator abundance but was not affected by predator family richness or energy use. While the positive effect of predator abundance has frequently been reported elsewhere (Dainese et al., 2019), the impact of richness and energy use remains ambiguous (Rusch et al., 2015). Although energy use has been suggested as a useful proxy for prey consumption (Perovic et al., 2018), it has also been argued that an increase in body size and energy requirement can alter predator-prey dynamics by shifting prey preferences or increasing intraguild predation, which can even result in a net negative effect of a higher energy requirement on pest consumption (Rusch et al., 2015). Similar mechanisms may be at work when richness increases, which may stimulate egg predation through resource partitioning and facilitation, but can also negatively affect pest predation due to negative intraguild interactions (Lu et al., 2021). Additionally, predator richness and energy use might have been better predictors if predators were identified to species level instead of family level, but this was not feasible due to the high number of juvenile specimens in our samples. Surprisingly, the PSEM analysis indicated that sentinel egg predation was mostly influenced by direct effects of landscape, with egg predation increasing with SNH cover and ED and being higher in the edges of the orchards compared to the center. It is likely that these effects of landscape were, in fact, mediated through natural enemies but that we were not able to detect them as such due to our sampling methodology. The beating

tray method for instance undersamples flying predators such as ladybugs and lacewings, or very small predators such as mites.

Compared to the semi-natural benchmark, both organic and IPM orchards showed a different predator community composition and supported lower abundance and family richness. The overall difference in effect size was relatively small, but was higher when looking at predator energy use and sentinel egg predation. These results indicate that negative effects of agricultural management on predator communities may translate in even more detrimental effects on the delivery of the ecosystem services they provide.

### 3.5.2 Cascading effects on pest infestation

Our PSEM analysis pointed out that pest infestation levels in our study were mainly driven by strong direct effects of organic orchard management, high SNH cover and high ED, indicating that the same factors that enhanced natural enemies were of even greater benefit to the pests. Additionally, pest infestation levels also showed an unexpected positive association with predator richness and energy use. Just like for sentinel egg predation, this may be due to mechanisms such as shifting prey preferences or higher intraguild predation, or it may indicate that pests and natural enemies are influenced by common drivers that were not captured in our analysis. Another likely explanation might be that pest abundance is actually driving predator richness and energy use, with high levels of pest infestation supporting predator communities with higher richness and higher energy requirements. Nevertheless, some variables also decreased codling moth infestation as lower percentages of infested apples were found in the orchard edges and with increasing orchard cover in the landscape. A decrease in both pests and natural enemies with higher orchard cover has also been reported in other studies and is often attributed to the "chemical umbrella effect", which entails that uniform landscapes with high pesticide application reduce biodiversity at the landscape level (Samnegård et al., 2019, Muneret et al, 2018b). In landscapes where pesticide pressure is very low, however, this effect might be absent and a higher orchard cover might actually stimulate pest abundances due to higher resource availability (Martínez-Sastre et al., 2021). Specifically for codling moth in our study, the chemical umbrella effect also applies to the pheromones that are used for mating disruption in both the organic and IPM orchards, which have been shown to be more effective when applied in areas with a large, continuous cover of orchards and few field edges with semi-natural habitat (Bangels & Beliën 2012; Witzgall et al., 2008). Additionally, a high orchard cover in the landscape might also reduce local infestation levels due to a resource dilution effect, where the abundance of a pest is found to be negatively associated with

host plant availability (Schneider et al., 2015). Both the umbrella effect and resource dilution can also provide an additional reason why pest infestation increases with higher cover of semi-natural habitat in the landscape, in this case by the lower landscape-level application of pesticides and limited availability of apple trees as resource. Contrary to our expectations, predation on sentinel eggs of codling moth was not linked to codling moth infestation levels at apple harvest. This may be explained by the inability of the sentinel egg cards to capture the entire predation pressure, since only one specific life stage of the pest species is exposed to natural enemies for only a limited timeframe (Lovei and Ferrante, 2017). Additionally, our study only focused on arthropod predators, while other natural enemies like birds and bats might also affect pest infestation by feeding on the larvae or adults of codling moths (Garcia et al. 2018).

## 3.6 Conclusion

While organic management and habitat conservation are known to enhance natural enemies and stimulate pest control of many pest species in different cropping systems (Muneret et al., 2018a, Karp et al., 2018), our study shows that these factors can also enhance pests and lead to an overall increase in pest-related crop damage. Indeed, our results indicate that pest infestation levels were predominantly shaped by strong direct effects of local management and landscape, and that impacts on pest infestation mediated through biological control were insignificant. This implies that an integrated approach utilizing a combination of pest management strategies that are adjusted to the specific landscape context is likely required to achieve more sustainable and effective pest suppression in apple orchards.

# Chapter 4

## Cascading effects of management and landscape on insect pollinators, pollination services and yield in apple orchards

Adapted from:

Hulsmans*, E., Daelemans*, R., Cuypers, V., Van Der Straeten, E., Vanderlinden, M., De Blanck, T., Vertommen, W., Boeraeve, M., Proesmans, W., Honnay, O., 2023. Cascading effects of management and landscape on insect pollinators, pollination services and yield in apple orchards. Agric. Ecosyst. Environ. 352, 108509.

* Shared first co-authors, both authors contributed equally to the field work, lab work, data analysis and writing of the manuscript

## 4.1 Summary

Recent insect pollinator declines, mainly due to the expansion and intensification of agricultural land use, are jeopardizing ecosystem service provisioning in agroecosystems. Organic farming has been suggested as a biodiversity-friendly alternative to conventional farming, but additional insights evaluating its effectiveness in perennial cropping systems are needed. Here, we provide a comprehensive analysis of local and landscape effects on the provided pollination services and yield in apple crops. We first used mixed models to disentangle effects of agricultural management and landscape on both taxonomic and functional diversity of wild bees and hoverflies during bloom in both organic and integrated pest management (IPM) apple orchards in Belgium, and then compared these biodiversity indicators with semi-natural grasslands as a benchmark. Next, we applied piecewise structural equation modeling to quantify the direct and indirect effects of orchard management type and landscape on fruit set, seed set and ultimately on crop yield. Orchards, regardless of their type of management, hosted lower taxonomic and functional pollinator diversity compared to the semi-natural benchmark. Yet, pollinator abundance and diversity were higher in orchard edges and increased with small-scale landscape diversity, which was positively associated with the presence of semi-natural habitat, as well as arable and urban land. Investigating the cascading effects on apple yield, we found that yield levels were not shaped by the observed pollinator diversity or by the measured pollination services, but were lower in organic orchards. Overall, we conclude that apple yield was likely not pollinator limited in our study system, but that conserving and restoring semi-natural habitats, maintaining and expanding orchard edges and promoting landscape diversity are the most promising avenues for pollinator conservation in orchard landscapes.

## 4.2 Introduction

Insect pollinators are key ecosystem service providers that are essential for the conservation of wild plant communities as well as for the production of more than 75% of the leading global food crops (Klein et al., 2007; Ollerton et al., 2011). However, over the last decades populations of wild bees and other pollinating insects have strongly declined, mainly attributed to the expansion and intensification of agriculture (IPBES, 2016; Wagner et al., 2021). Agricultural intensification and the conversion of natural habitats to farmland decrease the availability of resources and nesting sites, and negatively affect pollinator fitness and survival due to the use of agrochemicals (Lichtenberg et al., 2017; Potts et al., 2010). These factors have been associated with decreased species richness, abundance and diversity of wild pollinator communities, which in turn have been linked to lower seed and fruit set, lower long-term stability of yields and lower overall farmer income in pollinator-dependent crops (Albrecht et al., 2012; IPBES, 2016; Senapathi et al., 2021). Overall, a transition to more sustainable farming systems that can safeguard wild pollinators and their associated ecosystem services is urgently required.

Organic farming, which refrains from using synthetic fertilizers and pesticides and aims at capitalizing on biodiversity-based ecosystem services, has been proposed as a farming system that is more sustainable than conventional farming (Boone et al., 2019). Organic farming has indeed been associated with higher pollinator richness, abundance and diversity as well as higher crop pollination levels relative to conventional or integrated pest management (IPM) systems (e.g. Andersson et al., 2014; Holzschuh et al., 2010; Kennedy et al., 2013; Rundlöf et al., 2008). However, organic management is also typically associated with lower yields compared to IPM or conventional management systems (Seufert, 2019). Furthermore, the beneficial effects of organic management on pollinators and pollination services have been mainly found in annual cropping systems, while studies in perennial crops are more rare and often report inconsistent results (Pardo et al., 2020; Porcel et al., 2018). In apple crops, for instance, Samnegård et al. (2018) found higher species richness and flower visitation in organic orchards compared to IPM orchards, while other studies report similar species richness, abundance and pollinator visitation rates (Pardo et al., 2020; Porcel et al., 2018; Radzevičiūtė et al., 2021). These inconsistent results might indicate that local management practices have less impact on pollinators and pollination services in perennial crops as compared to annual crops (Brittain et al., 2010a; Porcel et al., 2018). This might be due to the lower disturbance and the presence of permanent structural elements in perennial cropping systems such as the crop trees and the grass strips

between the crop rows, which can provide sources of food, shelter and nesting sites for pollinators regardless of the farm management (Porcel et al., 2018).

However, even when resources for pollinators are higher in perennial cropping systems than in annual systems, they may still lack the capacity to support a diverse and abundant pollinator community because the resources are too limited in quantity and quality, or only sufficiently available during a very limited timeframe (e.g. mass flowering crops that only bloom for a few weeks) (Eeraerts et al., 2021; Garibaldi et al., 2011). Instead, most pollinator species present in agricultural fields are known to depend heavily on the availability of resources in the surrounding landscape (Garibaldi et al., 2011; Martins et al., 2015; Raderschall et al., 2021). A wide body of literature across multiple pollinator taxa and crop types has shown that the presence and proximity of semi-natural habitats such as grasslands, forest or hedgerows increases pollinator richness, abundance, flower visitation and long-term community stability (Garibaldi et al., 2011; Kennedy et al., 2013; Schoch et al., 2022). Furthermore, characteristics of the surrounding landscape have also been found to influence the impact of local farming practices on pollinators and pollination services (Brittain et al., 2010a). Beneficial effects of organic farming on pollinator richness and abundance have for instance mainly been found in relatively simple and homogenous landscapes (Lichtenberg et al., 2017). Consequently, it is necessary to simultaneously take into account the effects of local management and landscape context in order to correctly evaluate the performance of organic farming in stimulating pollinators and pollination services.

Most studies on the impact of agricultural management and landscape composition on pollinators have focused on taxonomic richness and diversity, while these are not necessarily good predictors of pollination efficiency (Cadotte et al., 2011; Ricketts et al., 2008). Several studies have indicated that ecological functions are often better explained by the identity and diversity of functional traits present in a community, with a high trait diversity for instance relating to more resilient pollination services (Forrest et al., 2015; Gagic et al., 2015; Roquer-Beni et al., 2021). Importantly, functional trait diversity does not necessarily respond in the same way to changes in land management or landscape context as species diversity metrics, for instance when there is high variation in responses between different functional groups (Forrest et al., 2015). Therefore, it is useful to use both taxonomic and functional metrics to study the effects of local management and landscape context on pollinators and pollination services.

Finally, to fully understand how different agricultural management systems affect pollinator communities, these systems should be compared against a (semi-)natural

reference (Katayama et al., 2019). Such a comparison can provide information on the extent to which pollinator communities in agricultural fields have been degraded as a result of agricultural management, and at the same time on the relative importance of (semi-)natural habitat for pollinator conservation. Studies that use such comparison in perennial systems are rare, and results seem inconsistent. Wild bee richness was for instance higher in natural habitats compared to both organic and conventional farms in South-African vineyards, while abundance did not differ between these systems (Kehinde and Samways, 2012). However, Forrest et al. (2015) found higher species richness of bees in organic farms compared to conventional farms, but lower functional diversity in both farm types relative to a natural reference habitat.

In this study, we investigated the impact of organic management versus conventional management following IPM practices on pollinator communities and pollination services in apple crops in Flanders, Belgium. As the implementation of Integrated Pest Management (IPM) became mandatory in the EU in 2014 (EU, 2009), we further refer to the conventional study sites as 'IPM orchards' in this text to clarify the difference between 'traditional' conventional management and current management with IPM practices. Apple (*Malus domestica*) is one of the most economically important fruit crops globally and typically requires insect pollination due to high levels of self-incompatibility (FAOSTAT, 2020; Pardo and Borges, 2020). The organic management of apple crops is rapidly increasing, mainly due to increasing consumer demands for organic fruits together with policy incentives such as the European Farm to Fork strategy, which aims to farm 25% of EU farmland organically by 2030 (European Commission, 2020b; Willer and Lernoud, 2020). This rapid increase in organic fruit production urges for a better evaluation of organic management in terms of the conservation of pollinators and pollination services relative to conventional management.

More specifically, we first aimed at quantifying the effects of local management (organic vs. IPM) and of landscape variables on both taxonomic and functional diversity of pollinators in 12 organic and 12 IPM apple orchards, and we compared diversity with 12 semi-natural grasslands as reference habitats. Second, we aimed to disentangle the direct and pollinator-mediated effects of local orchard management and landscape on fruit set, seed set and ultimately apple crop production. Because no synthetic pesticides are used in organic farming, we expected the organic orchards to harbor more taxonomically and functionally diverse pollinator communities relative to the IPM orchards, but we also expected both orchard types to have impaired pollinator communities relative to the semi-natural reference due to lower habitat quality and

resource availability. Additionally, we expected that more diverse pollinator communities in organic orchards would result in higher pollination services, but that this would not compensate for the lower yield levels that are often reported for organic agriculture. Furthermore, we also expected to find a positive influence of landscape diversity and surrounding semi-natural habitat on pollinator communities and pollination services in both organic and IPM orchards.

## 4.3 Methods

### 4.3.1 Study sites

Study sites (n = 36) included 12 IPM, 12 organic apple orchards, and 12 semi-natural grasslands, all with a similar soil type (sandy loam or loam), hydrology and slope. All orchards were planted with Jonagold apple trees (*Malus domestica*) that had reached production age and domesticated honeybees (*Apis mellifera*) were placed in or nearby each orchard during apple bloom to ensure pollination. In both management types, the drive rows are regularly mown. The selected semi-natural grasslands are managed extensively by mowing or grazing for nature conservation purposes. Semi-natural grasslands, organic orchards and IPM orchards were all characterized by differences in vegetation with highest levels of plant cover, richness and diversity in the semi-natural grasslands, intermediate levels in the organic orchards and lowest levels in the IPM orchards (Fig. S4.1). We randomly established three permanent sampling plots (4 m x 4 m) in the edge of each study site and three in the center.

### 4.3.2 Bee and hoverfly sampling, identification and functional traits

Wild bees and hoverflies were sampled by placing a set of three colored pan traps on ground level spaced one meter apart in each plot (n=216 sets) during apple bloom in 2019 and 2020. The pan traps were set out for four consecutive sunny days with a minimum temperature of 15°C and a maximal wind speed of 7 $ms^{-1}$, which coincided between April 20$^{th}$ and April 25$^{th}$ in both years. Each set of pan traps consisted of a fluorescent blue, a fluorescent yellow and a white trap (Ø 7 cm) with added nectar guides and filled with a soapy saline solution. On collection, the catch was sieved and stored in 70% ethanol until further identification. All bees were washed, dried, pinned and both bees and hoverflies were identified to species level (Falk and Lewington, 2017; Pauly, 2016, 2015a, 2015b; Schmid-Egger and Scheuchl, 1997; Smit, 2004). Identifications were verified by citizen scientists and local experts (T.D.B., M.B., W.V and M.B). We retrieved functional traits for all identified species from the literature

(Duchenne et al., 2020; Falk and Lewington, 2017; Kendall et al., 2019; Speight et al., 2020). Specifically, tongue length, diet, intertegular distance (ITD), nesting type, sociality, season and pollen carrying structure were identified for the bee species, and larval food, body size and larval microhabitat for the hoverfly species (Table S4.1).

### 4.3.3 Pollination services and apple yield

Within all orchards, seed set and fruit set were quantified at each sampling plot as proxies of the pollination services provided. Three branches with five clusters of three flowers each were marked within one tree, and on each branch a different pollination treatment was performed: (1) bagged flowers (control with only wind pollination), (2) open pollination (wind and insect pollination), and (3) hand-pollination (maximized pollination with pollen harvested from a compatible pollinizer tree within the same orchard). Pollination deficits for fruit set were calculated as the percentage difference between the number of developing fruits from the open pollination treatment and the number of fruits resulting from the hand-pollination treatment in late May, after flower moult. Pollination deficits for seed set were established by counting the number of developed seeds from three randomly selected apples per treatment, and again calculating the percentage difference between the number from the open treatment and the number from the hand-pollination treatment. Positive deficits indicate that the number of fruits/seeds is greater under supplementary hand pollination, while negative deficits indicate that the number of fruits/seeds is greater under open pollination. These apples were harvested in the beginning of September, right before commercial harvest. In the control treatment with bagged flowers, no fruits developed, confirming self-incompatibility (He et al., 2018; Orcheski and Brown, 2012). Finally, apple production, further referred to as yield, was quantified in each plot by calculating the average number of apples from two trees adjacent to the tree subjected to the pollination treatments and multiplying this number by the average apple weight in each plot.

### 4.3.4 Landscape variables

To investigate landscape effects on pollinators, pollination and yield, we first classified the landscape surrounding the sampling plots into seven categories (arable land, agricultural grassland, orchards, herbaceous and wooded semi-natural habitat, urban areas and other land uses), based on land cover data from the Biological Valuation map (De Saeger et al., 2017) and the Flemish agricultural land use parcels (LV, 2020) . We calculated the proportions of these land use classes surrounding each study site, as well as the land use Shannon-Weiner diversity (SHDI) and the distance to the nearest semi-natural habitat at seven spatial scales (50 m, 100 m, 250 m, 500 m, 1000 m, 1500 m and

2000 m) using QGIS v.3.16.10 (QGIS Development Team, 2021) (Table S4.2). After inspection of Pearson correlations between variables, we retained the proportion of agricultural land (both arable land and agricultural grassland) and SHDI as measures of landscape compositional heterogeneity, and the distance to the nearest semi-natural habitat (both herbaceous or woody) as a measure of landscape configuration. Next, the most appropriate spatial scale for each response variable was identified by constructing separate (generalized) linear models with all three landscape variables as predictors for each scale (Table S4.3). Finally, we used model selection based on the small sample–corrected Akaike information criterion (AICc) to identify the most predictive model and scale and applied that scale in all subsequent analyses (package MuMIn) (Barton, 2022).

### 4.3.5 Data analysis

All analyses were performed using R v. 4.0.0 (R Core Team, 2021). In order to explore the variation in wild pollinator community composition, we performed a principal coordinate analysis (PCoA) based on the Bray-Curtis dissimilarity index (package vegan) (Oksanen et al., 2020). To investigate the effect of both management system (semi-natural grassland *vs.* organic *vs.* IPM) and within-site location (center *vs.* edge) on the wild pollinator community, we performed a PERMANOVA with 999 permutations, followed by a pairwise PERMANOVA for post hoc testing (packages vegan and pairwiseAdonis) (Martinez Arbizu, 2020; Oksanen et al., 2020). We also performed an indicator species analysis with 999 permutations to identify typical species for all three management systems (package indicspecies) (De Cáceres and Legendre, 2009). All permutations were constrained to between-sites to account for the hierarchical sampling design. Applying the Hill number framework, species richness (diversity of order 0) and diversity (diversity of order 1) was calculated for the wild bee and hoverfly community in each plot, excluding honeybees as they are a domesticated pollinator in the region (package hillR) (Hill, 1973; Li, 2018). Bee and hoverfly species, further referred to as pollinators, were clustered into functional groups based on key traits related to taxon, diet, habitat and size class (Table S3). Next, functional group richness was determined by counting the number of groups in each plot, while also Rao's quadratic entropy was quantified for the wild bee community (package FD, Table S4.1) (Laliberté et al., 2014). The latter index is based on the trait dissimilarity between species, weighted by the relative abundance of species (Pavoine and Dolédec, 2005).

We investigated the effect of management system (semi-natural grassland *vs.* organic *vs.* IPM), as well as within-site location (edge *vs.* center) and the landscape variables on pollinator abundance and (functional) diversity using mixed models. Generalized linear

mixed models (GLMMs) following a Poisson distribution with log link function were composed for all abundance variables and functional group richness, while linear mixed models (LMMs) were used for all diversity variables and Rao's wild bee index. Management system, location and their interaction as well as the landscape variables at their appropriate scale were included as fixed factors in the full models together with site and year as random factors (package lme4) (Bates et al., 2015). To construct the final models, we then selected all predictor variables from the best fitting submodels ($\Delta AICc < 2$) based on the multimodel inference approach (package MuMIn) (Barton, 2022; Burnham and Anderson, 2004). Additionally, final models were checked for overdispersion in the case of GLMMs and for heteroscedasticity in the case of LMMs. We detected overdispersion in the GLMM for hoverfly abundance and accounted for this and we found heteroscedasticity between study sites for the LMM with hoverfly diversity as the response variable, correcting for this using the *VarIdent* option in function *lme* (package nlme) (Pinheiro et al., 2022; Pinheiro and Bates, 2000). The absence of spatial autocorrelation in all model residuals was confirmed both visually and using Moran's I (package ape) (Paradis and Schliep, 2019). Variance inflation factors (VIFs) were calculated to detect multicollinearity between the explanatory variables and were low (all < 3). Pairwise differences between the levels of all significant categorical variables were assessed using Tukey HSD post-hoc tests.

To investigate the direct and indirect effects of orchard management, location and the landscape variables on abundance and diversity, pollination services, and ultimately on yields, we developed a piecewise structural equation model (pSEM) based on a priori hypothesized relationships (Fig. 4). Wild pollinator abundance, wild pollinator richness, honeybee abundance, Rao's wild bee index and functional group richness were used as intermediary pollinator variables, while seed set and fruit set were included as intermediary pollination variables in the initial pSEM. As functional diversity is partly confounded by abundance and species richness, we applied a null model approach to obtain standardized metrics of the Rao's wild bee index and functional group richness. As such, trait associations were randomized using the option "independentswap" in the function randomizeMatrix by reshuffling the species in the species-trait matrix, while the observed abundance and species richness was kept constant (package picante) (Kembel et al., 2010). This procedure was iterated 999 times, allowing to quantify the mean value of the replicated null model ($x0$) and its standard deviation ($\sigma x0$). Standardized metrics were then calculated as $x - x0 / \sigma x0$ where $x$ is the initial observed value. These standardized values for Rao's wild bee index and functional group richness were then used in the pSEM. The pSEM was built using eight mixed models, excluding data from the semi-natural grasslands as pollination metrics and yield could not be

determined here. Therefore, the previously discussed models for the biodiversity variables were refit with only the data of the orchards. Additional models for seed set and fruit set were constructed, following a binomial distribution with logit link function, while the yield model followed a Gaussian distribution (package lme4) (Bates et al., 2015). Full models were composed based on their relationships in the initial pSEM and final models were selected and evaluated as above (Fig. 4). Correlated errors between Rao's wild bee index and functional group richness were included in the pSEM and the final model was selected using Shipley's test of d-separation to detect missing paths. The final pSEM was evaluated with Fisher's C statistics and the relative importance of pathways was determined using standardized path coefficients (package piecewise) (Lefcheck, 2016).

## 4.4 Results

### 4.4.1 Pollinator communities in semi-natural grasslands vs. organic and IPM orchards

A total of 2055 wild bee specimens from 83 species were identified across all management systems, belonging to 10 different genera and 3 families, mostly represented by the genera *Andrena*, *Lasioglossum* and *Osmia* (Fig. S4.2, Table S4.4). In both organic and IPM orchards, a total of 356 honeybee individuals were collected, compared to a total of 1280 wild bee individuals. Mean honeybee abundance per study site did not differ between organic and IPM orchards (8.0 ± 1.7 and 7.2 ± 2.6, respectively, $p = 0.094$). Additionally, 107 specimens of hoverflies from 29 species were identified, belonging to 18 genera of the subfamilies Eristalinae, Syrphinae and Pipizinae (Fig. S4.3). The identified bees mainly belonged to species that had polylectic diets and nested underground or in existing cavities (96%). A higher proportion of bees in semi-natural grasslands were oligolectic and nested underground (6%) compared to both orchard types (0.6% and 0.4% for IPM and organic, respectively. The larvae of the identified hoverflies were mostly zoophagous and their habitat was mostly associated with terrestrial plants (60%) (Fig. S4.4). PCoA followed by PERMANOVA revealed significant differences in community composition among all three management systems ($p = 0.001$) and both sampling locations ($p = 0.001$, Fig. 4.1, Table S4.5). Two wild bee species were identified as indicator species for the center of semi-natural grasslands (*Colletes cunicularius* IV = 0.23, $p = 0.03$; *Andrena vaga* IV = 0.23, $p = 0.01$) and two other species for the edge of organic orchards (*Andrena labiata* IV = 0.27, $p = 0.005$; *Andrena bicolor* IV = 0.18, $p = 0.01$).

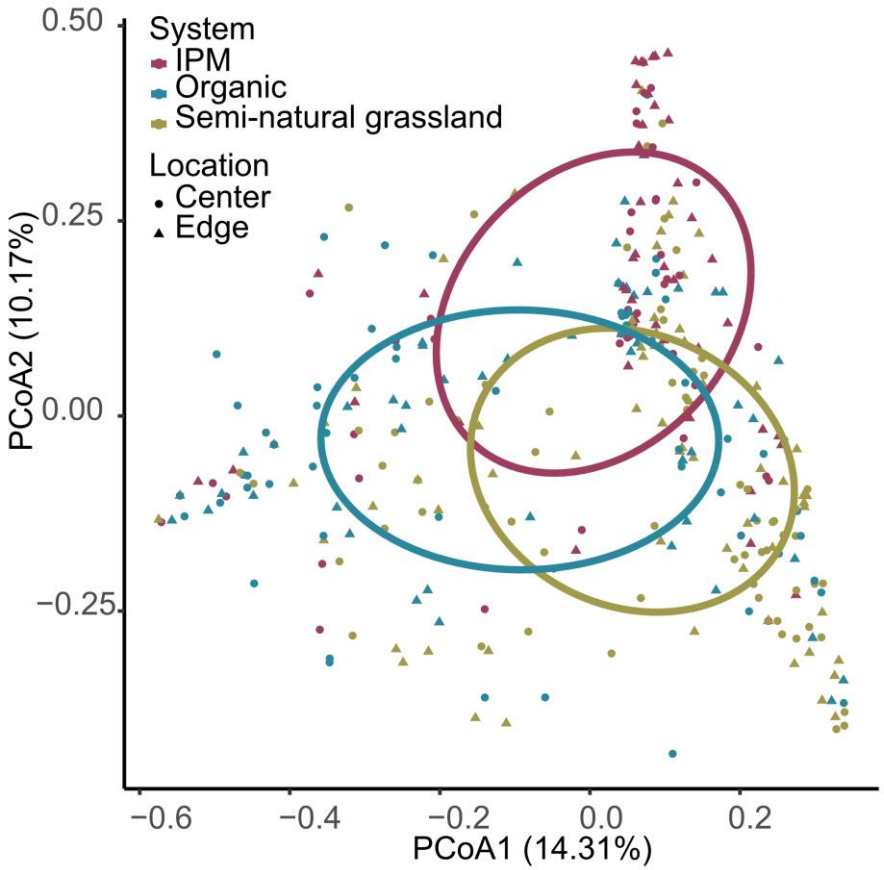



**Figure 4.1.** Results of the Principal Coordinate Analysis (PCoA) of wild bee and hoverfly communities in the center and edge of IPM and organic apple orchards and in reference semi-natural grasslands. Ellipses depict the standard deviation from the centroid for each management type.

The GLMM with wild pollinator abundance as response variable revealed significant effects of management system ($p < 0.001$), location ($p < 0.001$) and their interaction ($p < 0.001$) (Table 4.1, Fig. 4.2a). We found lower abundances in both orchard types compared to the center of semi-natural grasslands, except for the edge of organic orchards where the abundances reached the level of the semi-natural benchmark (Fig. 4.2a). Due to the low abundances of hoverflies in our study (Fig. S4.4), total abundance and diversity was mainly shaped by the wild bee community. As such, wild bee abundances followed the same pattern across management systems and sampling location as total abundance (Table 4.1, Fig. S4.5). Hoverfly abundance was significantly affected by management system ($p = 0.032$) with lower abundances in IPM compared to semi-natural grasslands (Table 4.1, Fig. S4.5). Total diversity was affected by management system ($p < 0.001$) and was higher in semi-natural grasslands compared to both orchard types (Table 4.1, Fig. 4.2b). Higher diversity levels were additionally found in the edges compared to the center of study sites ($p = 0.048$) (Table 4.1, Fig. 4.2b). Both wild bee and hoverfly diversity followed the same pattern across

management systems and locations (Table 4.1, Fig. S4.6). Wild bee abundance and diversity were both significantly affected by the interaction between honeybee abundance and management system ($p = 0.001$ and $p < 0.001$, respectively), with both wild bee abundance and diversity decreasing with increasing honeybee abundance in the organic orchards ($p = 0.003$ and $p = 0.001$, respectively), but showing no significant relationship in the IPM orchards or semi-natural grasslands. Rao's wild bee index was significantly affected by management system ($p = 0.025$), with higher values in semi-natural grasslands compared to both orchard types, while there was a marginally non-significant effect of the interaction between management system and location ($p = 0.063$) (Table 4.1, Fig. 4.2c). Functional group richness was also significantly affected by management system ($p < 0.001$) and was lower in IPM orchards compared to semi-natural grasslands, with intermediate levels for organic orchards (Table 4.1, Fig. 4.2d). Landscape SHDI at the 50 m scale had a significantly positive effect on total ($p = 0.0076$) and wild bee abundance ($p = 0.029$), while it had a marginal non-significant effect on Rao's wild bee index ($p = 0.052$) (Table 4.1, Fig. S4.7).

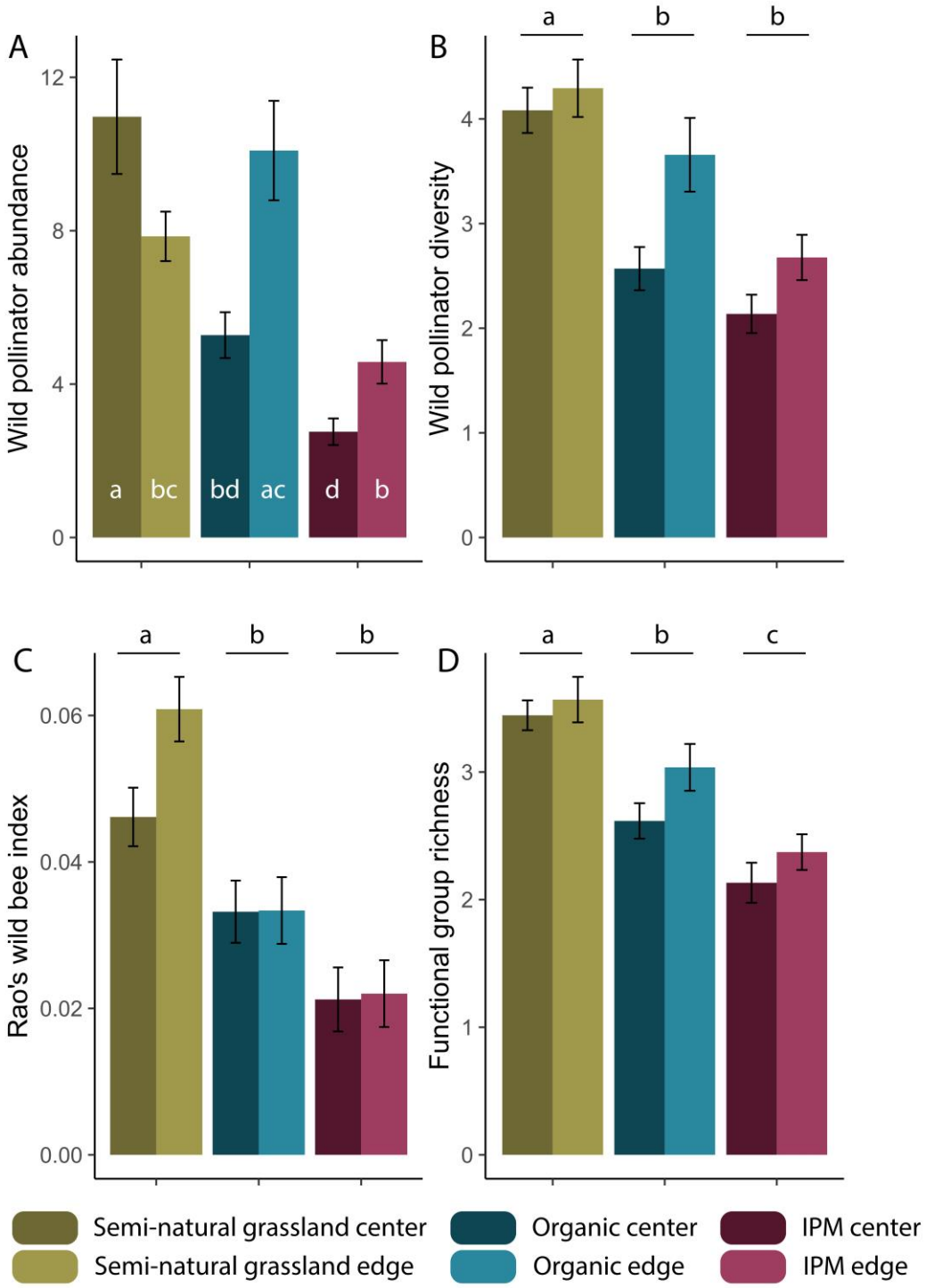



**Figure 4.2.** Abundance and (functional) diversity indices in IPM and organic orchards with a semi-natural reference. Mean values ±1SE of total wild pollinator abundance (A), total wild pollinator diversity (B), Rao's index for the wild bee community (C) and functional group richness (D) across management systems and within-site sampling locations. Same lowercase letters indicate no statistically significant ($p < 0.05$) difference after post hoc testing (A). Statistically significant differences between systems revealed by post hoc testing are indicated using brackets (B, C, D). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

**Table 4.1.** Output of mixed models on pollinator abundance and (functional) diversity. Marginal and conditional $R^2$ ($R^2_m$ and $R^2_c$) are provided for individual general(ized) linear mixed models regarding abundance and (functional) diversity in IPM and organic orchards and semi-natural grasslands. Test statistics ($\chi^2$) and p-values (*P*) are given for each predictor selected in the model selection procedure, while arrows depict the direction of the effect for significant continuous variables. Selected variables include system (IPM *vs*. organic *vs*. semi-natural grassland), location (center *vs*. edge), their interaction and the landscape variables landscape Shannon diversity (landscape SHDI), distance to the nearest semi-natural habitat (DSNH) and the proportion of agricultural land (agriculture) at different spatial scales.

| Response variables → Explanatory variables ↓ | Wild pollinator abundance $R^2_m = 0.30$ $R^2_c = 0.83$ | | Wild bee abundance $R^2_m = 0.29$ $R^2_c = 0.84$ | | Hoverfly abundance $R^2_m = 0.055$ $R^2_c = 0.17$ | | Wild pollinator diversity $R^2_m = 0.17$ $R^2_c = 0.39$ | | Wild bee diversity $R^2_m = 0.14$ $R^2_c = 0.34$ | | Hoverfly diversity $R^2_m = 0.034$ $R^2_c = 0.035$ | | Rao's wild bee index $R^2_m = 0.18$ $R^2_c = 0.31$ | | Functional group richness $R^2_m = 0.094$ $R^2_c = 0.094$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* | $\chi^2$ | *P* |
| System | 23.38 | <0.001 | 15.52 | <0.001 | 6.88 | 0.032 | 15.86 | <0.001 | 13.96 | <0.001 | 9.1 | 0.011 | 7.37 | 0.025 | 106.52 | <0.001 |
| Location | 18.82 | <0.001 | 18.3 | <0.001 | 1.77 | 0.18 | 3.9 | 0.048 | 5.01 | 0.025 | 4.22 | 0.04 | 0.06 | 0.81 | 24.60 | 0.29 |
| System x Location | 105.1 | <0.001 | 111.04 | <0.001 | 1.61 | 0.23 | | | 3.47 | 0.18 | | | 5.53 | 0.063 | | |
| Landscape SHDI 50 m | 7.12 ↗ | 0.0076 | 4.78 ↗ | 0.029 | | | 2.2 | 0.14 | 1.34 | 0.25 | | | 3.77 ↗ | 0.052 | 0.84 | 0.36 |
| Landscape SHDI 100 m | | | | | 1.47 | 0.11 | | | | | 0.031 | 0.86 | | | | |
| DSNH | | | 1.49 | 0.22 | 2.55 | 0.64 | | | 0.35 | 0.55 | 1.69 | 0.19 | 0.3 | 0.59 | | |
| Agriculture 50 m | 0.55 | 0.46 | 0.67 | 0.41 | 0.22 | 0.64 | 0.54 | 0.46 | | | | | 2.59 | 0.11 | | |
| Agriculture 100 m | | | | | | | | | | | 0.88 | 0.35 | | | | |

### 4.4.2 Direct and indirect effects of orchard management and landscape on pollinators, pollination and yield

The pSEM revealed direct positive effects of organic management on total abundance ($p = 0.0017$) and indicated positive, yet marginally non-significant, effects on diversity ($p = 0.081$) and honeybee abundance ($p = 0.094$) (Table S4.6, Fig. 4.3). Organic management also positively influenced seed set ($p = 0.0029$), yet it negatively affected yield ($p = 0.006$) (Fig. 4.5). A marginally non-significant positive pathway of organic management on wild pollinator diversity ($p = 0.081$) and further on fruit set ($p = 0.08$) could not mitigate the direct negative effect of organic management on yield. The sampling location also significantly affected the pollinator community, with positive effects of edge locations on wild pollinator abundance ($p < 0.001$), wild pollinator diversity ($p = 0.013$), honeybee abundance ($p < 0.001$) and functional group richness ($p = 0.024$), while a positive effect on Rao's wild bee index was suggested ($p = 0.058$). Additionally, edge locations were indicated to negatively affected seed set ($p = 0.079$), while yield was positively affected ($p = 0.029$). Most of the studied landscape variables were not retained in the final pSEM, except for the proportion of agricultural land. At the 50 m scale, it positively affected honeybee abundance ($p = 0.03$), while it negatively influenced functional group richness at the 2000 m scale ($p = 0.017$). Furthermore, pollination deficits based on fruit set did not differ between organic and IPM orchards ($0.08 \pm 0.23$ and $0.21 \pm 0.27$, respectively, $p = 0.152$) while deficits calculated based on seed set were higher in the IPM orchards ($0.06 \pm 0.19$ for organic and $0.23 \pm 0.21$ for IPM, $p = 0.017$) (Fig. S4.8).

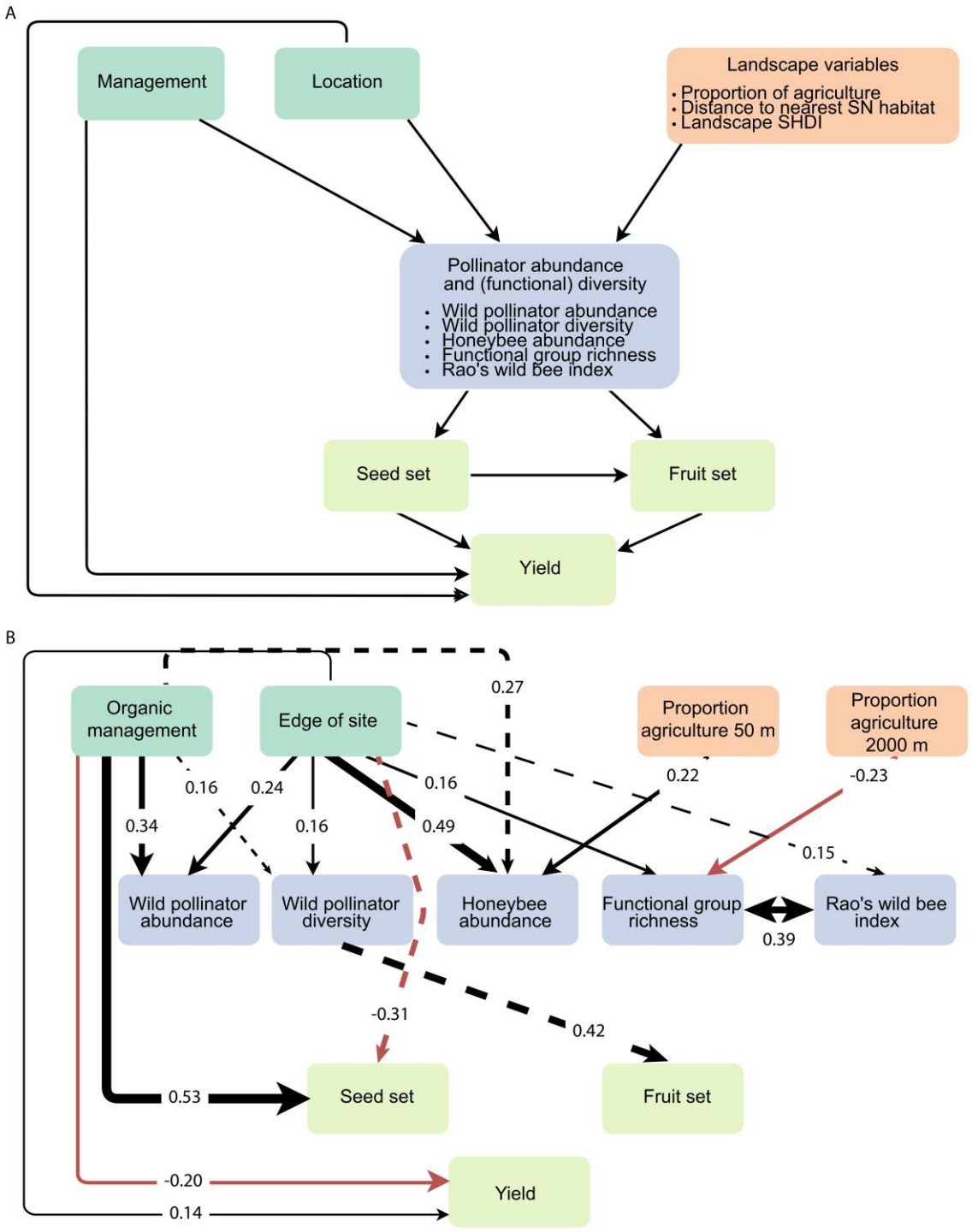



**Figure 4.3**. Initial (A) and final (B) piecewise structural equation model (pSEM). The model indicates significant direct and indirect paths from orchard management, within-site location and landscape variables on pollinator abundance and (functional) diversity, pollination and apple yield (Fisher's C = 107.98, p = 0.95). Arrow thickness is proportional to their respective standardized path coefficients, which are also indicated on the arrows themselves, and arrow color indicates the sign of the effect with red indicating negative effects. Full arrows represent paths with $p < 0.05$, while dashed arrows represent paths with $p < 0.1$. The final SEM includes correlated errors between functional group richness and Rao's wild bee index ($p < 0.001$), indicated by the double-sided arrow.

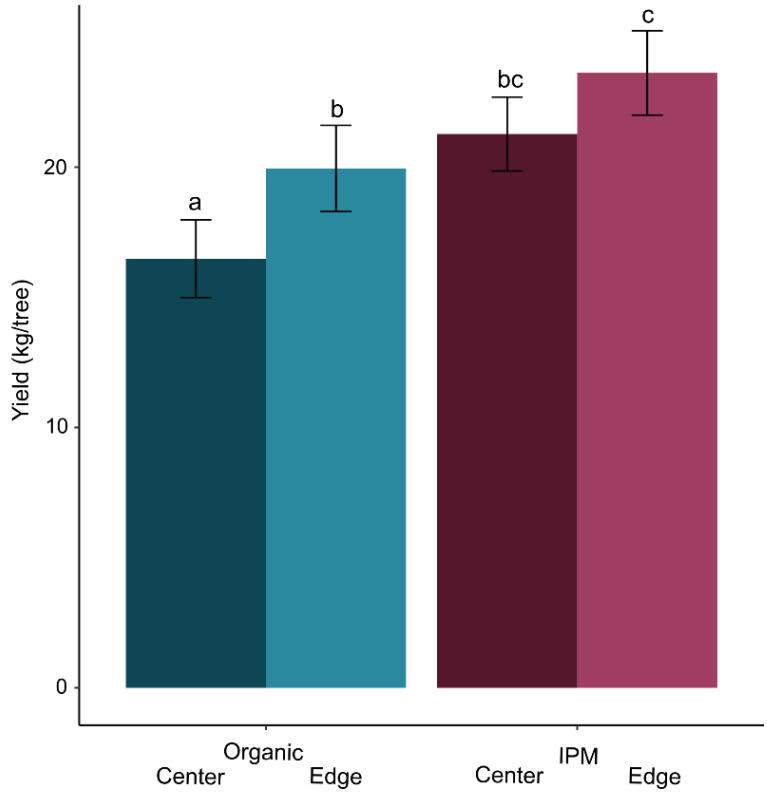



**Figure 4.4**. Apple yields in IPM and organic orchards. Mean values ±1SE of the yield across the center and edge of organic and IPM orchards, determined by the average number of apples per tree multiplied by the average apple weight. Different letters indicate significant differences ($p < 0.05$).

## 4.5 Discussion

In this study, we quantified the abundance and taxonomic and functional diversity of wild bees and hoverflies across organic and IPM apple orchards during bloom, and contrasted these with a semi-natural benchmark to fully assess the impact of agricultural management on pollinator communities in a perennial system. We also expanded on previous studies by identifying direct and indirect effects of management and landscape on pollinators, pollination services and eventually on yield, providing essential information for management and policy recommendations. Overall, we found that taxonomic and functional diversity were not strongly affected by orchard management, while semi-natural grasslands consistently harbored more diverse communities. Additionally, enhanced abundance and pollination services in organic orchards could not offset lower yield levels.

### 4.5.1 Pollinator communities in semi-natural grasslands vs. organic and IPM orchards

We found a distinct wild bee and hoverfly community composition across all three management systems. The observed abundance of hoverflies was very low in this study,

likely because we sampled relatively early in their flying season (Bot and Van de Meutter, 2019). Distinctive pollinator communities have also previously been found in organic, conventional and natural sites, indicating differences in available resources, such as nesting sites and food sources, across these systems (Andersson et al., 2013; Forrest et al., 2015; Rosas-Ramos et al., 2020). While this study focused on pollinator communities during apple bloom, differences between communities in the organic and IPM orchards might be even more pronounced outside of bloom. When the orchards do not host a mass-flowering display, pollinators are instead dependent on floral resources in the herb layer, which are likely higher in the organic orchards because these are characterized by a higher plant cover, species richness and diversity (Fig. S1). The abundance of wild pollinators was higher in the edge of organic orchards - but not in their center - compared to IPM orchards, with the abundance in the organic edges even reaching the levels found in semi-natural grasslands. In contrast, pollinator diversity did not differ between both orchard types, meaning a higher abundance did not directly translate into higher diversity levels in this study. This is in line with the results from a recent review where inconsistent effects of organic management on the abundance and diversity of insect pollinators were found (Pardo and Borges, 2020). Compared to IPM, we found that organic management enhanced functional group richness, but did not sustain a higher Rao's wild bee index. Similarly, Weekers et al. (2022a) found that organic management did not enhance wild bee functional diversity in apple orchards across Western Europe. The anticipated positive effects of organic orchard management on bee and hoverfly abundance and taxonomic and functional diversity were weak and inconsistent, both in this and other studies (Paiola et al., 2020; Pardo and Borges, 2020). This suggests that organic and IPM orchards both provide habitats of comparable quality to pollinators, which might have several reasons. First, IPM in itself might have the potential to support similar pollinator biodiversity levels as organic farming since it already uses relatively environmentally-friendly methods, especially when compared to conventional management (Kennedy et al., 2013; Porcel et al., 2018). Second, there often is a large heterogeneity between individual farms, even within organic and IPM management systems (Geldenhuys et al., 2021; Marliac et al., 2015; Orpet et al., 2020; Puech et al., 2014). In addition to following the specific regulations concerning IPM or organic farming, individual farmers may for instance widely vary in the implementation of wider ecologically-based management practices, such as the provisioning of artificial nesting opportunities for pollinators (Orpet et al., 2020; Tscharntke et al., 2021; Weekers et al., 2022b). As a result, organic and IPM systems might show some similarities in the practices applied, possibly also adding to the converging results in both management types. This may be especially true for perennial crops such as orchards, which generally have lower disturbance levels and a higher structural

complexity with permanent landscape elements, further minimizing the potential effects of management (Bruggisser et al., 2010; Porcel et al., 2018). Additionally, the pollinator communities in this study were sampled during apple bloom, a period in which organic and IPM orchards might be temporarily very similar due to the high level of floral resources and lack of pesticide application. However, pollinators might also be affected by pesticide use outside apple bloom. Furthermore, though organic pesticides used outside apple bloom might be less harmful to the environment, they may be applied at similar or higher quantities than synthetic pesticides due to their lower effectiveness, which may have equally or even more detrimental effects on populations of non-target organisms such as pollinators (Orpet et al., 2020; Tscharntke et al., 2022, 2021, but see Brühl et al., 2021). Finally, the beneficial effect of organic farming on mobile organisms, including pollinators, partially depends on the local landscape context, with stronger positive effects in more simple landscapes (Batáry et al., 2011; Concepción et al., 2012; Smith et al., 2020). Through controlling for landscape heterogeneity in our models, this effect may have lost importance (Chateil and Porcher, 2015). As this study was conducted in a landscape dominated by non-organic farming, there may also be a significant spill-over of synthetic pesticides into the organic orchards, diminishing potential positive effects of organic farming (Brittain et al., 2010b). Indeed, organic farming has been proposed to work best as a landscape-scale management strategy, as the proportion of organic farms in a landscape can increase arthropod diversity at the field scale (Holzschuh et al., 2008; Inclán et al., 2015).

The semi-natural grassland benchmark consistently harbored the highest abundance and taxonomic and functional diversity compared to both orchard types, underpinning the crucial role these habitats play in pollinator conservation (Eeraerts, 2023; Maurer et al., 2022; Tscharntke et al., 2021). Similarly, other studies also report higher species richness and functional diversity in (semi-)natural sites compared to different orchard types, though results for abundance are inconsistent (Forrest et al., 2015; Kehinde and Samways, 2012). This demonstrates that even relatively environmentally benign management practices, reduced diversity as compared to a semi-natural benchmark. Especially extensively-managed grasslands, such as the reference situation selected in our study, can play a crucial role in enhancing the local species pool. These habitats have been found to host distinct floral and wild bee communities compared to orchards, as they offer complementary and diverse resources to wild bees (Mallinger et al., 2016). Hedgerows, forest edges and flower strips on the other hand offer valuable complementary resources throughout the growing season as well (Eeraerts et al., 2021; Maurer et al., 2022).

Orchard edges harbored higher pollinator abundances and diversity regardless of the management system. These edges can be adjacent to other permanent landscape elements, such as herbaceous vegetation or hedgerows, or might be simple boundaries directly bordering other orchards or agricultural fields. Permanent elements may provide food sources and nesting sites and act as refuge for a variety of species, while direct borders with other agricultural fields might also act as linear elements that guide the dispersion of flying insects (Clough et al., 2020; Hass et al., 2018). Higher bee visitation rates were indeed also found in the edges of Californian almond orchards (Klein et al., 2012), and field margins in Central European arable fields have been found to support even rare and threatened species (Wuczyński et al., 2014). Edge locations were also indicated to have a lower seed set in the pSEM, while yield itself was higher. Deficiencies in seed set might have been counteracted by the higher light interception in edges, which enhances fruit yield (Aggelopoulou et al., 2010; Demestihas et al., 2017).

Landscape diversity was positively correlated with wild pollinator and wild bee abundance and had a marginally non-significant effect on Rao's wild bee index. The measure for landscape diversity, however, was negatively correlated with orchard cover ($r = -0.45$), and positively correlated with semi-natural habitat cover ($r = 0.25$), arable land cover ($r = 0.31$) and urban land cover ($r = 0.28$) at the small spatial scale of 50 m (Fig. S4.9). This implies that the landscape diversity effect that we found might be confounded with the effects of land use identity, with wild pollinator and wild bee abundance increasing with higher proportions of semi-natural habitat, arable land and urban land. Heterogeneous landscapes have indeed been shown to support more diverse wild bee communities, with bees depending on several partial habitats for nesting and food sources including semi-natural habitats, agricultural lands and urban areas (Biella et al., 2022; Kratschmer et al., 2019; Mallinger et al., 2016; Pardo et al., 2020; Westrich, 1996). Additionally, the presence of several habitat types within the immediate surroundings of our sampling plots might also reflect high configurational heterogeneity (high field border density), which has been shown to enhance pollinator movement and landscape connectivity regardless of the identity of the habitat types (Hass et al. 2018). Hoverfly abundance and diversity were not affected by the surrounding landscape in this study; they are known to be able to use resources from highly-modified land uses, such as agricultural fields (Raymond et al., 2014; Winfree et al., 2011). Furthermore, they are not restricted to a particular home range since they do not return to their eggs after egg-laying and do not provide their offspring with nectar and pollen, unlike bees (Doyle et al., 2020). In the pSEM, the proportion of agricultural land positively affected honeybee abundance at the 50 m scale and negatively influenced functional group

richness at the 2000 m scale, when standardized for abundance and species richness. Similarly, the proportion of arable land had an indirect negative effect on richness-corrected bee functional diversity, through plant species richness, in European agricultural landscapes (Papanikolaou et al., 2017). Agriculturally-dominated landscapes also reduced the phylogenetic diversity of wild bees in apple orchards, while intensive fruit cultivation positively affected honeybee abundance and negatively impacted both the abundance and species richness of cherry flower visitors in our study region (Eeraerts et al., 2017; Grab et al., 2019).

### 4.5.2 Direct and indirect effects of orchard management and landscape on pollinators, pollination and yield

The pSEM revealed direct positive effects of organic management on wild pollinator abundance and seed set. A positive indirect effect of organic management on fruit set ($p = 0.080$) through enhanced wild pollinator diversity ($p = 0.081$) was also indicated, but not significant. This suggested pathway combined with enhanced seed set was insufficient to offset the direct negative effect of organic management on yield. Samnegård et al. (2018) also found a lower apple yield in organic apple orchards compared to IPM, which could equally not be compensated by a positive indirect effect through higher visitation rates in organic farming. This is reflected in a meta-analysis in orchard landscapes showing that IPM achieves similar yield levels compared to conventional farming, while organic farming is associated with a 16-18% yield reduction (Katayama et al., 2019). Though organic farming may enhance pollination services (but see Porcel et al., 2018), this does not translate into higher yields, probably due to increased pests, diseases and perhaps limiting soil nutrient availability (De Ponti et al., 2012). The increased seed set in organic farming may however contribute to higher fruit quality, but this aspect was not investigated here (Buccheri and Di Vaio, 2005; Keulemans et al., 1996; Sheffield, 2014).

A positive but not significant effect of wild pollinator diversity on fruit set was indicated in the pSEM, while wild pollinators and honeybee abundance, and functional diversity did not affect fruit set, similar to another study in the region (Pisman et al., 2022). Growers often rely on managed honeybees for the provision of pollination services and introduce them into the landscape. However, wild bees and hoverflies have been shown to provide complementary and more effective pollination to apple, mainly in inclement weather conditions (Pardo and Borges, 2020). This is mainly due to more effective foraging behavior found in several important groups of wild bees as well as increased functional diversity that may enhance functional complementarity (Brittain et al., 2013;

Miñarro and García, 2018). The lack of a strong (functional) diversity effect on pollination services in our study indicates that other factors, such as specific management interventions or local microclimate, play an important role in determining seed set and fruit set in this context. Additionally, we did not sample apple flower visitors directly, instead opting to characterize the general wild bee and hoverfly community in the study sites using pan traps, potentially diluting the effect of pollinator diversity on pollination services. Pan trapping permitted the evaluation of the study sites for pollinator conservation in a standardized way across all three study systems. However, it is known to sample different pollinator communities than insect netting, catching less individuals and more solitary bee and hoverfly yet less social bee species (O'Connor et al., 2019; Prendergast et al., 2020).

## 4.6 Conclusion

Our results suggest that IPM and organic management have similar effects on pollinator taxonomic and functional diversity levels during apple bloom, and that both IPM and organic orchards show reduced diversity levels compared to a semi-natural benchmark. Pollinator abundance and diversity were also higher in edge locations, and increased with small-scale landscape diversity, which was positively associated with the presence of semi-natural habitat, but also arable and urban land. Therefore, maintaining and expanding orchard edges and conserving and restoring semi-natural habitat both locally and at a landscape scale seem important strategies for pollinator conservation in agricultural landscapes. Furthermore, our study found no strong link between pollinator diversity and pollination services on the one hand and apple yield on the other hand, which might indicate that pollination limitation is currently not jeopardizing yield levels. Instead, other factors might be more dominant in shaping yield levels, as illustrated by the direct negative effect of organic management on yield in our pSEM. This negative effect of organic management on yield levels further strengthens the importance of increasing semi-natural habitat and field edges for pollinator conservation, since these measures can be applied while sustaining yield levels (Tscharntke et al., 2021). In conclusion, our results highlight the need for a collaborative approach to achieve sustainable and productive farming systems, requiring a landscape-level joint action of farmers, land managers and policy makers.

# Chapter 5

## Agroecosystem multifunctionality of apple orchards in relation to agricultural management and landscape context

Adapted from:

Daelemans, R., Hulsmans, E., Fockaert, L., Vranken, L., De Bruyn, L., Honnay, O., 2023. Agroecosystem multifunctionality of apple orchards in relation to agricultural management and landscape context. Accepted for publication in Ecological Indicators

## 5.1 Summary

Managing agricultural landscapes to simultaneously provide multiple ecosystem services is crucial to meet both environmental and societal demands. This not only requires surveying and modeling many ecosystem services at the same time, but also quantifying the impact of agricultural management and the surrounding landscape on agroecosystem multifunctionality. In this study, we assessed the agroecosystem multifunctionality of 12 organic apple orchards and 12 orchards with integrated pest management (IPM) using field data on 23 indicators for agronomical, ecological and economic performance. Furthermore, we also quantified the ecological indicators in 12 semi-natural grasslands to obtain a benchmark for the overall impact of agricultural management on ecological performance. We found that organic farming at the field scale had relatively limited beneficial effects on ecological performance, yet it provided farmers with a similar income relative to IPM, despite lower yield levels. Overall orchard multifunctionality did not differ between organic and IPM orchards, regardless of hypothetical stakeholder interests, and a clear trade-off between biodiversity and yield was found within both systems. Structural equation models revealed that in addition to orchard management, also within-orchard location, the surrounding landscape and local biodiversity were directly and/or indirectly driving ecosystem service indicator levels. Surrounding semi-natural habitat and landscape complexity enhanced ecological performance, and the higher provisioning of several biodiversity-based services in the semi-natural benchmark further highlighted the importance of preserving semi-natural habitats within the agricultural landscape. Overall, our results indicate that reconciling ecological, agronomical and economic goals requires a vision that goes beyond the field-level agricultural management. Therefore, we argue that policy measures should not only address local farm management, but should also target actions towards other stakeholders such as land managers and agricultural markets.

## 5.2 Introduction

Agricultural landscapes cover more than one-third of the global ice-free land mass and provide a variety of goods and services needed by society (FAO, 2021). Especially since the second World War, these landscapes have been increasingly managed to maximize agricultural production, for instance through the use of agrochemicals, mechanization and the introduction of new crop varieties. This agricultural intensification, together with land use conversion and agricultural expansion, has led to a decrease in biodiversity and biodiversity-based ecosystem functions and ecosystem services (ES) that underpin agricultural production, as well as a decline in non-food ES such as carbon sequestration, erosion control and cultural values (Ramankutty et al., 2018; Tilman et al., 2017). As maintaining and enhancing this multitude of services is considered critical for long-term agricultural sustainability and food security (Seppelt et al., 2020), one of the main challenges for modern agriculture is to reconcile agronomical, ecological and socio-economic interests, or in other words, to maintain or restore ecosystem multifunctionality (Manning et al., 2018). Although the concept of ecosystem multifunctionality is increasingly used in ecological research (Garland et al., 2021), it is still poorly adopted in agroecosystems, where the most common approach is to focus on one or a few services (e.g. optimizing yield levels) and potential synergies or trade-offs with other ES (e.g. environmental or socio-economic performance) are often ignored (Winkler et al., 2017).

In order to sustainably manage agricultural landscapes to maximize the provisioning of multiple services, it is key to identify the mechanisms behind synergies and trade-offs among services (Bennett et al., 2009). Synergies relate to situations where different services simultaneously increase or decrease, whereas trade-offs indicate that one service increases as another service decreases, and *vice versa*. These relationships can either be the result of a direct interaction between services, a simultaneous reaction to a shared driver, or a combination of both (Bennett et al., 2009). To properly manage synergies and trade-offs, it is therefore essential to determine how the simultaneous provisioning of multiple ES is influenced by different drivers at multiple spatial scales (Le Provost et al., 2022).

On a local or field scale, organic agriculture is considered to be a promising system to enhance agroecosystem multifunctionality and sustainability, as it prohibits the use of synthetic inputs and aims to promote natural ecosystem functions and services to grow and protect crops (Wittwer et al., 2021). Several studies have shown that organic farming generally enhances farmland biodiversity, reporting higher diversity and

abundance of plants, natural enemies and pollinators compared to conventional farming systems (Muneret et al., 2018a; Tuck et al., 2014; Daelemans et al., 2022a). Consequently, also ecological functions and services supported by biodiversity, such as pollination and biological pest control, are expected to be enhanced under organic farming (Kennedy et al., 2013; Muneret et al., 2018a, but see Pardo et al., 2020; Porcel et al., 2018). Despite these potential environmental benefits, organic agriculture is often criticized because of its lower yields and reduced yield stability as compared to conventional agriculture (Knapp and van der Heijden, 2018; Ponisio et al., 2015), although this often does not compromise farmer income due to higher product valuation and subsidies (Shennan et al., 2017; Smith et al., 2020). Overall, the effects of organic farming on synergies and trade-offs between ecological, agronomical and socio-economic performance at the field scale are highly variable between studies and remain poorly understood (Couthouis et al., 2022; Ostandie et al., 2022; Wittwer et al., 2021).

Besides local agricultural management practices, also the landscape surrounding agricultural fields is likely to play an important role in shaping agroecosystem multifunctionality (Botzas-Coluni et al., 2021; Couthouis et al., 2022; Lamy et al., 2016). Especially biodiversity-based services have been shown to be affected by landscape properties, as most species that provide services heavily depend on diverse habitats in the surrounding landscape for resources like food, nesting sites and overwintering habitat (Tscharntke et al., 2012). However, in some cases landscape characteristics that enhance service providers can also stimulate pest species, resulting in unpredictable outcomes for agronomical performance (Karp et al., 2018; Daelemans et al., 2022a). While much attention has been paid to the effects of landscape on biodiversity and biodiversity-based services, most studies focus on a single aspect of biodiversity or a limited set of ES, and the effect of landscape factors on the simultaneous provisioning of a broader set of ES remains largely unknown (Martin et al., 2019). Additionally, effects of both local and landscape drivers on ES provisioning can be either direct or indirect, further complicating the assessment of mechanisms that affect agroecosystem multifunctionality (Allan et al., 2015; Le Provost et al., 2022). Direct effects include for instance the spill-over of organisms from surrounding habitat into the agricultural land, thus contributing to farmland biodiversity, or the direct effects of management practices (e.g. fertilizer applications) on agricultural production. Indirect effect are mainly biodiversity-mediated, for instance when management practices or landscape properties alter farmland plant communities, which in turn support ES providers like bees, natural enemies and soil microorganisms (Le Provost et al., 2022; Tscharntke et al., 2012).

Here, we used piecewise structural equation modelling to quantify how farm management, landscape and other environmental variables are either directly or indirectly driving the simultaneous provisioning of multiple ES in apple orchards in Flanders, Belgium. Orchards are an interesting study system due to the considerable (and increasing) proportion under organic farming, and their high dependence on a variety of ES (Demestihas et al., 2017; DLV, 2022; Garratt et al., 2014). Furthermore, little research has been done considering ecosystem multifunctionality in perennial systems (but see Ostandie et al., 2022; Winkler et al., 2017), although these have some unique properties that differentiate them from arable systems, such as the permanent presence of both crops and understory vegetation, and the low level of soil disturbance (Simon et al., 2010). In addition to the assessment of ES multifunctionality in apple orchards, we also measured biodiversity and biodiversity-based ES in semi-natural grasslands within the agricultural landscape to create a reference for the ecological performance of the orchards. Semi-natural grasslands are typically managed extensively either by mowing or grazing, and are considered essential for biodiversity conservation and ecosystem functioning in agroecosystems (Tamburini et al., 2022). Comparisons between different types of land use (in this case orchards vs. semi-natural grasslands) are rarely established, but they can provide important information about the maximum levels of biodiversity and ES provisioning that can be achieved in agricultural landscapes, and the extent to which ES provisioning in agricultural fields has deteriorated (Katayama et al., 2019).

The main aim of this study was to compare ES provisioning between organic and conventional apple orchards, and to gain understanding of the drivers and mechanisms behind ES multifunctionality. As the implementation of Integrated Pest Management (IPM) became mandatory in the EU in 2014 (EU, 2009), we further refer to the conventional study sites as 'IPM orchards' in this text to clarify the difference between 'traditional' conventional management and current management with IPM practices. We quantified 23 indicators relating to five ES (soil-based services, biodiversity, pollination, pest control and production) and economic performance in organic orchards and IPM orchards, and aimed to compare the indicators for ecological performance with those measured in reference semi-natural grasslands. Second, we aimed at identifying the main direct and indirect drivers of ES provisioning in the orchards and at quantifying synergies and trade-offs between different services. To incorporate potential stakeholder preferences concerning agricultural land-use, we finally calculated overall agroecosystem multifunctionality for both organic and IPM orchards by assigning weights to the different ES and economic performance, based on four hypothetical

scenarios ranging from a focus on production and farmer income to a focus on biodiversity conservation.

## 5.3 Materials and methods

### 5.3.1 Study sites and landscape characteristics

In this study, we used the data that was obtained in the study sites that were used in chapters 2, 3 and 4. In a total of 29 sites (9 semi-natural grasslands, 10 organic orchards and 10 IPM orchards), the full set of ecosystem service indicators could be determined. These sites were therefore used to calculate synergies and trade-offs between services and to assess overall agroecosystem multifunctionality in this study. Landscape variables were determined in the same way as described earlier, and the orchard cover (OR), semi-natural habitat cover (SNH), landscape Shannon diversity (SHDI), landscape edge density (ED) and distance to nearest semi-natural habitat (DSNH) were retained for further analysis.

### 5.3.2 Selection of ecosystem services and quantification of ES indicators

Within our study sites, we quantified 23 indicators for five ES (soil-based services, biodiversity, pollination, pest control and agricultural production), and economic performance (Table 1). All ES indicators are established estimators of ES provisioning and are either ecosystem functions that support ES (e.g. nitrogen mineralization for soil health) or general proxies of ES (e.g. predator abundance for pest control) (Garland et al., 2021).

### 5.3.3 Soil-based services

Soil ES indicators were obtained from Daelemans et al. (2022b). Aggregate soil samples were taken from each of the center plots by pooling five soil cores taken at three different depths (0-10 cm, 10-30 cm, 30-50 cm). In the orchards, separate samples were taken in the drive and the crop rows of each sampling plot to account for spatial variability in soil ES due to differences in soil management. While the drive rows are typically characterized by a permanent vegetation cover, the crop rows are kept open either by mechanical or chemical weed removal and are frequently subjected to fertilizer application. Soil samples were air-dried and soil C:N ratios were calculated based on soil organic carbon (SOC) and total nitrogen (N) concentrations as determined by elemental analysis (EA1108 Elemental Analyzer; CARLO ERBA Reagents, Italy).

**Table 1.** List of selected indicators corresponding to five ecosystem services (ES) and economic performance, and the scale at which the indicators were determined. Services are classified into different sections following the Common International Classification of Ecosystem Services (CICES, Haines-Young and Potschin, 2018).

| ES section | ES | ES indicator | Data collection |
|---|---|---|---|
| Regulating and maintenance | Soil-based ES (relating to soil health and carbon storage) | Soil respiration<br>Nitrogen mineralisation<br>Litter stabilisation<br>Litter decomposition | Top soil (0-10 cm) samples from center plots (n=3) of each site (n=36). In orchards, samples were obtained from two locations per plot (drive row and crop row) |
| | | Carbon stock | Similar to other soil-based ES, but summed over three depth layers (0-10, 10-30 and 30-50 cm) |
| | Biodiversity | Diversity plants<br>Diversity arthropods | Standardized surveys in center plots (n=3) and edge plots (n=3) of each site (n=36) |
| | | Diversity fungi<br>Diversity bacteria | DNA analysis on top soil (0-10 cm) samples from center plots (n=3) of each site (n=36) |
| | Pollination | Pollinator diversity apple<br>Apple seed set<br>Apple fruit set<br>Pollinator diversity strawberry<br>Strawberry seed set<br>Strawberry fruit set | Standardized surveys in center plots (n=3) and edge plots (n=3) of each site (n=36) |
| | Pest control | Natural enemy abundance<br>Natural enemy energy use<br>Natural enemy egg predation<br>Pest regulation | Standardized surveys in center plots (n=3) and edge plots (n=3) of each site (n=36) |
| Provisioning | Production | Yield<br>Yield stability | Center plots (n=3) and edge plots (n=3) of each orchard (n=24). Also estimated per orchard (n=24) |
| | Economic performance | Performance indicator | Data collection |
| | | Farmer income<br>Farmer income stability | Estimated at orchard level (n=24) |

Soil carbon stocks (Mg $ha^{-1}$) were calculated up to a depth of 50 cm using SOC concentrations and soil bulk density measures. To determine potential heterotrophic soil respiration and potential net nitrogen mineralization, fresh soil samples from the top layer (0-10 cm) were pooled, resulting in two samples per orchard (drive row and crop row) and one sample per semi-natural grassland. Average soil respiration rates (mg $CO_2$ $kg^{-1}$ $h^{-1}$) were determined with an *ex situ* respiration experiment, and are indicative for the metabolic activity of the soil microbiota. Potential net nitrogen mineralization rates (mg $kg^{-1}$ $d^{-1}$) were assessed by measuring $NO_3^-$ and $NH_4^+$ concentrations using colorimetric analyses before and after an *ex situ* incubation period of 25 days. Additionally, the 'Tea Bag Index' method was used to estimate the litter stabilization

factor (S) and decomposition rate (k), relating to long-term carbon storage and short-term carbon dynamics, respectively (Górecki et al., 2021; Keuskamp et al., 2013).

### 5.3.4 Biodiversity services

Indicators of soil bacterial and fungal diversity were obtained from Hulsmans et al. (2022). Genomic DNA was extracted from top soil samples (0 – 10 cm, October 2018) and sequenced on an Illumina Miseq platform (Illumina, San Diego, CA, United States) (see supplementary material, Methods S5.1, for details). Based on the resulting operational taxonomic units (OTUs), taxonomic richness and diversity of fungi and bacteria were calculated (hill numbers 0 and 1, respectively; Hill, 1973). Vegetation surveys were carried out using 3 x 1 m quadrats in each sampling plot in June 2019 to determine plant richness and diversity (hill numbers 0 and 1, respectively; Hill, 1973). In the orchards, the quadrats were laid out from the middle of the crop row towards the middle of the drive row to cover both sections equally. Wild bees and hoverflies were sampled using a set of three colored pan traps (blue, white and yellow, Ø 7 cm) with added nectar guides and filled with soap solution. These traps were placed in each sampling plot on ground level spaced one meter apart both during apple bloom (April 2019 and 2020) and in the summer (July 2019). They were set out for four consecutive sunny days with a minimum temperature of 15°C and a maximal wind speed of 7 $ms^{-1}$. True bugs and grasshoppers were sampled during August 2018 by sweep netting the vegetation in a 3 x 10 m strip in each sampling plot. Springtails were caught in June 2021 by taking soil samples with an open PVC cylinder (Ø 4.5 cm, 10 cm depth). Soil organisms were then extracted from these soil samples using Berlese-Tullgren funnels which were active during four weeks (Tullgren, 1918; Macfayden, 1953). All arthropods were store in 70% ethanol and later identified to species level. For all arthropod groups we determined abundance, richness (hill number 0) and diversity (hill number 1).

### 5.3.5 Pest control services

Pest control services were obtained from Daelemans et al. (2022a) and were estimated by the abundance and energy use of predatory arthropods, the predation rates on eggs of codling moth (*Cydia pomonella*) and the level of codling moth infestation. In both the center and edge plots of the orchards, natural enemies belonging to 14 different taxonomic families were sampled from the tree canopy with the beating-tray method during the second egg-laying period of codling moth in July 2020 and 2021. In addition to natural enemy abundance, we calculated the energy use of the natural enemies based on their body mass and metabolic rate, and used this measure as a proxy of the predation

potential of the natural enemy communities (Perović et al., 2018). In the egg predation experiment, three prey cards with eggs of codling moth were deployed in the tree canopy of each sampling plot for four consecutive days. After retrieval, the cards were inspected for predation marks and the total proportion of predated eggs was determined. Both the sampling of predator communities and the egg predation experiment were also performed in the semi-natural reference sites, but only in the edge plots due to a lack of trees or hedges in the center plots. Finally, we also estimated pest infestation rates as an indicator of pest control by counting the proportion of infected apples in the six sampling plots of each orchard. Infestation rates were inverted so that higher infestation values correspond to lower service provisioning, and the inverted measure is further referred to as 'pest regulation'.

### 5.3.6 Pollination services

Pollination services were partly obtained from Hulsmans et al. (2023a) and quantified by measuring pollinator diversity (bees and hoverflies), fruit set and seed set both during apple bloom (April 2019 and 2020) and summer (July 2019). Pollinators were captured using pan traps (see section 2.2.2) and fruit and seed set were determined by comparing the proportions of fruits and seeds that developed from open (insect) pollinated flowers to the proportions that developed from hand pollinated flowers (maximized pollination), correcting for self-pollination by wind (bagged flowers). To determine fruit and seed set in summer, three potted strawberry plants were introduced as phytometers in each of the sampling plots. Pollination services in the semi-natural reference sites were estimated by capturing pollinators and measuring fruit set and seed set on potted apple trees in April and potted strawberry plants in July.

### 5.3.7 Production services and economic performance

Apple yield (kg tree$^{-1}$) was calculated by counting the total number of apples from two trees per sampling plot, and multiplying this number with the average apple weight per plot. Next, the total yield per orchard (tonnes ha$^{-1}$) was determined using the average production per tree, the number of trees per orchard and the orchard area. Yield was measured in three consecutive years (2019, 2020 and 2021) and yield stability was calculated as 1 – [coefficient of variation over three years]. For the same years, farmer income and overall income stability were calculated as a measure of economic performance. Farmer income (FFI, family farm income) per ha was calculated for each parcel by subtracting the fixed and variable costs per ha from the revenues per ha. Estimates for both fixed and variable costs were calculated based on the formulas from Fockaert et al. (2023), which employ FADN data from the Flemish apple sector (DLV,

2021) as specific data for the studied farms were not available. This dataset contained five years of data (2016-2020) for 38 Flemish apple farms (= 190 observations), focusing only on the farms' apple production activities. To determine fixed and variable costs, data from IPM and organic farms were analyzed separately. For organic farming, only data from two farms were available (representing 7 observations, 5 for one farm and 2 for the other), but results were deemed realistic and usable for further analysis based on critical evaluation of literature and interviews with farmers. For IPM farming, data from 4 farms (out of 36) were excluded due to exceptionally high variable costs. Variable costs included fertilizer costs, crop protection costs, energy costs, costs for contract work, wages for seasonal labor, sales costs, preservation costs and miscellaneous variables costs. For both IPM and organic farms a linear-log model was constructed for yield dependent on variable costs, and inverted to enable calculation of variable costs from yield. Fixed costs consisted of depreciation and fictional interests of machinery, buildings, land or plantings and other factors, rent of fridges, rent of land, and fixed costs related to wages like social charges and insurance. Estimates for fixed costs were calculated by averaging the fixed costs per ha across all observations and farms, and were thus independent of yield but differed between IPM and organic farms. Revenues per ha were calculated for each year (2019, 2020 and 2021) by multiplying the yields per ha with the average selling prices per kg between September and June following each harvest. As the majority (83%) of Flemish fruit and vegetable farmers are members of large-scale marketing cooperatives that account for 85% of the market, the prices set by these cooperatives are used as a reference for the entire sector and were consequently used for the calculation of the revenues (Avermaete et al., 2018; Gijselinckx and Bussels, 2012). The average selling prices were obtained from datasets of weekly IPM and organic apple prices per kg and were provided by the Association of Belgian Horticultural Auctions (DLV, 2022). All values of fixed costs, variable costs and revenues were corrected for inflation with April 2022 as base (Statbel, 2022). Subsidies for organic farming (€210 $ha^{-1}$) were added to the revenues, while other subsidies, such as direct payments, are generally rather low in Flemish pit fruit farming and were therefore excluded from the analysis. Family farm income (FFI) was calculated as follows:

$$FFI\ \left(\frac{€}{ha}\right) = Revenues - \left(Cost_v + Cost_f\right)$$

$$Revenues\ \left(\frac{€}{ha}\right) = Price\ \left(\frac{€}{kg}\right) * Yield\ \left(\frac{tonnes}{ha}\right) * 1000\ \left(+ Subsidies_{\ organic}\left(\frac{€}{ha}\right)\right)$$

$$Cost_{IPM}\ \left(\frac{€}{ha}\right) = Cost_{v,IPM} + Cost_{f,IPM} = \ 2025.034 * \exp\left(\frac{Yield}{25.904}\right) + 6721$$

$$Cost_{org}\ \left(\frac{€}{ha}\right) = Cost_{v,org} + Cost_{f,org} = \ 2685.034 * \exp\left(\frac{Yield}{30.320}\right) + 14099$$

### 5.3.8 Ecosystem service multifunctionality

To further assess service provisioning, ES multifunctionality was calculated for five ES (soil-based services, biodiversity, pollination, pest control and yield) and for economic performance by applying the averaging approach to the individual indicators (Garland et al., 2021; Manning et al., 2018). First, all measured variables were scaled relative to the average of the five highest and the average of the five lowest values measured across all sites, allowing for direct comparison among different variables. When necessary, variables were inverted so that the lowest and highest values corresponded to the lowest and highest service provisioning, respectively. When variables were closely related, they were averaged into one single indicator: bees, hoverflies, springtails, true bugs and grasshoppers were averaged into 'arthropod diversity' as a proxy for biodiversity conservation, and bees and hoverflies were grouped into 'pollinator diversity' as a proxy for pollination services. Scaled indicators were averaged for each of the five ES and economic performance at the sampling plot level, assigning an equal weight to each indicator. For biodiversity multifunctionality, the indicators for fungal, bacterial and springtail diversity were only determined in the center plots, so we used their average values within the study site to calculate multifunctionality in the edge plots. For some sampling plots one or more indicator values were missing, for instance due to a damaged sampling setup or errors in the sample processing, in which case multifunctionality metrics were calculated for a subset of indicators, allowing for one missing indicator per multifunctionality metric per sampling plot.

Overall agroecosystem multifunctionality was calculated separately for the organic and the IPM orchards by averaging the multifunctionality metrics of the five ES and economic performance. For the averaging procedure, different weights were assigned to the different multifunctionality metrics, based on four scenarios representing different land-use interests by stakeholders. These hypothetical stakeholder preferences range from a focus on production and farmer income to a focus on biodiversity, and were adapted from Allan et al. (2015) and Herzog et al. (2019). The "yield and income" scenario focused on production and profitability, with 60% of the weight for yield and income and 40% for the other services. In the "sustainability" scenario 60% of the weight was allocated to yield and soils, 30% to regulating services and 10% to biodiversity and income. In the "equal weights" scenario all multifunctionality measures were represented equally, and in the "biodiversity conservation" scenario 60% of the weight was assigned to biodiversity, 30% to regulating services based on biodiversity and 10% to yield and income.

### 5.3.9 Data analysis and statistics

Linear mixed-effects models were constructed to assess the effects of management, within-site location, landscape and environmental variables (soil pH, soil C:N ratio and soil texture) on the different ES indicators and economic performance variables. When ES indicators or economic performance variables were expected to be influenced by other (intermediate) ES indicators, these were also included as explanatory variables in the models. For all soil-based variables, within-site location refers to the difference between drive rows and crop rows, while for all other variables this implies the difference between center and edge sampling plots. Prior to model building, variance inflation factors (VIFs) were calculated between landscape variables and only variables with VIF < 2.5 were retained to avoid multicollinearity. For each of the models, the assumptions of normality and constant variance were met. The presence of spatial autocorrelation was checked both visually and using Moran's I (package ape), and when necessary, distance-based Moran's eigenvector maps (dbMEMs, package adespatial) were added to the models to account for trends resulting from the spatial structure of the study system (Dray et al., 2021; Paradis and Schliep, 2019). Study site was included as random factor in all models, and final model selection as well as parameter estimations were based on a multimodel inference approach (package MuMIn; Bartoń, 2022).

First, all models were fitted to data from both orchard types as well as the semi-natural reference sites to assess how the provisioning of our selected ES in the orchards differs from service provisioning in a semi-natural system. Model effect sizes were calculated based on differences in marginal means between organic orchards, IPM orchards and the semi-natural references. Next, all models were refitted excluding data from the semi-natural sites to further study the drivers of ES provisioning in organic and IPM orchards. To this end, we first constructed a conceptual model with hypothesized direct and indirect causal relationships between all predictors and response variables (Fig. 5.1, Table S5.1). Based on the significant variables from the linear mixed models, we then fitted separate piecewise structural equation models (PSEMs) for each ES indicator and each multifunctionality measure (package piecewiseSEM; Lefcheck, 2016). Models were evaluated using D-separation tests and Fisher C statistics, and direct and indirect effects were estimated using standardized path coefficients, allowing for comparisons between models. For each ES indicator or multifunctionality measure, the relative importance of the different predictors was calculated as the proportion of the summed absolute effects across all predictors. Finally, all ES indicators and multifunctionality measures were averaged per orchard, weighing values from center and edge plots relative to their surface area (considering the outer 5 m of each orchard as edge area).

Trade-offs or synergies between different ES indicators and between different multifunctionality measures at the orchard level were calculated using Pearson correlations. All statistical analysis were performed in R v.4.0.0 (R Core Team, 2021).

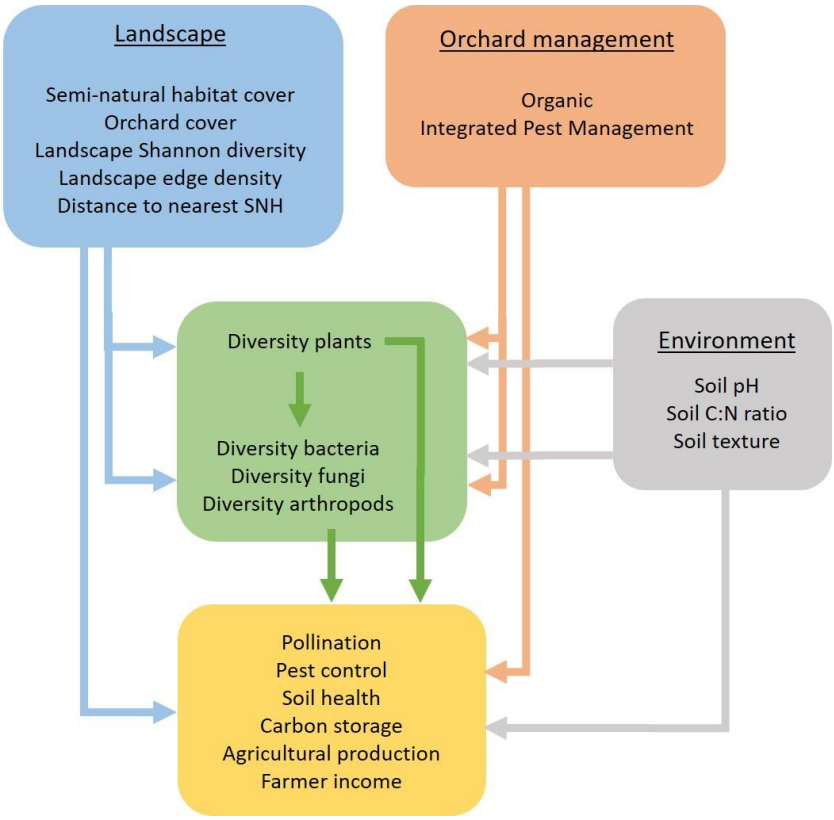



**Figure 1.** Conceptual framework illustrating the hypothesized direct and indirect relationships between the fundamental predictors (landscape, management and environment), the intermediate variables (biodiversity indicators) and the ultimate response variables (indicators and multifunctionality measures for pollination, pest control, soil-based services, production services and farmer income) that were tested using a series of PSEMs.

# 5.4 Results

## 5.4.1 Indicators for ecological, agronomical and economic performance

A total of 23 indicators were obtained, from which multifunctionality measures were calculated for each of the five ES and economic performance. Soil-based services, biodiversity, pollination and pest control all relate to ecological performance and were determined in both orchard types as well as in the semi-natural reference habitats. Eight out of 19 ecological performance indicators differed significantly between the orchards

and the semi-natural references, with soil respiration, plant diversity, strawberry pollinator diversity, strawberry seed set, natural enemy egg predation and natural enemy abundance being lower in the orchards than the semi-natural grasslands, and bacteria diversity and natural enemy energy use being higher in the orchards (Fig. 5.2, Tables S5.2-5.6). For arthropod diversity, apple seed set, apple pollinator diversity and strawberry fruit set, estimated mean values were significantly higher in the semi-natural references relative to the IPM orchards, but not in comparison to the organic orchards. Litter decomposition, on the other hand, was significantly higher in the organic orchards compared to the semi-natural reference sites. Significant pairwise differences between organic and IPM orchards were found for soil respiration, plant diversity, apple seed set, strawberry pollinator diversity and pollination multifunctionality, with the IPM orchards consistently having lower ES provisioning levels.

The multifunctionality measures for the five ES and economic performance did not significantly differ between orchards and semi-natural reference sites, except for biodiversity and pollination multifunctionality, which were both lower in the IPM orchards relative to the reference. Additionally, pollination multifunctionality in the IPM orchards was also found to be significantly lower than in the organic orchards. Pest regulation, yield, yield stability and yield multifunctionality were only quantified in the orchards, and all were higher in the IPM orchards compared to the organic orchards, except for yield stability which was lower in the IPM orchards (Fig. S5.1, Tables S5.5-5.6). The indicators for economic performance (income, income stability and income multifunctionality) did not differ between organic and IPM orchards (Fig. S5.1, Table S5.6).

### 5.4.2 Drivers of ES provisioning in the organic and IPM orchards

Orchard management (organic vs. IPM) was a significant driver for all ES indicators and multifunctionality measures, except for fungal and bacterial diversity and natural enemy energy use (Fig. 5.3). For three indicators (plant diversity, apple seed set and yield), orchard management accounted for more than 50% of the total explained variation. For all soil-based indicators, most of the total variation was explained by the location within the orchard (drive row vs. crop row). Soil-based indicators generally reached higher values in the drive rows than the crop rows, except for litter decomposition, which was higher in the crop rows (Fig. S5.2). Concerning the other response variables, spatial variability within the orchards was especially important for pollination indicators and pollination multifunctionality, which reached higher levels of service provisioning in the edges of the orchards compared to the center (Fig. 5.3, Fig.

S5.4). Plant diversity significantly affected the soil-based variables, arthropod and strawberry pollinator diversity, strawberry seed set, apple fruit set and pest control multifunctionality. Arthropod diversity, on the other hand, significantly contributed to apple fruit set, natural enemy egg predation and pest regulation. The characteristics of the landscape surrounding the orchards explained most of the variation in all pest control variables. Also the fruit set of both strawberry and apple, the diversity of plants, arthropods, fungi and pollinators, and yield stability and multifunctionality were significantly affected by the landscape. To a lesser extent, landscape characteristics also influenced soil-based variables, but mostly indirectly as a result of their relationship with plant diversity (Fig. 5.3, Table S5.7). None of the identified drivers had a significant effect on the economic performance indicators (Table S5.6).

Overall, local drivers explained most of the variation in the soil-based variables, biodiversity, pollination and yield, while the landscape characteristics were the dominant drivers of pest control and yield stability. Biodiversity drivers had relatively low effects on ES indicators and multifunctionality measures, and were the highest for apple fruit set, where plant and arthropod diversity together explained 46% of total variation.

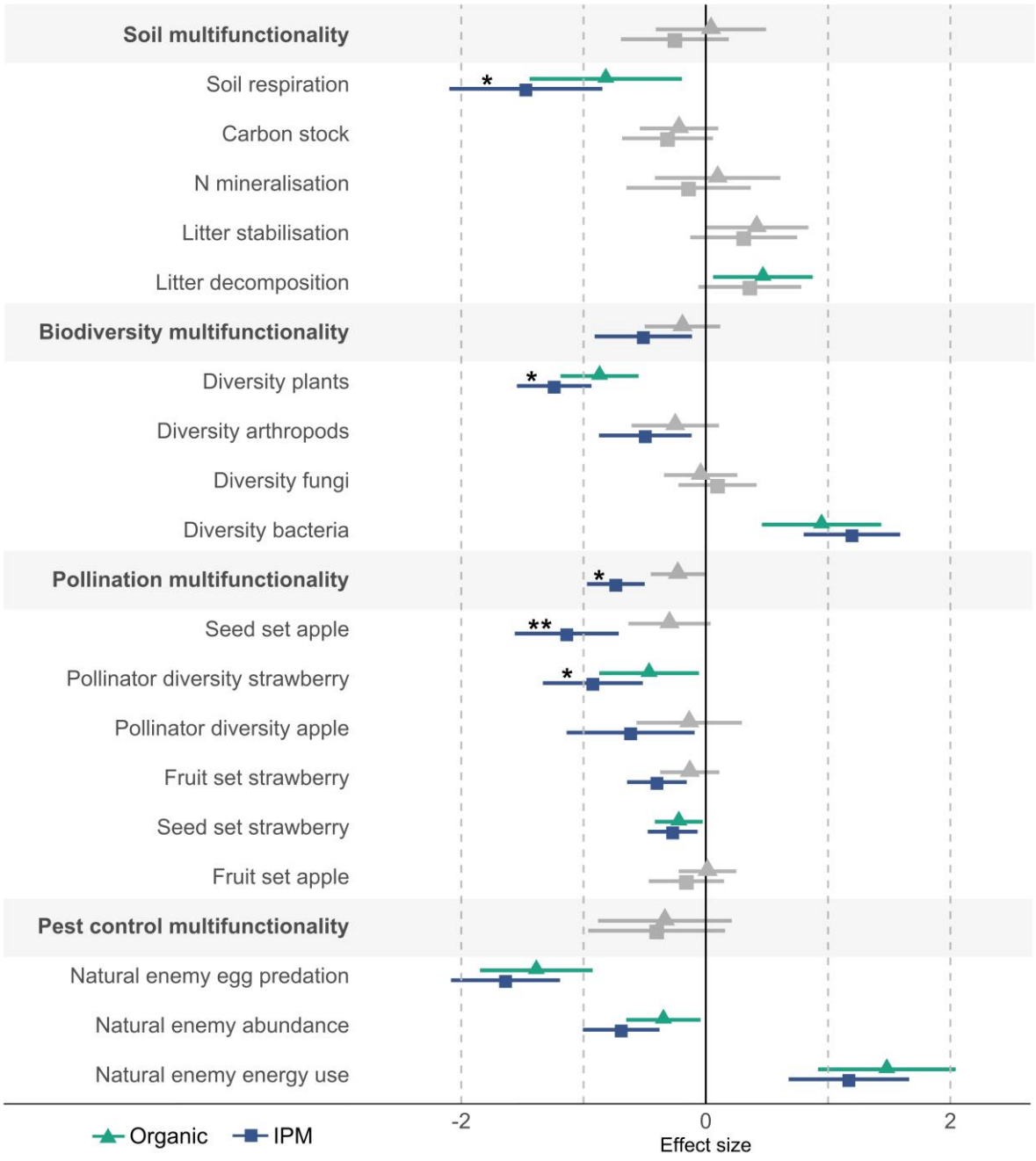



**Figure 5.2.** Model effect sizes and 95% confidence intervals for organic and IPM orchards relative to semi-natural grassland references. Effect sizes were calculated for both the ES indicators and the multifunctionality measures, with negative effects indicating lower marginal means than the semi-natural reference and positive values indicating higher marginal means. Values for organic and IPM orchards that do not significantly differ from the semi-natural reference are represented in grey, and significant differences between organic and IPM orchards are indicated with asterisks (*$P < 0.05$, **$P < 0.01$). The LMM statistics of the full models that were used to calculate the effect sizes and confidence intervals can be found in Tables S5.2-5.6.

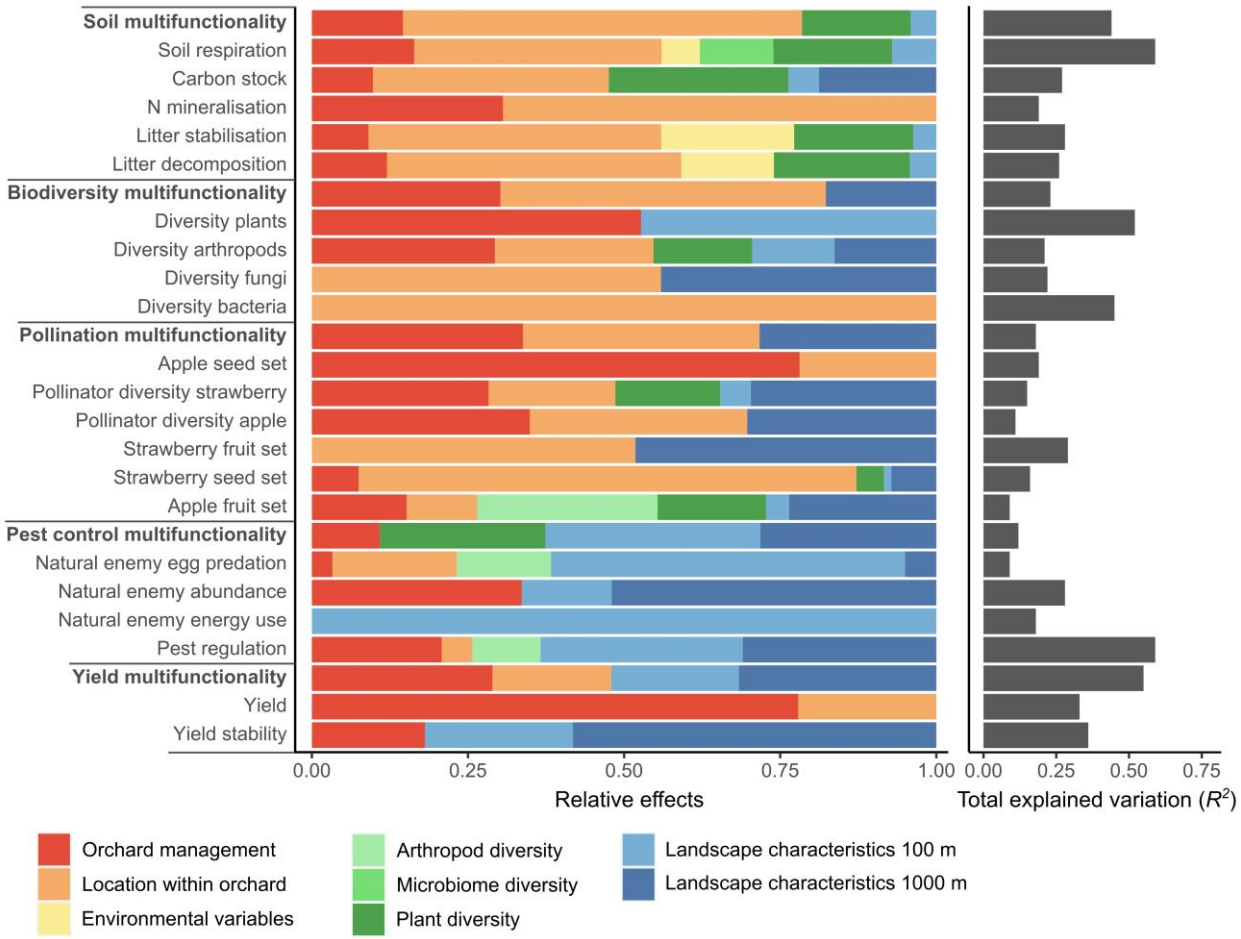



**Figure 5.3.** Relative importance of different drivers of ES indicators and multifunctionality measures. For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Drivers were grouped into three local variables, three biodiversity variables and landscape variables at two spatial scales. The total explained variation (R2) of each PSEM is shown on the right. Details about the drivers of each response variable, with indication of the direction of the effects, are shown in Fig. S5.2-5.6. Variables relating to farmer income are not included as they were not significantly affected by any of the drivers (Table S5.6). Summary statistics for all PSEM models can be found in Tables S5.7-5.11.

### 5.4.3 Synergies, trade-offs and orchard multifunctionality

Possible trade-offs and synergies were assessed using the multifunctionality measures for the five ES and economic performance. Considering all orchards, synergies were found between soil services on the one hand and pollination and biodiversity on the other hand (Fig. 5.4a). Looking at the organic and IPM orchards separately, these synergies were also present in the organic orchards but not in the IPM orchards (Fig. 5.4b,c). Furthermore, in the organic orchards also a synergy between biodiversity and pest control was detected. Yield and income measures were positively correlated in both orchard types. An overall negative correlation or trade-off was found between biodiversity and yield, which also held within the organic and IPM orchards separately. In the IPM orchards, biodiversity was also negatively correlated with farmer income.

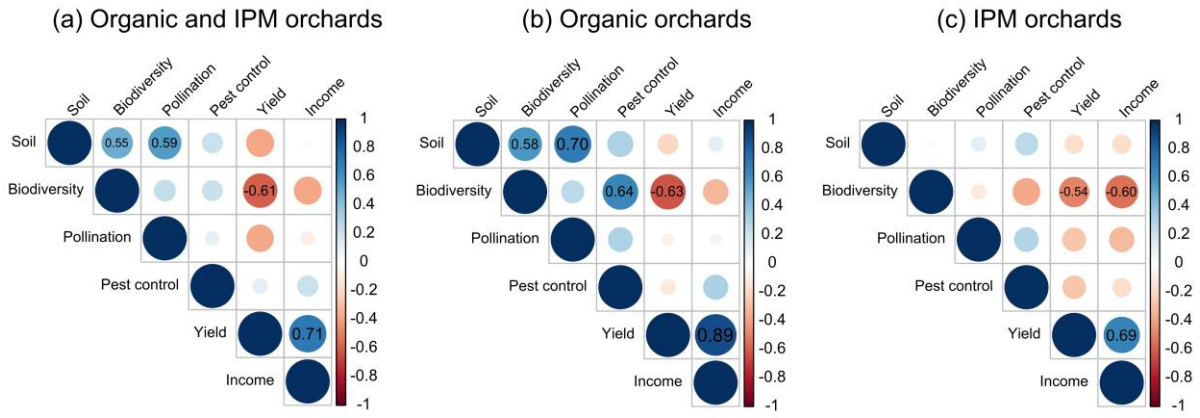



**Figure 5.4.** Pairwise Pearson's correlations between the five ecosystem service multifunctionality measures and income multifunctionality for (a) all orchards combined, (b) the organic orchards and (c) the IPM orchards. Blue dots indicate positive correlations (synergies) and red dots indicate negative correlations (trade-offs). Pearson correlation coefficients are shown for all significant correlations ($P < 0.05$).

Overall orchard multifunctionality, calculated by averaging the multifunctionality metrics for biodiversity, pollination, pest control, soil-based services, yield and income, did not differ between organic and IPM orchards in any of the four scenarios of potential stakeholder preferences concerning agroecosystem service provisioning (Fig. 5.5). Despite this insignificance, a pattern is visible where organic orchards have lower multifunctionality in the scenarios prioritizing yield and income (scenario a), and sustainable yields, soils and regulating services (scenario b). In the scenarios where all six metrics were weighted equally (scenario c) and where the focus was on biodiversity conservation (scenario d), organic orchards tended to score higher overall

multifunctionality. Additionally, the variation in overall multifunctionality was highest for organic orchards in all four scenarios, with both the highest and lowest values consistently obtained in the organic orchards.

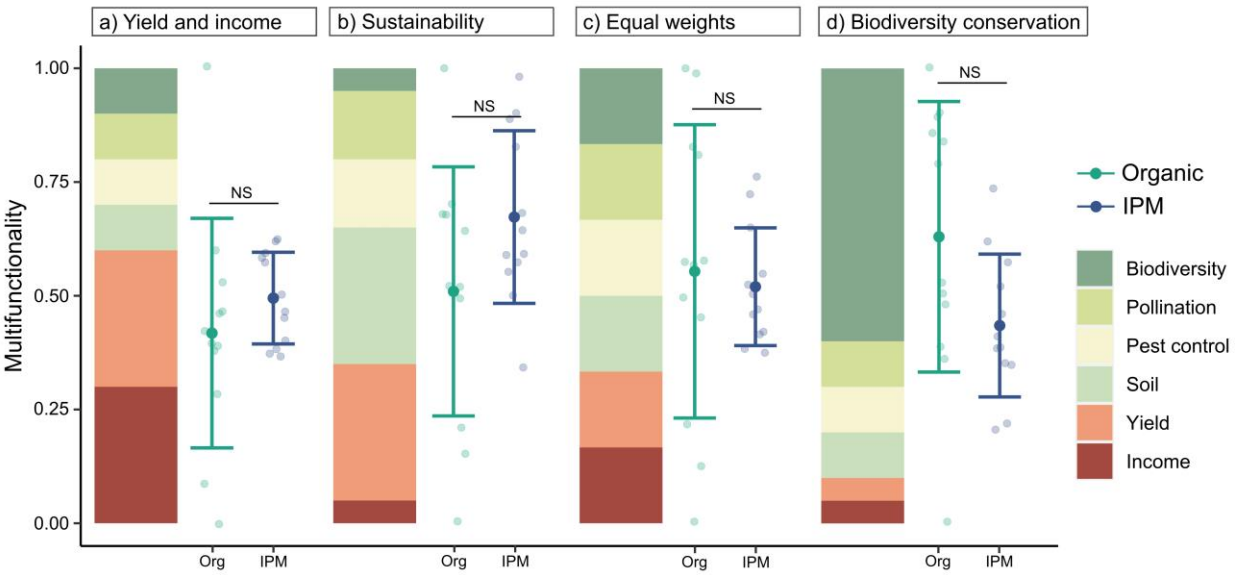



**Figure 5.5.** Overall multifunctionality for organic and IPM orchards in response to different hypothetical stakeholder preferences: (a) "yield and income" with 60% of the weight for yield and income and 40% for the other services, (b) "sustainability" with 60% of the weight for yield and soils, 30% for regulating services and 10% for biodiversity and income, (c) "equal weights" with 16.7% of the weight for each group and (d) "biodiversity conservation" with 60% of the weight for biodiversity, 30% for regulating services based on biodiversity and 10% for yield and income. For each scenario, the stacked bars represent the weight distribution, and mean ±1 SE is given for the organic and IPM orchards with points representing individual orchards. NS = non-significant ($P > 0.05$).

## 5.5 Discussion

In this study, we compared ecosystem multifunctionality between organic and IPM apple crops by analyzing indicators of ecological, agronomical and economic performance. Out of 23 indicators and six multifunctionality measures, ten significantly differed between organic and IPM orchards, mainly those relating to pollination services and yield. In addition to orchard management, also within-orchard location, the surrounding landscape and to a lesser extent local biodiversity were key factors shaping ES indicator levels. A clear trade-off was found between yield and biodiversity measures in both the organic and IPM orchards, while the organic orchards were also associated with several synergies among services. Overall ecosystem multifunctionality

did not differ between orchard types, although the IPM orchards had a tendency to score better in scenarios of stakeholder preference focusing on yield, income, and sustainable yields and soils, while the organic orchards tended to score higher when biodiversity conservation was the main interest.

### 5.5.1 Ecological performance indicators in organic and IPM orchards relative to a semi-natural reference

Organic and IPM orchards had similar levels of soil-based ES, except for potential heterotrophic soil respiration, which was lower in the IPM orchards. These lower respiration rates are likely the result of lower soil organic carbon (SOC) content in the IPM orchards (Daelemans et al., 2022b), since SOC is an important resource for soil microbial communities and largely determines microbial activity rates (Awale et al., 2017; Luján Soto et al., 2021). Overall comparable levels of soil health between organic and IPM apple cultivation systems were also found in other studies (Orpet et al., 2020; Reganold et al., 2001). Also relative to the semi-natural grasslands, few differences in soil health indicators and soil multifunctionality were found, indicating that both orchards types can maintain soil health compared to a semi-natural reference. Concerning the biodiversity indicators, only plant diversity differed between the organic and IPM orchards. The less diverse plant communities in the IPM orchards are likely due to the negative effects of herbicide use (Rundlöf et al., 2016). The diversity of arthropods, fungi and bacteria as well as biodiversity multifunctionality did not differ between organic and IPM orchards, which is surprising since several reviews report overall beneficial effects of organic farming for biodiversity conservation (Muneret et al., 2018a; Tuck et al., 2014). However, most of these studies are performed in annual crops, while the effects of organic vs. conventional management on farmland biodiversity are often less clear or even absent in perennial crops (Bruggisser et al., 2010; Muneret et al., 2019; Ostandie et al., 2022). Additionally, our use of general diversity metrics and the classification of species in broad taxonomic groups might have caused individual responses of different species to remain obscured. Compared to the semi-natural reference, both orchard types harbored less diverse plant communities, but higher diversity of bacteria in the soil. Both these effects likely result from the higher disturbance and nutrient availability in agricultural soils, which has been shown to negatively affect plant diversity, but is often associated with higher bacterial diversity (Lammel et al., 2021; Szoboszlay et al., 2017). Pollination and pest control services showed a mixed response to orchard management. While service provisioning was generally higher in the organic orchards, differences with the IPM orchards were rarely significant. An exception was the indicator for pest regulation potential, which was

lower in the organic orchards due to higher levels of pest infestation. While most studies generally report higher levels of pollination and pest control services in organic farms compared to IPM or conventional farms, these differences are often rather small and several studies also report inconsistent outcomes, especially in perennial crops (Muneret et al., 2018a; Porcel et al., 2018; Weekers et al., 2022a). Compared to the semi-natural grasslands, service providers of pest control and pollination services were generally less abundant and diverse in the organic and IPM systems, likely contributing to the lower levels of several service indicators in the orchards. These results indicate that negative effects of agricultural management on service providers may also translate into detrimental effects on ES delivery.

### 5.5.2 Drivers of ES provisioning in organic and IPM orchards

The majority of the ES indicators were strongly affected by orchard management, location within the orchards and landscape characteristics, indicating that both local and landscape scale drivers are important for ES provisioning. Although most drivers were directly affecting service indicators, the PSEM analyses also revealed several indirect, mainly biodiversity-mediated pathways. The small positive effects of organic management on soil-based services including soil respiration, carbon stocks, litter mineralization and litter stabilization, for instance, were mainly a result of an indirect pathway where organic management positively affected plant diversity, and higher plant diversity in turn led to higher levels of soil-based services. Biodiversity drivers in general, however, explained less variation than expected based on the fact that most of the ES are biodiversity-based. Pollination and pest control services were, for instance, only weakly driven by arthropod diversity metrics, with small positive effects on apple fruit set and natural enemy egg predation, respectively. For pollination this might imply that there are currently no pollinator shortages in the orchards, and that variation in pollinator communities will not cascade down towards differences in pollination services or yield levels. Another possible explanation might be that diversity metrics based on taxonomy are not necessarily good predictors of ES provisioning. Several studies have for instance shown that ecological functions and services are often more strongly correlated with the functional diversity of a community than with the taxonomic diversity (Gagic et al., 2015; Roquer-Beni et al., 2021).

In addition to the orchard management, also the sampling location within the orchards was identified as a strong local driver of the variation in ES provisioning, especially for soil-based services, biodiversity and pollination. For soil-based services and the diversity of soil fungi and bacteria, the within-orchard variability refers to the difference

between the drive rows and the crop rows. For the other biodiversity indicators and pollination, within-orchard variability refers to the difference between the center and the edge of the orchards. Both drive rows and orchards edges were generally associated with higher levels of ES indicators, highlighting the importance of these elements for ES provisioning. Both the drive rows and orchard edges are zones within the orchards that are typically managed less intensively, and are characterized by vegetative elements such as a permanent grass cover or edge habitat consisting of herbaceous vegetation, hedges or hedgerows. The presence of hedgerows and higher plant diversity at the field scale have also been found to promote ecological performance indicators in other studies (Couthouis et al., 2022; Le Provost et al., 2022). Additionally, also high plant diversity and the presence of semi-natural habitat in the surrounding landscape have been found to enhance ES (Dainese et al., 2019; Le Provost et al., 2022; Tamburini et al., 2022). In our study, higher semi-natural habitat cover, landscape diversity and edge density were all frequently associated with higher ES provisioning, indicating the importance of preserving and restoring semi-natural habitats and maintaining heterogeneity within the agricultural landscape. These beneficial effects, however, were not found for pest regulation and yield stability, confirming that beneficial factors for service providers can also enhance pest species (Karp et al., 2018), and further suggesting that this might result in lower yield stability levels (but see Redhead et al., 2020).

Despite the ubiquitous effects of the surrounding landscape on most ES indicators and yield stability, average yield levels were not influenced by landscape characteristics and were entirely driven by orchard management and, to a lesser extent, by within-orchard location. Yield levels were on average 29% lower in organic orchards relative to IPM orchards, which falls within the expected range for the yield gap between organic and conventional systems (De Ponti et al., 2012; Knapp and van der Heijden, 2018). Farmer income, on the other hand, did not differ between organic and IPM orchards, nor was it affected by any of the other drivers included in our analyses. Despite lower yields and higher overall costs in organic farms, the higher prices for organic apples in combination with subsidies for organic farming thus resulted in similar farmer income and profitability among organic and IPM systems. Overall, these results illustrate that the ecological, agronomical and economic performance of apple cultivation systems depends on a variety of drivers at multiple spatial scales, which are controlled by a variety of stakeholders including farmers, land managers, markets and policy makers. Adequately managing agricultural landscapes to ensure environmental sustainability, while simultaneously obtaining sufficiently high yield levels and a sustainable farmer

income, thus transcends the management of individual fields or farms and requires a multidisciplinary approach.

### 5.5.3 Synergies, trade-offs and agroecosystem multifunctionality

Our analysis of synergies and trade-offs between ES and farmer income revealed a strong trade-off between biodiversity and yield, which was present in both the organic and IPM orchards. This suggests that agricultural management practices that enhance yield levels negatively affect biodiversity, also under organic management. These results challenge the widespread view that organic farming is the key farming approach to reconcile agricultural production with biodiversity conservation, and further emphasize the need to go beyond the organic/conventional dichotomy to achieve sustainable, biodiversity-friendly agricultural landscapes (Ostandie et al., 2022; Tscharntke et al., 2021). In the IPM orchards also a trade-off between biodiversity and farmer income was found, but no other significant trade-offs were detected in either of the management systems, suggesting that increasing apple production intensity, although negatively affecting biodiversity, does not jeopardize the provisioning of other biodiversity-based services. Overall synergies were found between biodiversity and soil-based services, soil-based services and pollination, and in the organic orchards an additional synergy between biodiversity and pest control was detected. Based on the analysis of ES drivers, it is likely that several of these synergies are the result of similar reactions to shared underlying drivers such as plant diversity and surrounding semi-natural habitat. If not involved in significant trade-offs with other important ES, these underlying drivers might be valuable management targets to simultaneously enhance the provision of multiple ES, further strengthening ES resilience (Bennet et al., 2009).

In our assessment of overall orchard multifunctionality, we found that orchard management had no significant effect on multifunctionality in any of the four scenarios of stakeholder preference, although the IPM orchards had a tendency to score better in scenarios focusing on yield and income, and on sustainable yields and soils, while the organic orchards tended to score higher when biodiversity conservation received the highest valuation. Comparable multifunctionality levels between organic and IPM farming systems have also been reported by other studies (Couthouis et al., 2022; Herzog et al., 2019; Ostandie et al., 2022, but see Wittwer et al., 2021) and can be explained by several factors. First, our identification of ES drivers showed that orchard management only had a limited impact on ES provisioning, with large parts of variation also attributed to within-orchard location and landscape influences. Second, the organic and IPM systems might not be that different in practice, since IPM is considered to be

already quite environmentally-friendly, especially compared to conventional management (Porcel et al., 2018). Moreover, also organic farms can be managed relatively intensively, for instance by frequent and heavy use of organic pesticides and fertilizers, increased mechanization and large-scale monocultures (often referred to as 'organic conventionalization', Rover et al., 2020). Especially in perennial crops, the contrast between practices applied in organic and IPM systems might be less pronounced (Bruggisser et al., 2010). Third, there was considerable variation between individual orchards, especially within the organic system. Although the comparison between legislation systems as a whole provides useful information to evaluate and guide policy, it would be interesting to further assess the effects of different practices used within these systems to gain an even better understanding of the mechanisms behind ES provisioning. Additionally, it is also important to mention that in this study, we assumed linear supply-benefit relationships for all ES indicators, and did not include any thresholds above which the provisioning of a service is considered sufficient (Manning et al., 2018). Finally, although we included a wide variety of measures for ecological, agronomical and economic performance, it is possible that be the specific selection of indicators might have impacted multifunctionality outcomes, or that important indicators were missing from our selection. However, it was unfeasible to consider all possible functions and services that might be of importance to different stakeholders, especially since our study focused at service provisioning at the field scale, while some services such as biodiversity conservation, the retention and purification of water, cultural and esthetic services are more relevant when assessed at a landscape level. While our study shows that on-field ES in apple orchards are affected by on both local and landscape influences, more studies are needed that assess ES provisioning across entire landscapes, considering a large number of fields with different crop types as well as non-crop habitat.

## 5.6 Conclusion

To achieve long-term agricultural sustainability and food security, it is necessary to develop multifunctional agricultural landscapes that meet both environmental and societal demands. By investigating a comprehensive set of ecological, agronomical and socio-economic performance indicators in organic and IPM apple orchards, our study provides insights in the factors driving ES multifunctionality in these systems. We found that organic management at the field scale only had few beneficial effects on ecological performance indicators and, despite lower yield levels, also provided farmers with a similar income relative to conventional management. Limited differences in overall agroecosystem multifunctionality between organic and IPM orchards and the

clear trade-off between biodiversity and yield in both systems furthermore indicates that there is a need to go beyond the organic/conventional dichotomy to optimize orchard multifunctionality. In addition to farm management, also within-orchard location, landscape characteristics and farmland biodiversity were key factors driving on-field ecosystem service provisioning. The positive impact of surrounding semi-natural habitat and landscape complexity on ecological performance, together with the higher provisioning of several biodiversity-based services measured in semi-natural grasslands, further highlights the importance of preserving semi-natural habitats within the agricultural landscape. Overall, managing agricultural landscapes to optimize agroecosystem multifunctionality will require a joint effort of farmers, land managers and other stakeholders within the agricultural landscape, and needs to be supported by adequate policy at regional, national but also international level.

# Chapter 6

General discussion and conclusions

## 6.1 Overview of the research goals and main results

Agricultural intensification and expansion have led to environmental degradation, biodiversity loss, and erosion of biodiversity-based ecosystem functions and services in rural landscapes (Bommarco et al., 2013; Ramankutty et al., 2018). Organic farming is promoted as an environmentally-friendly alternative to conventional farming, but its actual performance in sustaining and enhancing biodiversity and multiple ecosystem services remains poorly understood, especially in perennial crops. Additionally, most studies to date lack a comparison with a semi-natural benchmark, although this can provide valuable insights into the extent to which biodiversity and biodiversity-based services are affected by agricultural management. With this thesis, our aim was to gain further insights in the role of organic farming in supporting soil-based ecosystem services, biological pest control, pollination, biodiversity, yield, farmer income, and overall agroecosystem multifunctionality in Flemish apple farms. As local farm management interacts with properties of the surrounding landscape in shaping within-field communities of service-providing organisms, we also aimed to quantify the influence of landscape factors on ecosystem service provisioning. Furthermore, we assessed the biological conservation potential of both organic and IPM orchards by comparing functional and taxonomic diversity of service-providing organisms, as well as their services, with a semi-natural reference. An overview of the obtained results in presented in Table 6.1.

**Table 6.1** Overview of the main results in relation to the specific objectives of the thesis.

| Identified drivers | Quantified findings for ecosystem services and farmer income |
|---|---|
| Soil health and soil-based ecosystem services (chapter 2,5) | |
| Agricultural management | Similar physical, chemical and biological soil health indicators in organic and IPM orchards. |
| Within-field location | Higher levels of soil health indicators in IPM drive rows relative to IPM crop rows. This difference is less pronounced in organic orchards. Differences only exist in the top soil layer (0-10 cm). |
| Landscape | Indirect positive effect of landscape diversity on carbon stocks through increased plant diversity (chapter 5) |
| Biodiversity | Positive effects of plant diversity on soil respiration, carbon stocks, and litter stabilization, but negative effect on litter decomposition. Higher soil respiration with increased fungal richness (chapter 5). |

| | |
|---|---|
| Comparison with SN land use | Similar soil health among semi-natural grasslands, organic and IPM orchards (slightly lower litter decomposition rates in SN grasslands, but likely due to drought). |
| Biological pest control (chapter 3,5) | |
| Agricultural management | Different community composition and higher abundance and richness of natural enemies in organic orchards, but no difference in natural enemy energy use. Also higher levels of pest infestation, despite slightly higher sentinel egg predation rates in organic orchards. |
| Within-field location | Higher sentinel egg predation rates and lower pest infestation in orchard edges. |
| Landscape | Positive effects of semi-natural habitat cover and landscape edge density on natural enemies, but also on pest infestation levels. Negative effects of orchard cover on both natural enemies and pest species. |
| Biodiversity | Higher predator abundance increases sentinel egg predation rates. |
| Comparison with SN land use | Degraded predator communities in both organic and IPM orchards, resulting in an impaired delivery of biological control services. |
| Pollination (chapter 4,5) | |
| Agricultural management | Higher wild pollinator abundance and apple seed set in organic orchards, but no effect on other pollinator community metrics and apple fruit set. Lower overall yield levels under organic management. |
| Within-field location | Higher taxonomic and functional diversity of pollinators in orchard edges. |
| Landscape | Higher pollinator abundance and diversity with increased landscape diversity and semi-natural habitat cover. |
| Biodiversity | Higher pollinator diversity with increased plant diversity in summer (chapter 5). Differences in pollinator community metrics are not linked to yield differences. |
| Comparison with SN land use | Lower taxonomic and functional pollinator diversity in both orchard types (chapter 4). Higher overall pollination services on phytometer plants in semi-natural grasslands (chapter 5). |
| Yield and farmer income (chapter 5) | |
| Agricultural management | Lower yields but higher yield stability in organic orchards compared to IPM orchards. Similar farmer income and income stability between both systems. |

| | |
|---|---|
| Within-field location | Higher yield in orchard edges |
| Landscape | No effects on yield or farmer income, but lower yield stability in diverse landscapes with higher semi-natural habitat cover. |
| Biodiversity – overall patterns for plants, arthropods, fungi and bacteria (chapter 5) | |
| Agricultural management | Overall positive effects of organic management on plant diversity, but no effects on fungal and bacterial diversity. Varying effects on different taxonomic groups of arthropods, but overall no significant difference in arthropod diversity between management systems. |
| Within-field location | Higher arthropod diversity in orchard edges. Higher fungal diversity but lower bacterial diversity in orchard drive rows compared to crop rows. |
| Landscape | Positive effects of landscape diversity on plant diversity, of landscape diversity and edge density on arthropod diversity, and of semi-natural habitat cover and orchard cover on fungal diversity. Increased orchard cover at small spatial scale has a negative impact on within-field arthropod diversity. |
| Biodiversity | Higher within-field plant diversity has a positive effect on arthropod diversity. |
| Comparison with SN land use | Less diverse plant communities in both orchard types, but higher diversity of fungi and bacteria (but these communities never match the complexity and connectivity of those in a semi-natural benchmark, Hulsmans et al. 2022). Service providers for pest control and pollination are less abundant and diverse in the orchards, but overall arthropod diversity is not lower in the organic orchards compared to the semi-natural reference. |
| Multifunctionality, synergies and trade-offs (chapter 5) | |
| Agricultural management | No difference in overall agroecosystem multifunctionality between organic and IPM orchards, regardless of potential scenarios of stakeholder interest. A strong trade-off between biodiversity and yield in both orchard types. Synergies between biodiversity and soil-based services, soil-based services and pollination, and biodiversity and pollination (the latter only in the organic orchards). |

## 6.2 Drivers of multiple ES and implications for sustainable orchard management

### 6.2.1 Agricultural management

Less than half of the indicators for ecological, agronomical, and economic performance that were quantified in this study differed significantly between organic and IPM apple orchards. Differences between the two management systems were mainly related to aspects of biodiversity, pollination, and yield. Concerning biodiversity measures, organic agriculture enhanced plant diversity, wild pollinator abundance, and natural enemy abundance compared to IPM, but had no effect on overall arthropod diversity, bacterial diversity, or fungal diversity. This confirms earlier findings that the effects of organic farming differ between functional groups, with greater beneficial effects on primary producers, pollinators, and natural enemies relative to other functional groups such as decomposers (Bengtsson et al., 2005; Lichtenberg et al., 2017; Tuck et al., 2014). The higher abundance but similar diversity in organic orchards furthermore indicates that organic farming mainly enhances the abundance of species that are already quite common and present in both organic and IPM farms. Additionally, as many taxonomic diversity metrics (abundance and richness of fungi and bacteria, pollinator diversity, overall arthropod diversity…) as well as the entire set of functional diversity metrics included in this study did not differ between organic and IPM orchards, the benefits of organic farming in terms of maintaining biodiversity were rather limited.

A similar observation was made for biodiversity-based ecosystem services and overall ES multifunctionality, with only small positive effects of organic farming on apple fruit set and sentinel egg predation rates, which were used as indicators for pollination and biological control services, respectively. These differences in ES levels were also too small to positively affect apple production, as the PSEM analyses did not point out causal relationships between levels of ES provisioning and yield. Instead, yield levels were directly affected by orchard management, with yields in organic orchards being on average 29% lower than those in IPM orchards. However, a large variation in yield levels within the IPM system, and even more so within the organic system, was observed, with some organic orchards for instance generating higher yields than the average of the IPM orchards. Possible reasons for the average yield gap include i) lower effectiveness of organic pesticides and herbicides, leading to higher infestation levels of weeds, pests, and diseases in organic orchards, ii) difficulties in regulating the release of various nutrients from organic fertilizers in accordance with crop demands (both in quantity and timing), and iii) differences in management practices such as pruning,

thinning, use of phytohormones, orchard planting configuration, and weather risk management (Seufert, 2019; Seufert et al., 2012; Seufert and Ramankutty, 2017).

Several factors may contribute to the limited beneficial effects of organic farming on biodiversity and biodiversity-based services. For example, the focus on waiving synthetic pesticides in organic farming does not necessarily translate into lower environmental impacts compared to IPM. Pesticides allowed in organic farming need to be derived from natural substances, but these can be as harmful for biodiversity as synthetic pesticides (Biondi et al., 2012). Additionally, it has also been shown that certain practices that are used in both organic and IPM systems play an important role in shaping within-field community assemblages. For instance, increased soil copper content resulting from the use of copper sulfate has been shown to greatly determine the abundance and diversity of earthworms, pot worms, fungi, springtails, and mites (Karimi et al., 2021; Mackie et al., 2013; Ostandie et al., 2021; Peigné et al., 2009). Although pesticide applications are typically lower in organic arable crops, organic perennial crops are often heavily treated with natural pesticides, leading to equal or sometimes even higher application levels than in conventional fields (Annaert et al., 2017; Muneret et al., 2018b; Nascimbene et al., 2012). The heavy use of organic pesticides, together with the increased mechanization and use of large-scale monocultures that is frequently observed in organic farms, can contribute to a convergence in management intensity between organic and IPM systems (Rover et al., 2020). This might be further reinforced by the fact that IPM in itself already uses relatively environmentally-friendly methods, especially compared to conventional farming (Kennedy et al., 2013; Porcel et al., 2018).

Additionally, also the high variability among individual farmers within both the organic and IPM systems might contribute to the converging results in both systems. On top of meeting IPM and organic regulations, farmers from both systems can voluntary choose to implement wider environmentally-friendly practices. Measures that are known to increase within-field biodiversity without jeopardizing yield levels include for instance the incorporation of grass strips, hedges and hedgerows within and around agricultural fields, or creating more field edges by reducing field sizes (Tscharntke et al., 2021). While these practices fit strongly within the principles of organic farming, they are no formal part of organic certification, and therefore their uptake greatly varies among individual farms (Tscharntke et al., 2021). In our study, we indeed found that field edges and grass strips (drive rows) were positively associated with biodiversity, and that yields were on average higher in the edges of the orchards compared to the center, regardless of the management system.

Furthermore, our analysis of synergies and trade-offs between different ecosystem services revealed a strong trade-off between biodiversity and yield in both the organic and IPM systems. This suggests that farming practices that enhance yield levels inevitably lead to lower within-field biodiversity, irrespective of the management system in which they are applied. This highlights the need to go beyond the organic/IPM certification to understand which practices are actually driving trade-offs, and to further investigate how these negative associations can be mitigated. Interestingly, no trade-offs were found between yield levels and biodiversity-based ecosystem services in either system. This indicates that enhancing yield levels, although leading to lower overall biodiversity, is possible while still maintaining the species that are key to supporting agricultural production. The overall limited differences in biodiversity and biodiversity-based ecosystem services between organic and IPM farms were furthermore in sharp contrast with the higher taxonomic and functional diversity, as well as higher service provisioning found in the semi-natural reference habitats. Although the semi-natural grasslands represent a different type of land use with a focus on nature conservation, they provide a benchmark for regional biodiversity that allows the assessment of the impact of both IPM and organic management on biodiversity conservation. The lower overall diversity and few unique species in both orchard types relative to the semi-natural grasslands indicate that the remaining biodiversity in orchards, although providing important ecosystem services, is generally of low value from a biodiversity conservation perspective (Hulsmans et al., 2023b). These results, together with the strong trade-off between biodiversity and yield, suggest that both organic and IPM orchards have little potential to contribute to regional biodiversity conservation. Instead, a focus on maintaining functional agrobiodiversity to safeguard ES provisioning and yield levels might be more feasible and realistic.

### 6.2.2 Landscape context

Our identification of local and landscape drivers of ES provisioning showed that landscape characteristics were at least equally important for biodiversity and biodiversity-based ecosystem services as local orchard management. The proximity and cover of semi-natural habitat, landscape diversity and edge density were found to enhance the diversity of plants, arthropods and fungi, and were positively associated with apple fruit set and sentinel egg predation, as indicators for pollination and biological control services, respectively. Also several indicators of soil-based services like soil respiration, carbon stocks, and litter stabilization were indirectly stimulated by landscape characteristics, as they all benefited from the higher within-field plant diversity that was found in more diverse landscapes. On the other hand, a higher

proportion of orchards in the landscape generally decreased arthropod diversity. As discussed in chapter 3, this can be assigned to the chemical umbrella effect, which entails that a high pesticide pressure in uniform landscapes negatively affects biodiversity at the landscape scale (Muneret et al., 2018b; Samnegård et al., 2019). An exception was found for pollinators during apple bloom, who could likely benefit from the high resource availability during mass flowering and were thus not negatively affected by a high orchard cover. Because the positive effects of surrounding semi-natural habitat and landscape complexity on most aspects of biodiversity, as well as on several ecosystem services, were not accompanied by a production cost, this opens up opportunities to stimulate biodiversity in agricultural fields, and further highlights the importance of landscape-level greening measures relative to local management interventions. However, it should be noted that surrounding semi-natural habitat might also provide some disservices for agriculture, such as the higher levels of pest infestation that were found for codling moth in chapter 3. Especially when also other pest species and diseases are taken into account, it is very likely that a high cover of semi-natural habitat in close proximity to agricultural fields also comes with a certain yield cost. Therefore, we stress the need to carefully balance the possible services and disservices when considering measures that might enhance biodiversity in agricultural landscapes.

### 6.2.3 General conclusions

Altogether, five main conclusions can be formulated based on the results of our study.

**First**, the limited ecological benefits of organic farming practices in combination with the high yield gap with the IPM system, indicate the need to go beyond the organic/IPM dichotomy to improve orchard sustainability. Maintaining and increasing orchard edges, semi-natural habitat, and overall landscape complexity seem more effective strategies and can be beneficial for both organic and IPM orchards.

**Second**, as both orchard types were able to maintain soil health compared to our semi-natural reference system, measures to improve ecosystem service provisioning in the apple orchards should be mainly targeted at above-ground services. However, the high spatial variability in soil health between drive and crop rows also indicates that there is still opportunity to improve soil management in the crop rows of the IPM system.

**Third**, better characterization of the effectiveness of different management practices and crop protection strategies might help farmers in streamlining their management

towards optimal results for biodiversity, biodiversity-based services and yield. In this context, development of result-based certification policies instead of the current input-based certification schemes would be more effective to achieve more sustainable orchard management.

**Fourth**, the potential disservices that might originate from increasing semi-natural habitat, the clear trade-off that was observed between biodiversity and yield, and the fact that biodiversity was much higher in our semi-natural benchmark, all suggest that both orchard types have little potential for biodiversity conservation. The focus in the apple orchards should therefore be rather on maintaining functional agrobiodiversity and achieving a steady supply of ecosystem services that support crop production. Additionally, the local conditions in agricultural land (e.g. high nutrient availability and high disturbance) are not suited to maintain high overall biodiversity, further stressing the indispensable role of (semi-) natural habitats for proper biodiversity conservation.

**Finally**, integration of these guidelines requires an improved collaboration between a variety of stakeholders including farmers, farmer associations, research institutes, agri-food chains, land managers and governments, and needs to be supported by appropriate policies at regional, national and international level.

## 6.3 Shortcomings and research perspectives

### 6.3.1 Selection of study sites and data collection

The study system used in this thesis consisted of organic apple orchards, orchards with integrated pest management, and semi-natural grasslands as reference habitats. Concerning the orchards, the categorization into either organic or IPM enabled us to compare these management systems in their entirety, which is relevant in a policy context that is mainly focused on management systems rather than specific management practices. However, this approach also has some drawbacks, as specific information on the applied practices would give a more precise idea about what exactly we are comparing, and could provide additional insights or explanations for the obtained results. This is especially true because there might be high variability in applied practices between farms, even within the organic and IPM systems (Orpet et al., 2020; Porcel et al., 2018; Rover et al., 2020). In addition to the specific regulations concerning organic or IPM farming, both systems may vary widely in the implementation of more environmentally friendly management practices (Tscharntke et al., 2021; Weekers et al., 2022b). While we were also able to observe this variability in the field and in our

data (parcel identity explained a large part of the total variation in most of our models), we were unfortunately unable to collect specific data on the applied practices and the types and quantities of fertilizers and crop protection products used in each of the orchards. Furthermore, as organic and IPM orchards might both be relatively environment-friendly, a comparison with real conventional management (without IPM practices) would also have been interesting. However, as all professional farmers within the EU are obliged to apply IPM, this comparison would only be possible in an experimental setup, and thus unsuitable for translation to larger spatial scales and different socioeconomic and policy contexts.

In our study, both organic and IPM orchards were compared with semi-natural grasslands in terms of their biodiversity and provisioning of biodiversity-based ecosystem services. While this allowed us to assess the extent to which biodiversity and related services in the orchards were degraded due to agricultural management, this comparison also has some limitations. For example, the applied nature management in the semi-natural grasslands might also vary between sites, for instance in terms of the frequency and timing of mowing or grazing, or in terms of management history. As a result, also the habitat quality might vary between different semi-natural grasslands, making it less clear against which baseline the orchards are being compared. With respect to habitat quality, another limitation of this reference system is that real pristine grasslands do not exist within the study area. All semi-natural grasslands, and by extension all semi-natural habitats within the study area, are to a certain extent degraded, for instance due to increased nutrient availability following excessive nitrogen deposition. This implies that our results concerning the effects of orchard management on biodiversity and biodiversity-based ecosystem services are likely to be underestimated, and that comparison with a real natural system would indicate an even higher degree of biodiversity erosion under agricultural management. Thus, our comparison with (degraded) semi-natural grasslands is subject to a shifting baseline. Additionally, the sampling of pollinators and quantification of pollination services was centered around the flowing period of the apple trees, during which the resource availability in the orchards was exceptionally high for a short period of time. This mass-flowering event might attract a large number of pollinators that use the orchards only as a partial habitat, and do not establish or reproduce. During this period, a comparison with semi-natural grasslands might be biased, as these do not exhibit such a mass-flowering event. To obtain a better understanding of the real potential of the orchards to contribute to biodiversity conservation, it would therefore be useful to sample more frequently throughout the entire year and study the population dynamics of the species present.

Finally, to fully estimate the effects of agricultural management on biodiversity, it would be advisable not only to sample in the orchards, but also in the (semi-natural) habitats surrounding the orchards. Orchards can, for instance, negatively affect biodiversity in the surrounding landscape by spillover of fertilizers and harmful agrochemicals, or because they might be ecological 'sinks' with below-replacement population growth rates. This might be especially important for resident and less mobile species, which are less flexible in moving between different habitats.

### 6.3.2 Selection of ecosystem services and their indicators

In this study, we described the impact of orchard management on a selection of biodiversity-based ecosystem services, yield and farmer income. Each of these services were represented by one or more indicators that were chosen based on recommendations from previous research, and after careful consideration of their quantification feasibility. In addition to our selection, however, several other indicators would be worth investigating. For the pest control services, we focused on the impact of orchard management on a generalist community of natural enemies, and examined the extent to which they preyed on codling moth eggs and whether this affected codling moth infestation levels. However, as apple cultivation suffers from a wide variety of pests and diseases, it would be interesting to also investigate the impact on other pests such as different species of aphids, weevils and true bugs. The combined effects on different pest and diseases would allow for better estimation of the biological control potential of organic management, and the assessment of overall infestation levels could provide additional insights in the possible causes of the observed yield gap between organic and IPM orchards. Additionally, yields were only approached quantitatively in our study, while organic farming might also have effects on the quality and food safety of the produced apples. For instance, the increased fruit set that was found under organic management might contribute to higher fruit quality due to increased shape, weight, flesh firmness and calcium content (Buccheri and Di Vaio, 2005; Keulemans et al., 1996; Sheffield, 2014). Also the food safety of organic apples might be important to consider, as fruit crops generally contain a relatively high concentration of pesticide residues, and because this is one of the main reasons why consumers and farmers choose organic (Baker et al., 2002; Montiel-León et al., 2019; Seufert et al., 2017). Several studies far have reported that organic apples have overall lower concentrations of pesticide residues and are less likely to exceed the maximum residue level (MRL) compared to conventional or IPM apples, although the actual health benefits remain debated (Barański et al., 2014; Kazimierczak et al., 2022; Smith-Spangler et al., 2012).

In addition to our focus on within-field biodiversity, biodiversity-based services, yield and farmer income, agricultural lands also depend on, or contribute to, a variety of other ecosystem services. Especially when we extend our view to not only include organic management practices but also wider nature-oriented measures, such as the implementation of hedgerows, grass strips and other semi-natural elements, we can expect that regulating services like erosion control, habitat provisioning, and the prevention of pesticide and fertilizer runoff will also be impacted (Holland at al., 2017). Furthermore, the implication of environment-friendly measures both within and outside agricultural fields might also increase the provisioning of cultural ecosystem services. Aesthetic beauty, cultural heritage and potential for recreation are for instance among the most valued services by the users and residents of the agricultural landscape, and were indicated to increase in landscapes with high complexity and a mosaic of small fields, forest patches, tree lines and hedgerows (Van Berkel and Verburg, 2014).

Considering a wider set of ecosystem services and service indicators would increase our understanding of the effects and possible trade-offs that might arise when implementing specific management types and other nature-oriented measures. However, also different methods for the quantification of ecosystem service indicators should be addressed. In our study, we assumed a linear relationship between the supply of an ecosystem service and the benefit it provides to humans, but this approach might not fit all services (Manning et al., 2018). For instance, while a linear relationship might be suited for carbon stocks (the higher the better), other services such as production levels might only provide profit for farmers, and thus contribute to human well-being, above a certain threshold. Also for pest control services this might be the case, as a minimum amount of predation by natural enemies might be required to actually decrease pest populations, depending on the ecological strategies and life history traits of both the natural enemies and pest species (Roy et al., 2020). Overall, supply-benefit relationships can be defined using a variety of methods, including extensive examination of ecological relations, economic models, expert knowledge and stakeholder consultations, and should always be clearly explained and justified as they might have a great impact on the quantification and interpretation of ecosystem service levels (Manning et al., 2018). When the quantification of supply-benefit relationships is difficult or uncertain, it is advisable to explore the sensitivity of ecosystem services or ecosystem service multifunctionality to a range of possible relationships. In this context, our study provides a first step towards a more extensive ecosystem service multifunctionality assessment, including a wide variety of services and supply-benefit relationships in order to approach the complex reality of agricultural landscapes and their link with human well-being as close as possible.

### 6.3.3 Upscaling from field-level to landscape level

In addition to expanding the set of considered ES, a fully integrated assessment of agroecosystem multifunctionality also requires the upscaling of parcel-level research to the landscape level, as many ecosystem services are affected at the landscape scale. More specifically, agricultural intensification generally has a negative impact on biodiversity and biodiversity-based ecosystem services like biological pest control and pollination through simplification of the agricultural landscape (Landis, 2017; Tscharntke et al., 2021). Simplified landscapes with large fields of monocultures, little or no semi-natural habitat at field edges, and overall low crop diversity will have a lower multifunctionality compared to more complex landscapes. To restore multifunctionality in these landscapes, it is therefore necessary to take actions on a scale larger than individual fields or farms. Moreover, nature-oriented interventions at the landscape level have been shown to provide much larger benefits for biodiversity, biodiversity-based ecosystem services and overall multifunctionality than changes in local farm management (Landis, 2017; Tscharntke et al., 2021, 2012). Reconciliation of possibly competing objectives in terms of biodiversity conservation, biodiversity-based ES, food production, and farmer income can be achieved by smart land use planning and a well-considered spatial allocation of different land use types at the landscape scale. To accomplish this, a better understanding of the multifunctionality of different land use types is required, which for instance includes different crop types, but also different types of semi-natural habitat within the landscape. Semi-natural habitats play a key role in landscape-level biodiversity and service provisioning, as they greatly determine the landscape-level species pool from which agricultural fields are colonized. While we used semi-natural grassland with patches of woodland and hedgerows as a benchmark in our study, also other habitat types should be considered as they all harbor specific species communities and all contribute to the regional species pool.

Additionally, optimizing the simultaneous delivery of a broad range of services also requires a better understanding of the interactions between multiple ES across different land uses. Synergies and trade-offs among ES are highly management- and context-dependent, but very few studies have quantified these relationships across different land use types and across gradients of agricultural intensification (but see Felipe-Lucia et al., 2020; Finch et al., 2019). Most studies, like ours, primarily focus on comparing different agricultural management systems rather than examining continuous gradients of agricultural management intensity. However, acknowledging these existing gradients can lead to a more accurate evaluation of various land use strategies at the landscape scale, such as for instance land sharing vs. land sparing strategies (Box 1). To this end, fine-grained field monitoring networks should be established across the agricultural

landscape, to allow parameterization of detailed predictive models for biodiversity and ES outcomes based on a wide range of local management practices and parcel characteristics. Furthermore, as many services like water regulation and pollination involve the exchange of matter and organisms among different areas within the landscape, also the spatial configuration of landscape features and land use types should be taken into account as this will influence such ES (Manning et al., 2018). Therefore, the adoption of spatially explicit methods is seen as a necessary path to further increase the understanding and optimization of local ES provisioning. Finally, high-resolution trade-off functions among ES that take into account the specific spatial context can be used to evaluate different land use scenarios in terms of their impact on agroecosystem multifunctionality. In the context of our study, this can for instance be used to evaluate the impact of different proportions and spatial allocations of organic farming within the agricultural landscape (e.g. the Farm to Fork objective of 25% of the total agricultural land area under organic farming by 2023). Further optimization techniques can then be used to balance trade-offs among different land use objectives, with the final goal of maximizing landscape-scale outcomes for biodiversity conservation, biodiversity-based ecosystem services, food production and economic viability (Gao et al., 2021b; Liu et al., 2022).

**Box 1. Going beyond the organic-IPM dichotomy**

In this study, we compared organic and IPM farming systems in terms of the provisioning of multiple ecosystem services. While this is relevant in a policy context where organic farming is increasingly supported, the observed heterogeneity within both organic and IPM farms also advocates for a more detailed assessment of the relationship between agricultural intensification levels and agroecosystem multifunctionality. Especially for the translation of field-level trade-offs to the scale of entire landscapes, considering a large variability in management intensities across different land uses allows for a more accurate and realistic evaluation of land use scenarios. In this context, quantifying how levels of ES vary over an intensification gradient allows to determine at what level of agricultural intensity the provisioning of these services is optimized. To maintain rare and specialist species of high conservation value, for instance, the optimal land use intensity is expected to be lower than for the conservation of functional agrobiodiversity, which typically consists of common and abundant species that can cope with a high degree of disturbance. Assessing relationships between species and land use intensity (often represented by yield levels) is also at the core of the land sharing – land sparing framework, where species are identified as winners or losers depending on whether their abundance

increases or decreases with agricultural intensification, and where the shape of the response curve is used to determine whether land sharing or land sparing provides the optimal strategy for their conservation (Green et al., 2005; Phalan et al., 2011). Here, extreme land sharing refers to low-intensity cultivation of the entire landscape by integration of nature conservation into the agricultural land, while extreme land sparing implies the spatial segregation of high-yielding agriculture and nature conservation.

In our study, the taxonomic and functional diversity of most groups decreased with agricultural intensification (higher yields). This is for instance the case for plant and arthropod diversity, for which the convex curve additionally indicates that land sparing is the optimal strategy to maximize diversity at the landscape scale (Fig. 6.1a,b). For fungi, however, a small increase in diversity was found under agricultural land use, with a maximum at intermediate production levels (Fig. 6.1c). Curves were also fitted for several ES (Fig. 6.1d,e), but these cannot be interpreted in the same way as service provisioning is intrinsically defined relative to the agricultural demand, and can thus not be spatially separated from the agricultural land (e.g. a land sparing scenario for ES would be meaningless). However, the combined response curves of multiple ES to agricultural intensification can be used to investigate whether trade-offs vary among production levels, and thus to determine the optimal farming intensity to maximize ecological, agronomical and economic objectives.

A realistic assessment of land sharing – land sparing strategies and different production intensities at the landscape scale would require quantification of response curves for species abundances across a wide range of crop types and land uses, in addition to the apple orchards and semi-natural grasslands that we investigated in our study. Furthermore, a more holistic approach to the land sharing – land sparing framework would also require taking into account a wider set of regulating and cultural services. When cultural services are included, for instance, the importance of land sharing would likely increase because complex landscapes with a mix of agriculture and natural elements are better appreciated by the general public (Van Berkel and Verburg, 2014). Recently, the attention of the scientific community has also been shifting to more intermediate land use strategies, as the land sharing – land sparing framework mainly focusses on either low or high productivity while many species have more complex relationships with agricultural intensity (Balmford, 2021; Finch et al., 2019; Fockaert et al., 2023; Simons and Weisser, 2017). It has for instance been shown that a three-compartment system with zero, low and high intensity areas across the landscape results in the highest biodiversity benefits (Finch

et al., 2019). Furthermore, land sharing and land sparing can also be simultaneously implemented as they mainly operate at different spatial scales; while land sharing is mostly relevant at local and landscape scales, land sparing is most effective at a regional scale. Also in the densely populated and highly fragmented landscapes in Flanders, a combination of both approaches seems most appropriate. Land sharing at the local scale can for instance be beneficial to maintain functional agrobiodiversity in agricultural fields, while land sparing at a regional scale can be important for the conservation of regional biodiversity.

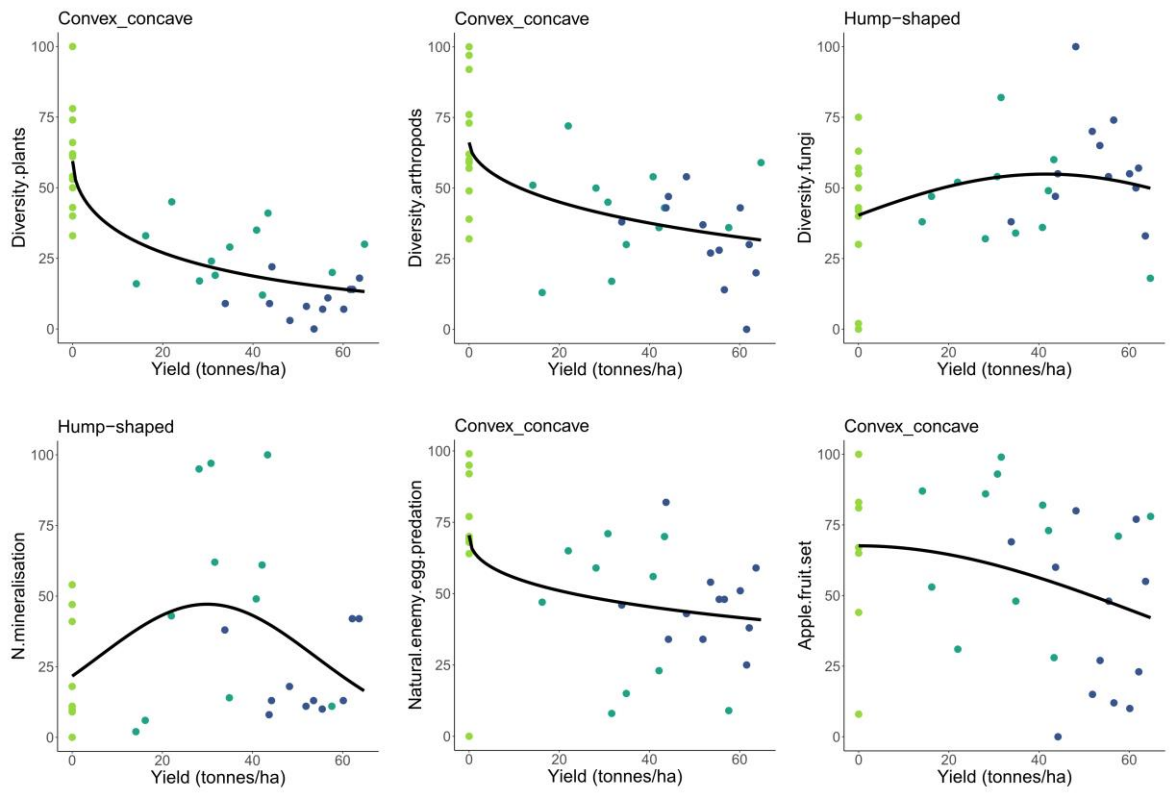



**Figure 6.1.** Relationships between the diversity of a selection of taxonomic groups (a-c) and the provisioning of a selection of ecosystem services (d-f) and yield levels. The best fitting curve (linear, hump-shaped or convex-concave) is indicated for each relationship. Light green points indicate semi-natural reference sites, dark greed points indicate organic orchards and blue points indicate IPM orchards.

### 6.3.4 Stakeholder engagement and policy evaluations

As we defined ecosystem service multifunctionality as the co-supply of multiple ecosystem services relevant for human well-being, designing agricultural landscapes to optimize multifunctionality requires the consideration of different stakeholders and

socio-economic factors (Manning et al., 2018). As different stakeholders might prioritize different (sets of) ecosystem services, overall multifunctionality estimates can greatly vary between stakeholder groups. In our study, we investigated how orchard multifunctionality might be perceived by different stakeholder groups with different interests, by incorporating hypothetical stakeholder weights, ranging from a focus on production and farmer income to a focus on biodiversity conservation. When quantifying multifunctionality at the landscape scale, however, all relevant stakeholders should be consulted, and weights should ideally be based on standardized surveys. In this way, different stakeholder objectives can be taken into account when determining optimal land use allocations, thereby minimizing trade-offs and possible conflicts between them (Allan et al., 2015). In a next step, optimal land use allocations should be brought into practice by effective policy support. As farmers are the main decision-making agents in the agricultural landscape, this requires insights in the factors that drive their farm management and land use decisions. This includes for instance economic and financial incentives, but also their social network, social norms and individual preferences (Dessart et al., 2019; le Polain de Waroux et al., 2021). These factors can be quantified, and subsequently used to model how different policy interventions mediate the uptake of greening measures by farmers, ultimately resulting in optimal policy strategies that maximize outcomes for biodiversity, food production and other ecosystem services. Overall, it can be concluded that stakeholder engagement is crucial to ensure that policies are implemented in a manner that is socially, economically, and environmentally sustainable.

## 6.4 Management and policy recommendations

To limit further environmental degradation, biodiversity loss, and erosion of ecosystem services in intensive farming landscapes, ecological principles should be better integrated in agricultural management and landscape planning (Tamburini et al., 2020). However, this will only be successful when also social and economic objectives are met, thus requiring careful consideration of different ecosystem services valued by various stakeholders. The EU CAP recognizes this need for multifunctionality, and increasingly supports environmental goals within a framework of fair income support and a competitive agri-food sector. For instance, the new Flemish CAP SP (2023 – 2027) aims to further increase the area under organic farming in Flanders to more than 30 000 ha (from 1.7% to more than 5%) by providing higher income support relative to the previous CAP period (DLV, 2023b). Whereas this holds a significant increase in the share of organic farming, these ambitions are clearly lower than those of the European Farm to Fork Strategy, which aims at achieving 25% of total EU agricultural land area

under organic farming by 2030. Since a clear substantiation of these objectives is lacking in both the EU CAP and the Flemish CAP SP, further scenario analyses and monitoring should investigate the impact and effectiveness of these objectives in improving agricultural sustainability.

In our study in apple orchards, organic farming had overall limited beneficial effects on biodiversity and ecosystem services, but came at a high yield cost. This can be partly attributed to the high focus of organic certification on regulation inputs rather than results, leading to a high variability in the outcomes for ecosystem services among farms. Consequently, a more promising approach to maximize ecosystem service delivery would be the introduction of result-based payments, for instance by Payment for Ecosystem Services (PES) (Capodaglio and Callegari, 2018). Such initiatives might stimulate the uptake of practices that effectively enhance service provisioning. Based on our study in apple orchards, interventions that increase the amount of orchard edges, semi-natural habitat, landscape diversity and landscape edge density seem most promising to enhance ecosystem service provisioning in both organic and IPM orchards. In comparison to the previous CAP, some new opportunities for ecosystem service payments have been established by the introduction of voluntary eco-schemes in Pillar I. These schemes allow higher payments for implementing nature-oriented measures than just compensating the costs, and thus offer opportunities for farmers to also receive payment for the results achieved. However, this approach also has several disadvantages. Our study for instance highlights the importance of landscape-scale parameters for biodiversity and ES outputs, which are often beyond the control of individual farmers. Additionally, practical estimation of results proves challenging, and demands considerable time and resource investment. Our research has revealed that the effects on biodiversity, ecosystem services, and yield at the parcel-level show significant variation, so in order to create effective result-based payment schemes high-resolution data is needed that allows to accurately estimate outcomes for ecosystem services based on local management and parcel characteristics. In this context, our approach of quantifying local and landscape drivers, as well as trade-offs between services, can help to gain insights in the effectiveness of current agricultural policy, and to formulate further recommendations for achieving multifunctional farming landscapes with lower environmental impact. Based on the findings of our study and a more general evaluation of the current agricultural policy, several recommendations can be formulated (Table 6.2).

**Table 6.2.** Overview of recommended actions that can be taken at various levels and by different actors to more effectively lower the environmental impact of agriculture and improve overall agroecosystem multifunctionality.

| Necessary actions | Context and involved actors |
|---|---|
| National and international | |
| Prioritize management systems and management practices that provide real and significant environmental benefits | The effectiveness of different management systems and management practices should be further assessed. This requires close collaboration with farmers and scientists, and a regular evaluation of both policy and management systems/practices |
| Improve the effectiveness of agricultural systems and practices by implementing result-based compensation schemes | Result-based compensations instead of area- and input-based schemes stimulate farmers to implement practices that effectively contribute to environmental sustainability |
| Promote the establishment of appropriate monitoring networks to evaluate policy and management results | As results are strongly context-dependent, high-resolution data is needed to model and evaluate the results of different policies, land use strategies and specific management practices. This requires close collaboration between farmers, scientists, landscape managers, and local or regional governments. Policy should promote these networks and facilitate collaborations |
| Acknowledge temporal variability in the expected results | Certain measures (e.g. enhancing semi-natural habitats) provide increasing benefits when they are maintained for a longer period (multiple years). Compensations should stimulate long-term maintenance of these measures |
| Acknowledge variability in ES trade-offs depending on local/regional conditions and objectives | Policy guidelines for ecosystem service provisioning should take into account the spatial context and prioritized ES within a region, and should be adjusted accordingly. This requires close collaboration between scientists, farmers, landscape managers and landscape planners |

| | |
|---|---|
| Integrate environmental ambitions within different policy domains | The environmental objectives of the CAP should be set jointly with other frameworks from other policy domains (e.g. environment, spatial planning) |
| Regional | |
| Identify regional objectives to optimize multiple service provisioning within the landscape | Farmers, land managers, regional governments and all other stakeholders should collaborate to determine regional objectives that can guide the optimization of land use planning |
| Establish monitoring networks to identify trade-offs and to evaluate policy and management results under regional conditions | As results are strongly context-dependent, high-resolution data is needed to model and evaluate the results of different policies, land use strategies and specific management practices. This requires close collaboration between farmers, scientists, landscape managers, and local or regional governments |
| Integrate knowledge about trade-offs in regional landscape planning | Farmers, land managers, regional governments and all other stakeholders at regional scale should work together to determine the optimal spatial allocation of different land uses within the region that minimizes trade-offs between environmental and societal demands |
| Acknowledge the role of farmers as landscape managers | As the main decision-making agents within agricultural landscapes, farmers can greatly contribute to regional multifunctionality. This should be acknowledged and appreciated by other stakeholders in the landscape (including tourists, citizens…) to enhance the support for environmental sustainability on a regional scale |
| Farm | |
| Stimulate sustainability as a proper part of farming | Implementation of measures that increase environmental sustainability should become common practice within farms. Adequate, result-based compensation schemes can stimulate the adoption of such measures and positively change farmers' attitudes |

| | |
|---|---|
| Adoption and evaluation of farming systems based on the location and landscape context | The adoption of agricultural management systems like organic farming is a voluntary decision made by individual farmers. Farmers should be supported in their decision making process by providing them with sufficient information about the different possibilities and potential results for their specific context and location within the landscape. This requires collaboration with policy makers, NGOs, farmers associations, agri-food chains, scientists, landscape planners and their social network |
| Field | |
| Minimize trade-offs between ecosystem services | Management should be adjusted to the local environmental conditions (e.g. soil type, soil texture and hydrology) and the specific landscape context (e.g. the proximity and cover of semi-natural habitat) to minimize trade-offs between ES |
| Agricultural practice | |
| Select effective practices that contribute to achieving environmental and societal/economic goals | Within the specific context (management system, landscape context), the most optimal and effective measures should be applied. This includes, for instance, different types of pesticides and fertilizers and their application frequency, of the selection of specific plant species to be included in hedges, hedgerows and grass strips to optimize biodiversity and ecosystem services (or to minimize disservices) |
| Monitor and evaluate selected practices | As the most optimal measures or farming practices might change over time, frequent monitoring and evaluation is needed. Also new technologies and new scientific insights can call for adjustments in the applied measures. This involves collaborations between farmers, scientists, NGOs and farmer associations. |

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# SUPPLEMENTARY MATERIAL

## SUPPLEMENTARY MATERIAL CHAPTER 1

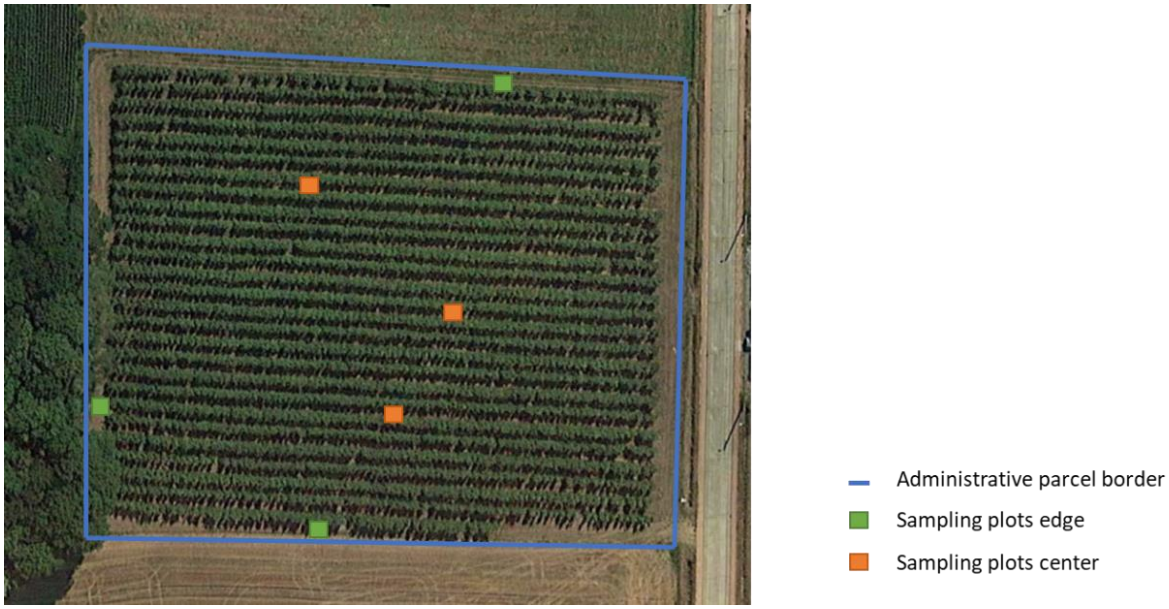



**Figure S1.1.** Example of a study orchard with indication of the six sampling plots. Sampling plots were established at random, with the edge plots containing the outer crop row and the grass strip between the outer crop row and the administrative field border. Field borders of both orchards and semi-natural references varied in complexity, ranging from relatively simple borders with minimal vegetation and no clear structural elements to complex borders with diverse vegetation cover and structural elements like wide verges or ditches, hedges, hedgerows, forest edges… The center plots contained a crop row and grass strip in the center of the orchard, situated at least 10 m from the outer tree rows. All sampling plots were situated at least 10 m from one another.

**Table S1.1.** Example of products used in IPM apple orchards in Flanders based on the guidelines for farmers (PCFruit vzw, 2022). The table lists different possibilities in commonly applied crop protection schemes, meaning that only a selection will be used by the farmers. Application and dosage depend on the presence and severity of pests/fungi/herbs and varies widely between individual orchards.

| Period of application | Type | | | |
|---|---|---|---|---|
| | **Insects/mites** | **Fungicides** | **Fertilizer** | **Herbicides** |
| **Before swollen bud** | | Copper hydroxide<br>Delan | Max. 125 E active N/ha<br>Max. 45 - 85 E $P_2O_5$/ha<br>Can be entirely from synthetic fertilizers | Isoxaben |
| **Bud burst until pink bud** | Gazelle<br>OR Teppeki<br>OR Sivanto Prime<br>OR Primor + Trend/Vivolt<br>Oviphyt<br>OR Vernotex<br>OR Promanal HP<br>< 15 °C: Steward<br>Nissorun SC | Syllit 544 PRO<br>Sulfur<br>Delan Pro<br>OR Delan (+ Soriale)<br>OR Captan (+ Soriale)<br>Faban<br>< 15 °C: Captan + Scala<br>OR Captan + Chorus<br>> 15 °C: Captan + Geyser OR Difol<br>Luna Privilege OR Sercadis | Urea<br>Mg-nitrate<br>Ammonia nitrate<br>Calcium nitrate | Glyfosate |
| **During bloom** | Mimic<br>Shirudo | Luna experience<br>OR Sercadis<br>Topaz | Boron preparation | |
| **After bloom** | Movento<br>Teppeki<br>OR Gazelle<br>OR Pirimor + Trend/Vivolt<br>Steward<br>Insegar<br>OR Exirel<br>OR Minecto One<br>Kanemite<br>Pheromone disruption | Topaz<br>Nimrod<br>Captan<br>OR Delan Pro<br>Captan + Geyser<br>OR Delan + Geyser<br>OR Faban<br>Candit<br>OR Flint + Captan<br>OR Luna care | Boron preparation + Mg nitrate OR Mg sulfate<br>Mn or Mn nitrate + Zn<br>Triplesuperfosfate | Glyfosate<br>Fluazifop-p-butyl<br>Propaquizafop<br>Chloortoluron<br>Pendimethalin<br>Diflufenican |
| **Half July until end of shoot growth** | Movento<br>Primor + Trend/Vivolt<br>Steward<br>Coragen<br>OR Exirel<br>OR Minecto One<br>Siltac SF/Stix<br>OR Kanemite<br>Pheromone disruption | Captan (+ Soriale)<br>Nimrod<br>Nissodium<br>Topaz | Calcium nitrate OR chloride<br>Mn OR Mn nitrate<br>Landamine OR MKP<br>Color tect<br>Phosphorus-calcium foliar feed<br>OR MAP | |
| **Summer** | Delegate<br>OR Affirm<br>OR virus preparation<br>OR Imidan<br>*Bacilus thuringensis*<br>Pheromone disruption | Bellis<br>Geoxe<br>OR Captan<br>OR Switch<br>OR Pomax | | MCPA<br>MCPA + MCPP-p + DP-p (growth enhancers) |
| **After harvest** | Pirimor + Trend/Vivolt | Penbotec (+Funds)<br>OR Deccopyr<br>Captan<br>Copper hydroxide | Urea<br>Lime | Propyzamide |

**Table S1.2**. Example of products used in organic apple orchards in Flanders based on the guidelines for farmers (PCFruit vzw, 2022). The table lists different possibilities in commonly applied crop protection schemes, meaning that only a selection will be used by the farmers. Application and dosage depend on the presence and severity of pests/fungi and varies widely between individual orchards. In organic orchards weeds are managed mechanically, so no herbicides are used.

| **Period of application** | **Type** | | |
|---|---|---|---|
| | **Insects/mites** | **Fungicides** | **Fertilizer** |
| **Before swollen bud** | Mineral oil | Copper | Bloedmeel<br>Biomix<br>Kieseriet |
| **Bud burst until pink bud** | Mineral oil<br>Xentari<br>Natria-antisect<br>Spruzit<br>Tracer<br>Eradicoat | Copper<br>Sulfur<br>Lime sulfur<br>Karma (vitisan)<br>Vacciplant | $MgSO_4$<br>Solubor |
| **During bloom** | Xentari<br>Neemazal | Karma (vitisan) | |
| **After bloom** | Pheromone disruption<br>Xentari<br>Natria-antisect<br>Quassia<br>Eradicoat<br>Spruzit<br>Tracer<br>RAK 3-4 | Karma (vitisan)<br>Copper<br>Sulfur<br>Lime sulfur<br>Vacciplant | Mangaspor<br>Zink Ultra<br>$CaCl_2$ |
| **Half July until end of shoot growth** | Pheromone disruption<br>Xentari<br>Natria-antisect<br>Eradicoat<br>Spruzit<br>Tracer | Karma (vitisan)<br>Vacciplant | Mangaspor<br>$CaCl_2$<br>$MgSO_4$ |
| **Summer** | Pheromone disruption<br>Xentari<br>Natria-antisect<br>Eradicoat<br>Spruzit<br>Tracer<br>Folisec | Karma (vitisan)<br>Boni Protect<br>Vacciplant | |
| **After harvest** | | WWB | |

**Table S1.3.** Description of the land use classes used to classify the landscape surrounding the sampling plots, based on land cover data from the Biological Valuation map and the Flemish agricultural land use parcels.

| Land use class | Description |
|---|---|
| Arable land (AL) | Land under temporary agricultural crops, e.g. potatoes, grains, seeds, legumes, vegetables, herbs, corn, fodder crops, hemp, flax, sugar beets… |
| Agricultural grassland (AG) | Land area that is primarily dominated by grasses and used for agricultural farming (mostly for feeding livestock). |
| Orchards (OR) | Trees and shrubs that are used for food production (fruits and nuts). Within the study region this mostly concerns cherry, apple and pear orchards. |
| Herbaceous semi-natural habitat (SNH) | Semi-natural habitat concerns the part of the land area in which flora and fauna have spontaneously established, but have been influenced by human intervention (real natural habitats without human intervention are not present in the study area). Herbaceous semi-natural habitat refers to semi-natural habitat in which the vegetation is dominated by vascular plants without persistent woody stems aboveground, e.g. grasslands (excluding agricultural grasslands), heathlands, swamps, moors, fens, bogs, linear vegetation at plot edges, ditches and verges… |
| Wooded semi-natural habitat (SNW) | Semi-natural habitat concerns the part of the land area in which flora and fauna have spontaneously established, but have been influenced by human intervention (real natural habitats without human intervention are not present in the study area). Wooded semi-natural habitat refers to semi-natural habitat in which the vegetation is dominated by vascular plants with persistent woody stems aboveground, e.g. different types of forests (mesophilic-, valley-, swamp-, peat-, ruderal- …), different types of tree plantations (coniferous-, poplar-…), tree rows, hedgerows, hedges… |
| Urban areas (U) | Land area dedicated to human settlement and associated infrastructure, e.g. agricultural infrastructure, all types of buildings, recreational area (sport fields, camp sites, parks, playgrounds…), industrial zones, roads and railways… |
| Other (OT) | All land areas not included in any of the other land use classes, e.g. dumps, quarries, rivers, stagnant water (ponds, lakes, pools… ) … |

# SUPPLEMENTARY MATERIAL CHAPTER 2

**Methods S2.1.** Diversity indices vegetation cover.

Diversity indices of the vegetation cover and percentage of bare soil were calculated based on data from an parallel study at the study sites. At each sampling plot, vegetation surveys were conducted within 1x1 m quadrats using the method of Braun-Blanquet (1932). Quadrats were placed both in the drive and the crop rows for the orchards, and in the grassland for the semi-natural grasslands. For each quadrant a species list was constructed and the relative percentage cover of each species was estimated to serve as a proxy for species abundance. This data was then used to calculate Hill numbers for species richness (S_Plant), shannon entropy (H_Plant) and inverse Simpson index (IS_Plant) using the function 'hill_taxa' from r package hillR (Li, 2018).

**Methods S2.2.** Diversity indices soil microbiome.

Several covariates relating to the soil microbiome were calculated based on data from a parallel study at the study sites, and were included in the analysis of the biological soil health indicators. At each 2-$m^2$ sampling plot (n=180), five top soil samples were taken with a 2-cm diameter auger, thoroughly mixed and stored at -20 °C. Next, genomic DNA was extracted from 250 mg of soil using the soil DNA Isolation Plus Kit (Norgen Biotek Crop., Thorold, ON, Canada). The DNA extracts were diluted 10 times before PCR amplification. Fungal communities were profiled through PCR amplification targeting the ITS2 region of the rRNA gene using the sample-specific barcode-labeled versions of the primers ITS86F and ITS4 (Kozich et al., 2013; Waud et al., 2014). Bacterial communities were characterized targeting the 515F/806R 16S rRNA primer pair (Walters et al., 2015). PCR was performed in a 25 µl volume, containing 0.25 mM of each dNTP, 0.5 µM of each primer, 1× HiFi Buffer, 1 U ALLin HS Red Taq Mastermix (HighQu, Kraichtal, Germany) and 1 µl genomic DNA. DNA samples were denatured at 95 °C for 2 min, followed by 35 cycles of 15 s at 95 °C, 15 s at 60 °C and 15 s at 72 °C, and finally 3min at 72 °C. Amplicons were purified using the Agencourt AMPure XP kit (Beckman Coulter Life Sciences, Indianapolis, IN, USA). Next, purified double-stranded DNA (dsDNA) amplicons were quantified using the Quant-iT PicoGreen dsDNA Assay Kit and Qubit fluorometer (Invitrogen), and pooled in equimolar quantities in three amplicon libraries. These amplicon libraries were loaded on an agarose gel and the amplicon of the expected size was excised and purified using the QIAquick Gel Extraction Kit (Qiagen). After dilution to 2 nM, the amplicons were sequenced at the Genomics Core UZ Leuven on an Illumina Miseq platform using

2 × 250 paired end Illumina chemistry with v2 500 cycle reagent kit (Illumina, San Diego, CA, USA).The resulting sequences from the Illumina run were clustered into operational taxonomical units (OTUs) following the recommended pipeline in USEARCH (v. 11) (Edgar, 2013). Paired-end reads were merged to form consensus sequences, followed by quality filtering with a maximum expected error of 0.5 for the individual sequences. Next, sequences were dereplicated and sorted by abundance. Singletons were removed before clustering as this has been shown to improve the accuracy of diversity estimates (Brown et al., 2015). Sequences were clustered into OTUs defined at 97% sequence similarity using the Uparse algorithm in Usearch, during which chimeric sequences were also removed (Edgar, 2013). To prevent bias due to differences in sequencing depth, reads were randomly resampled from each sample to an equal number of reads. The resulting OTUs for both bacteria and fungi were then used to calculate Hill numbers for species richness (S_Bac and S_Fun), shannon entropy (H_Bac and H_Fun) and inverse Simpson index (IS_Bac and IS_Fun) using the function 'hill_taxa' from r package hillR (Li, 2018).

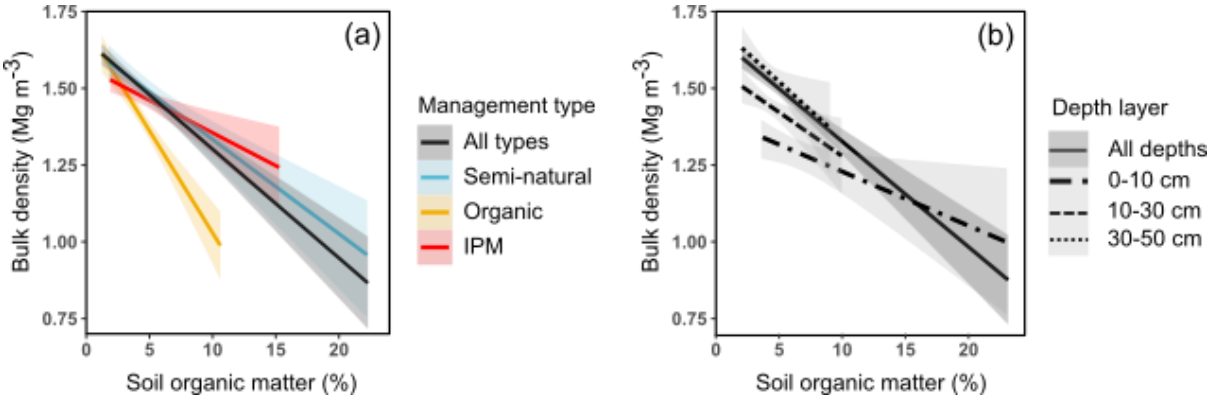



**Figure S2.1.** Relationship between soil bulk density and soil organic matter content for a) the different management types and b) the different depth layers.

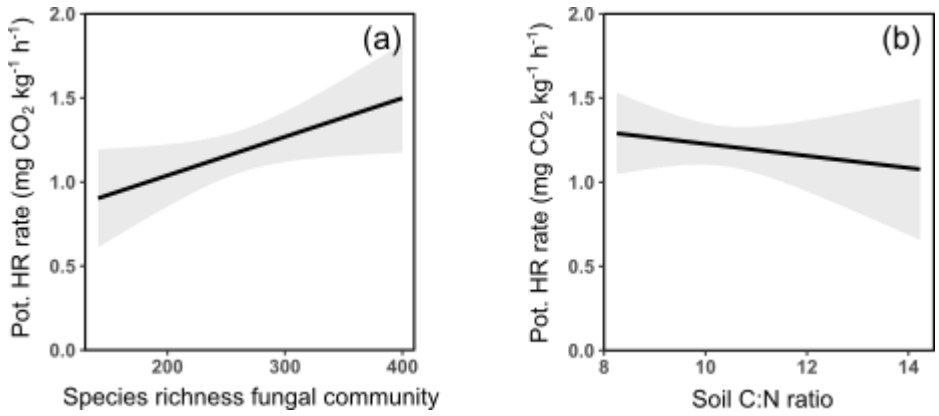



**Figure S2.2.** Relationship between potential heterotrophic respiration rate and a) species richness of the fungal community and b) soil C:N ratio.

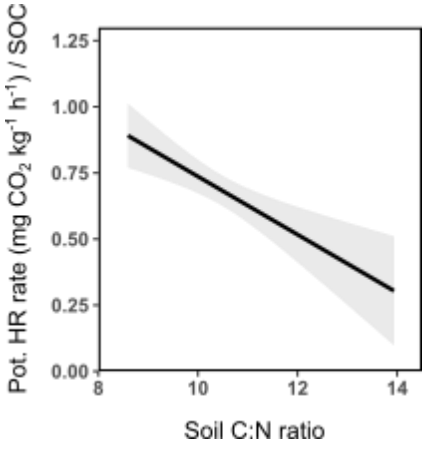



**Figure S2.3**. Relationship between potential heterotrophic respiration rate divided by soil organic carbon content (SOC) and soil C:N ratio.

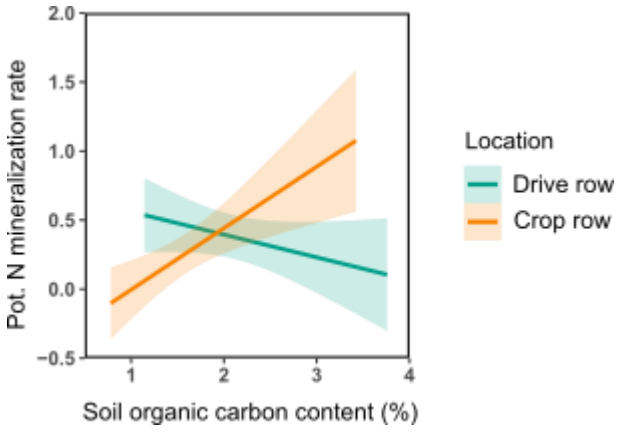



**Figure S2.4.** Relationship between potential N mineralization rate and soil organic carbon content (SOC) for the drive rows and crop rows.

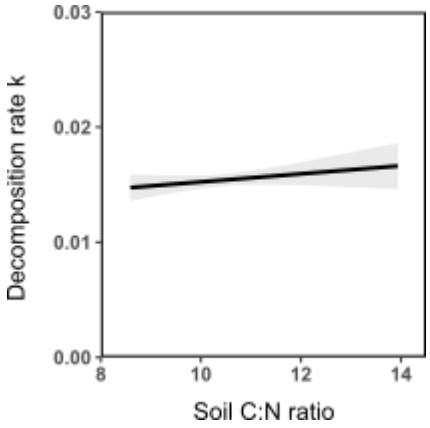



**Figure S2.5.** Relationship between decomposition rate k, as measured by the tea bag method, and soil C:N ratio.

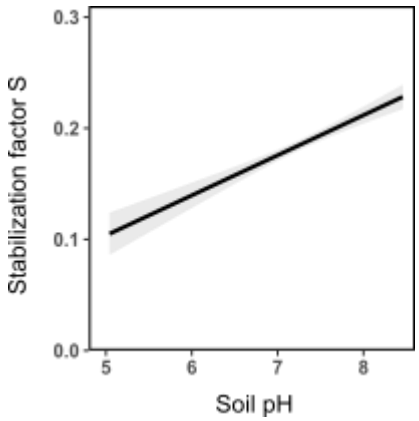



**Figure S2.6.** Relationship between stabilization factor S, as measured by the tea bag method, and soil pH.

**Table S2.1.** Results of the final linear mixed-effects models for potential heterotrophic respiration rate divided by soil organic carbon (SOC) content, showing marginal ($R_m^2$) and conditional ($R_c^2$) $R^2$-values. Test statistic (F) and semi-partial $R_\beta^2$ are given for each retained explanatory variable after model reduction. C = total organic cabon, N = total nitrogen, S_Fun = richness fungi, IS_Fun = inverse Simpson index fungi, IS_Bac = inverse Simpson index bacteria, IS_Plant = inverse Simpson index plants. *$P$ < 0.05, **$P$ < 0.01, ***$P$ < 0.001.

| Soil biological indicator | Pot. heterotrophic resp. / SOC $R_m^2$= 0.564 ; $R_c^2$ = 0.722 | |
|---|---|---|
| | *F* | $R_\beta^2$ |
| Management | 1.6 | 0.123 |
| Location | 8.3** | 0.195 |
| pH | - | - |
| C | - | - |
| C:N | 22.2*** | 0.277 |
| S_Fun | - | - |
| IS_Fun | - | - |
| IS_Bac | 1.4 | 0.119 |
| IS_Plant | - | - |
| Management x Location | 2.0 | 0.118 |
| Management x S_Fun | - | - |
| Location x C | - | - |
| Location x N | 3.3 | 0.066 |
| Location x IS_Plant | - | - |

**Methods S3.1.** Metabolic model for the calculation of predator community energy use

Predator energy use, integrating predator abundance, body mass and metabolic rate, is a key trait in predator-prey dynamics and has recently been adopted for the assessment of biological pest control potential (Happe et al., 2019; Perović et al., 2018). Predator community energy use was calculated for each sampling plot separately, using the phylogenetic metabolic model of Ehnes et al. (2011), adapted by Happe et al. (2019) to account for the entire community:

$$\ln C = \sum_{f=1}^{f} \left[ \left( \ln i_f + a_f \ln M_f - E_f \left( \frac{1}{kT} \right) \right) x \, A_f \right]$$

with $C$ = predator community energy use (J $h^{-1}$), $M_f$ = average dry mass (mg) of predator family $f$, $k$ = Boltzmann's constant (8.62 x $10^{-5}$ eV $K^{-1}$), $T$ = average local temperature in Kelvin and $A_f$ = total abundance of predator family $f$. Parameters $i_f$, $a_f$ and $E_f$ are the taxon-specific normalization factor, allometric exponent and activation energy, respectively (see Table 2 in Ehnes et al. (2011)). Average dry mass (mg) of each family was calculated separately for each sampling plot by drying all specimen at 50 °C for at least 48 h, weighting them together on an analytic balance (0.01 mg) and dividing the total weight by the number of specimen. When size differences between specimen of the same family were big (e.g. between larval and adult stages), the specimen were sorted into different morphotypes and energy use was calculated separately for each morphotype.

**Methods S3.2.** Preparation of sentinel egg cards

To assess the predation potential of the natural enemy community, sentinel prey cards with eggs of codling moth were made and exposed to the predators for four days (Lövei & Ferrante, 2017). Eggs were obtained from a laboratory strain of *C. pomonella* (Andermatt Group AG, Switzerland) by placing egg laying sheets in plastic jars with a male-female pair of moths, and allowing the females to lay eggs for 36 h. Egg laying sheets were fixed on double sided tape and cut into smaller cards of approximately 2 x 2 cm containing on average 10 (+/- 4) eggs. Within 24 h, these cards were sterilized under an UV lamp (30 W, 5 min) and taken to the field where they were stuck to the abaxial side of leaves to avoid desiccation.

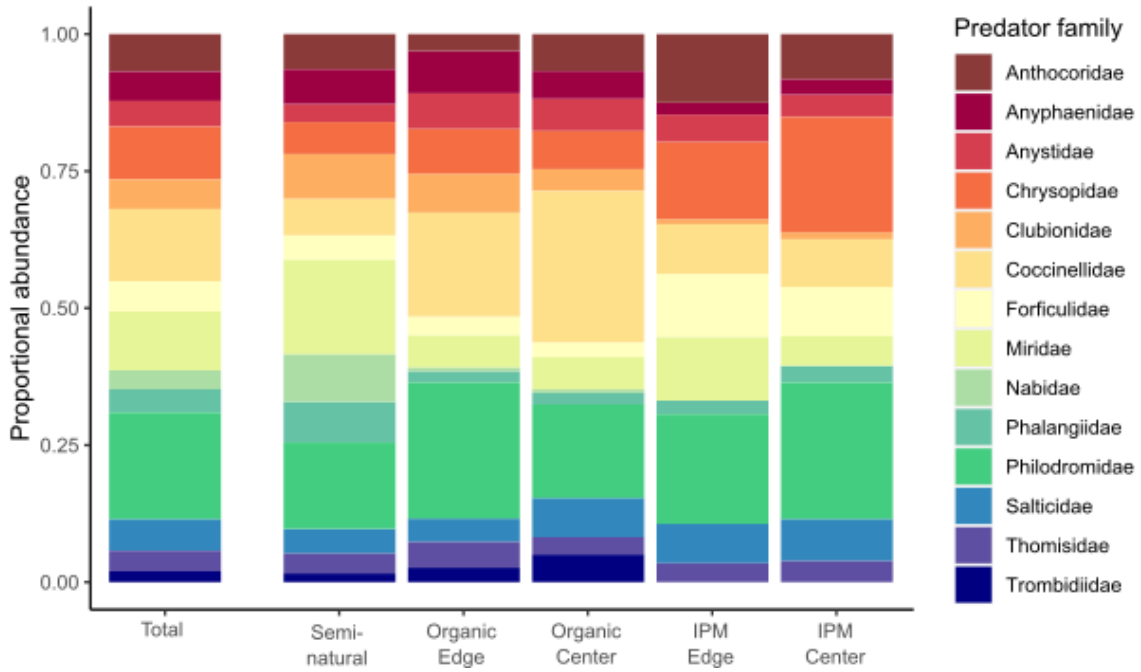



**Figure S3.1.** Proportional abundance of each predator family per management type (Organic orchards, Integrated Pest Management orchards and semi-natural references) and location of the sampling plots (center vs. edge of the orchards).

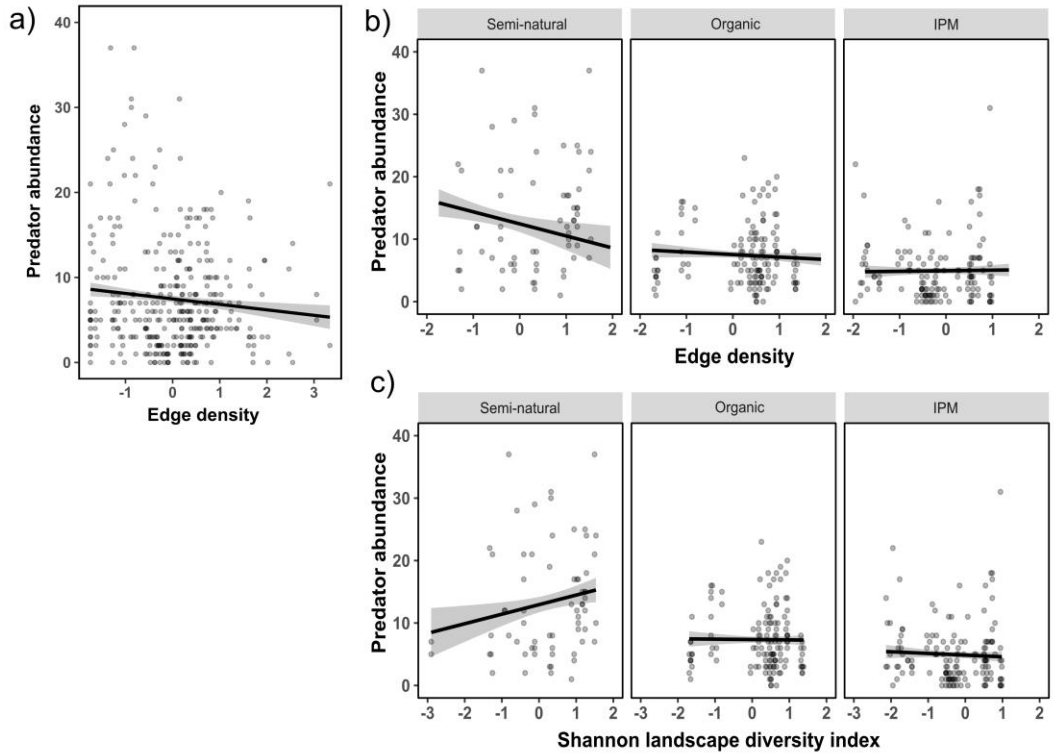



**Figure S3.2.** Relationship between predator abundance and (a) landscape edge density and the interactions between management and (b) landscape edge density and (c) Shannon landscape diversity index. Landscape variables are all standardized. Corresponding GLMM statistics are shown in Table S3.7a-b.

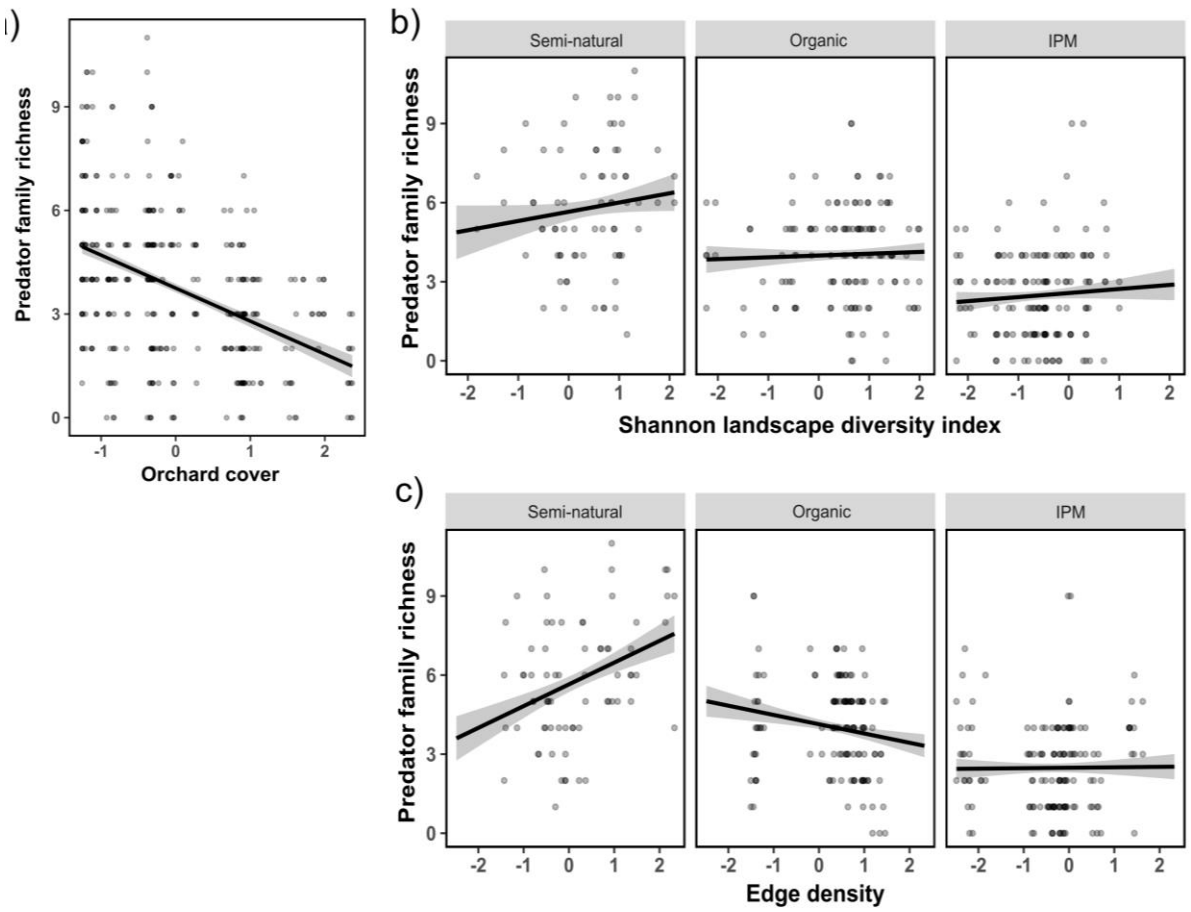



**Figure S3.3.** Relationship between predator family richness and (a) landscape orchard cover and the interactions between management and (b) Shannon landscape diversity index and (c) landscape edge density. Landscape variables are all standardized. Corresponding GLMM statistics are shown in Table S3.7a-b.

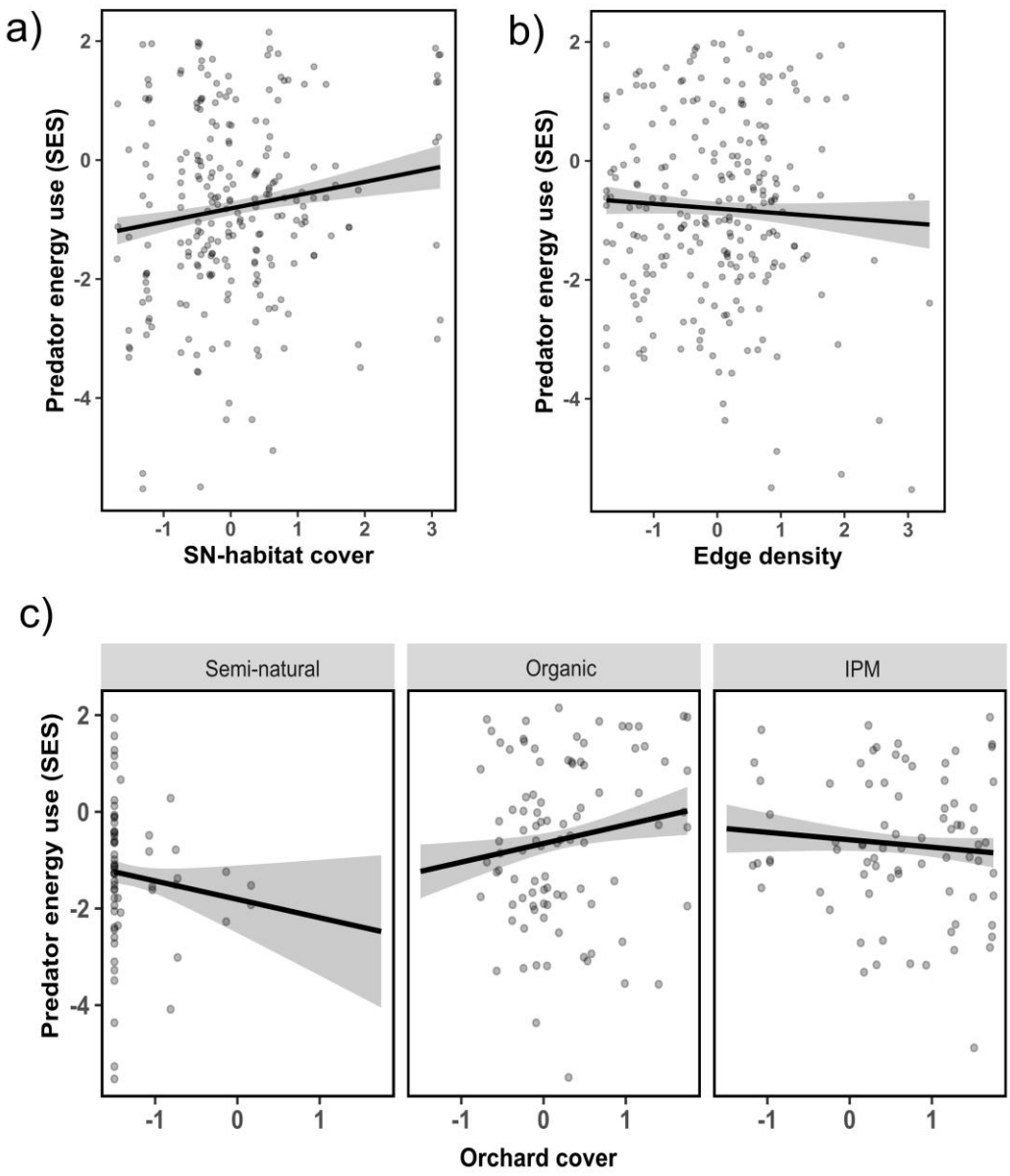



**Figure S3.4.** Relationship between the standardized effect size (SES) of predator energy use and (a) semi-natural habitat cover in the landscape, (b) landscape edge density and (c) the interaction between management and landscape orchard cover. Landscape variables are all standardized. Corresponding GLMM statistics are shown in Table S3.7a-b.

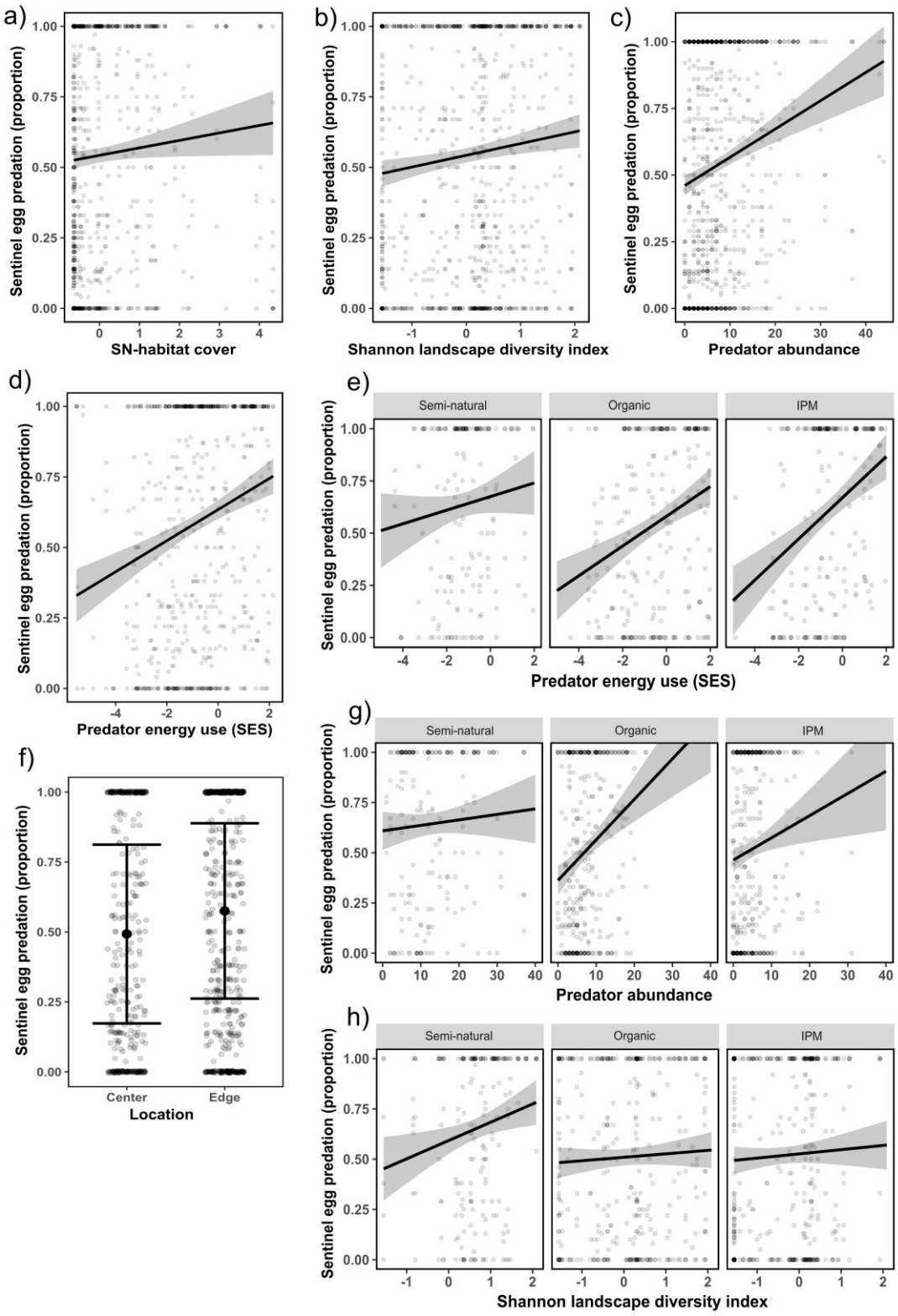



**Figure S3.5.** Relationship between sentinel egg predation and (a) semi-natural habitat cover in the landscape, (b) Shannon landscape diversity index, (c) predator abundance, (d) standardized effect size (SES) of predator energy use, (e) the interaction between management and predator energy use, (f) location within the orchard and the interactions between management and (g) predator abundance and (h) Shannon landscape diversity index. All explanatory variables were standardized (except location). Corresponding GLMM statistics are shown in Table S3.9a-b.

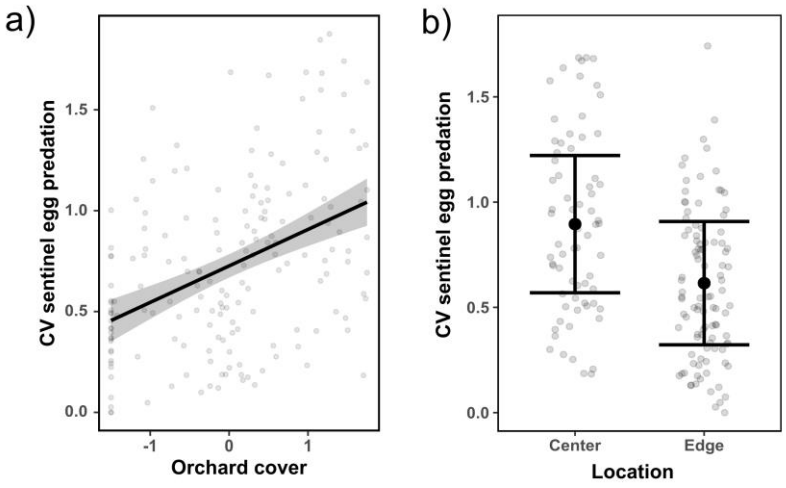



**Figure S3.6.** Relationship between the coefficient of variation (CV) of sentinel egg predation and (a) landscape orchard cover and (b) location within the orchard. All explanatory variables were standardized (except location). Corresponding GLMM statistics are shown in Table S3.9a-b.

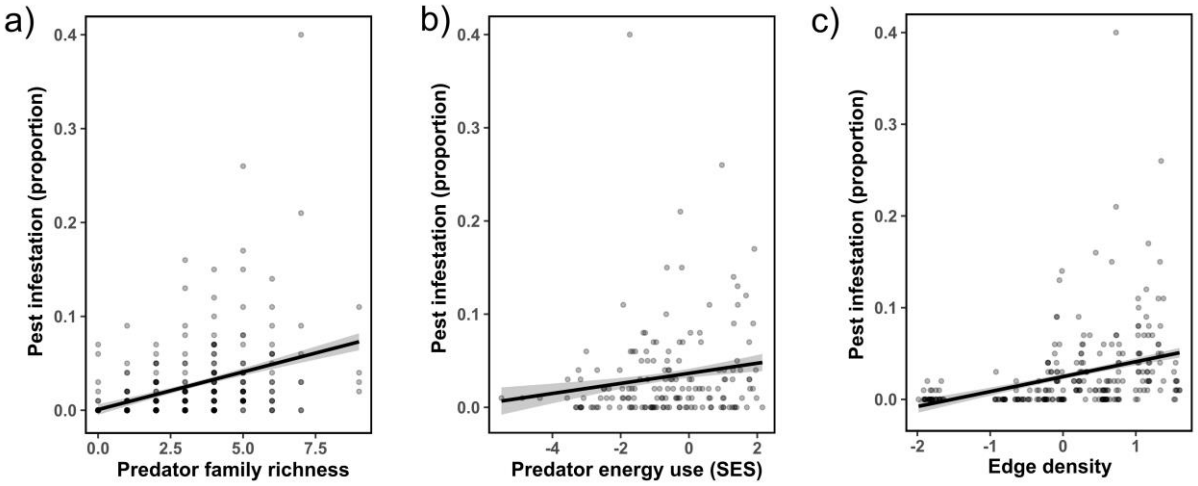



**Figure S3.7.** Relationship between pest infestation and (a) predator family richness, (b) standardized effect size (SES) of predator energy use and (c) landscape edge density. All explanatory variables were standardized. Corresponding GLMM statistics are shown in Table S3.9a-b.

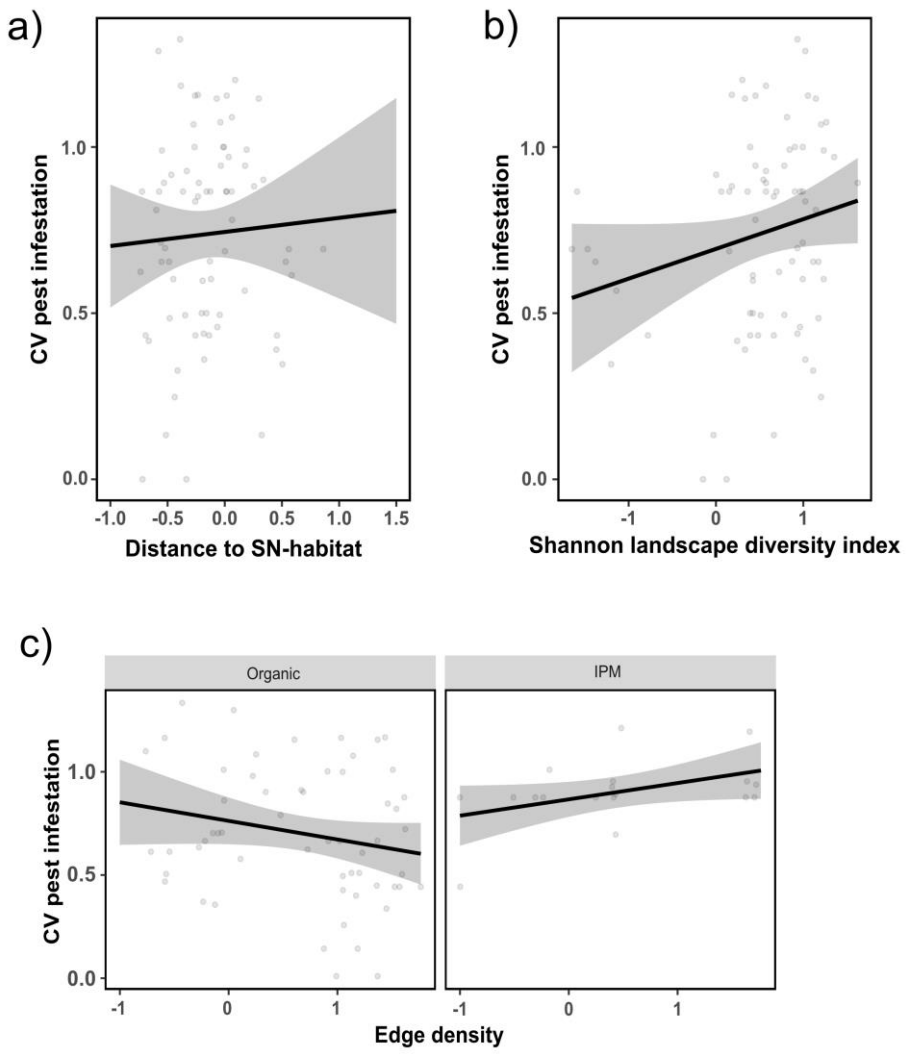



**Figure S3.8.** Relationship between the coefficient of variation (CV) of pest infestation and (a) distance to semi-natural habitat, (b) Shannon landscape diversity index and (c) the interaction between management and landscape edge density. All explanatory variables were standardized. Corresponding GLMM statistics are shown in Table S3.9a-b.

**Table S3.1.** Overview of all landscape metrics for each of the study sites, calculated at a spatial scale of 1000 m. The last letter of the site name indicates the respective management (N = semi-natural reference, O = organic orchard and C = IPM orchard). AG = agricultural grassland cover, AL = arable land cover, OR = orchard cover, OT = cover of other land uses, U = urban land cover, SN = semi-natural habitat cover, DSN = distance to nearest semi-natural habitat, PR = patch richness, SHDI = Shannon landscape diversity index, SHEI = Shannon landscape evenness index, ED = landscape edge density, NP = number of patches, MPAR = mean perimeter to area ratio.

| Site | Longitude | Latitude | AG | AL | OR | OT | U | SNH | DSNH | PR | SHDI | SHEI | ED | NP | MPAR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 27N | 4.7781528 | 50.91272 | 11.85 | 21.4 | 12 | 0 | 21.89 | 32.87 | 0 | 6 | 1.55 | 0.86 | 220.5 | 504 | 1.88 |
| 25N | 4.8584759 | 50.8953 | 15.79 | 48.11 | 0.92 | 0.32 | 10.35 | 24.51 | 0 | 7 | 0.74 | 0.75 | 295.43 | 619 | 1.99 |
| 26N | 4.91728 | 50.88512 | 11.71 | 36.47 | 17.08 | 2.64 | 14.85 | 17.26 | 0 | 7 | 1.68 | 0.89 | 266.31 | 523 | 1.72 |
| 14N | 4.5370579 | 50.92553 | 10.6 | 32.26 | 3.78 | 1.4 | 38.53 | 13.42 | 0 | 7 | 1.25 | 0.81 | 203.14 | 291 | 1.48 |
| 30N | 4.2121653 | 50.95811 | 17.87 | 51.64 | 0.09 | 0 | 24.11 | 6.28 | 0 | 6 | 1.45 | 0.68 | 205 | 326 | 1.88 |
| 24N | 5.4063151 | 50.78372 | 18.37 | 33.53 | 13.68 | 1.08 | 15.89 | 17.45 | 0 | 7 | 1.72 | 0.88 | 197.54 | 351 | 1.65 |
| 9N | 4.519408 | 50.93599 | 10.67 | 20.16 | 7.18 | 1.47 | 23.14 | 37.38 | 0 | 7 | 1.45 | 0.8 | 121.88 | 170 | 1.91 |
| 7N | 4.8511743 | 50.82234 | 4.46 | 72.92 | 7.68 | 0 | 6.64 | 8.4 | 0 | 6 | 1.21 | 0.46 | 156.82 | 288 | 2.31 |
| 2N | 5.4495739 | 50.80154 | 17.99 | 36.14 | 12.54 | 0.24 | 13.53 | 19.57 | 0 | 7 | 1.71 | 0.86 | 249.1 | 578 | 2.18 |
| 13N | 4.8603017 | 50.7994 | 15.92 | 59.76 | 1.88 | 0.05 | 5.54 | 16.85 | 0 | 7 | 1.42 | 0.64 | 204.82 | 474 | 2.24 |
| 4N | 4.86391 | 50.77304 | 17.89 | 58.47 | 0 | 3.39 | 8.16 | 12.09 | 0 | 6 | 1.19 | 0.61 | 255.6 | 388 | 2.09 |
| 18N | 5.2670589 | 50.76203 | 15.17 | 21.47 | 18.73 | 0.07 | 23.3 | 21.26 | 0 | 7 | 1.75 | 0.9 | 266.53 | 599 | 2.3 |
| 15O | 5.08162 | 50.92705 | 17.86 | 41.21 | 16.28 | 0 | 7.81 | 16.84 | 124.8 | 6 | 1.58 | 0.88 | 294.39 | 375 | 2.19 |
| 14O | 5.07678 | 50.93709 | 13.47 | 44.83 | 13.38 | 0.17 | 17.54 | 10.61 | 22.59 | 7 | 1.52 | 0.78 | 273.5 | 602 | 2.08 |
| 26O | 5.02499 | 50.93227 | 10.26 | 38.86 | 32.89 | 0.26 | 6.81 | 10.93 | 192.94 | 7 | 1.66 | 0.75 | 232.95 | 517 | 2.09 |
| 20O | 4.9459 | 50.92608 | 21.96 | 34.8 | 27.32 | 0.1 | 8.26 | 7.56 | 143.39 | 7 | 1.52 | 0.78 | 281.12 | 651 | 1.93 |
| 19O | 4.9351 | 50.92462 | 21.66 | 40.56 | 12.7 | 0.01 | 15.29 | 9.79 | 16.65 | 7 | 1.40 | 0.79 | 286.01 | 705 | 2.04 |
| 4O | 4.61912 | 50.8028 | 10.53 | 21.35 | 8.76 | 1.86 | 17.66 | 39.84 | 60.71 | 7 | 1.62 | 0.85 | 225.6 | 524 | 1.98 |
| 1O | 4.91326 | 50.91381 | 13.61 | 48.16 | 6.53 | 0 | 23.11 | 8.59 | 2.1 | 6 | 1.7 | 0.78 | 215.67 | 451 | 1.9 |
| 10O | 5.1393444 | 50.92353 | 21.25 | 35.34 | 17.35 | 0 | 12.91 | 13.15 | 57.56 | 6 | 1.04 | 0.9 | 242.68 | 594 | 2.41 |
| 9O | 5.12864 | 50.94523 | 16.19 | 18.46 | 14.88 | 0.6 | 31.17 | 18.7 | 84.34 | 7 | 1.52 | 0.87 | 260.24 | 533 | 2.37 |
| 2O | 5.19897 | 50.7625 | 3.11 | 58.94 | 31.07 | 0 | 3.51 | 3.38 | 183.06 | 6 | 1.54 | 0.58 | 175.01 | 278 | 2.35 |
| 12O | 5.34184 | 50.90284 | 17.44 | 14.41 | 8.62 | 0.21 | 43.72 | 15.59 | 111.98 | 7 | 1.42 | 0.73 | 262.95 | 660 | 2.3 |
| 15C | 5.16993 | 50.79227 | 7.19 | 43.37 | 31.13 | 0 | 10.7 | 7.61 | 69.65 | 6 | 1.38 | 0.77 | 142.94 | 499 | 1.72 |
| 23C | 5.23682 | 50.86415 | 9.44 | 22.16 | 35.65 | 0 | 16.94 | 15.81 | 71.65 | 6 | 1.52 | 0.83 | 185.11 | 372 | 2.21 |
| 17C | 5.1802 | 50.84799 | 15.02 | 32.61 | 28.14 | 0.14 | 12.04 | 12.05 | 49.29 | 7 | 1.56 | 0.83 | 143.99 | 481 | 2.06 |
| 24C | 4.90508 | 50.87777 | 12.23 | 44.3 | 12.97 | 1.74 | 13.12 | 15.63 | 1.62 | 7 | 1.41 | 0.83 | 270.88 | 545 | 1.99 |
| 5C | 5.15041 | 50.78554 | 10.68 | 58 | 17.67 | 0 | 6.49 | 7.16 | 641.69 | 6 | 1.17 | 0.63 | 145.25 | 487 | 1.72 |
| 25C | 4.89168 | 50.87483 | 14.6 | 42.47 | 5.15 | 0.14 | 25.85 | 11.79 | 90.85 | 7 | 1.2 | 0.76 | 252.12 | 570 | 2.19 |
| 9C | 5.14716 | 50.9336 | 7.86 | 38.47 | 12.61 | 0.06 | 26.47 | 14.54 | 56.1 | 7 | 1.56 | 0.78 | 225.8 | 475 | 1.94 |
| 11C | 5.14584 | 50.93979 | 11.56 | 28.41 | 5.07 | 0.08 | 35.79 | 19.1 | 99.17 | 7 | 1.49 | 0.8 | 219.85 | 503 | 2.07 |
| 19C | 5.23631 | 50.8459 | 14.38 | 12.58 | 41.39 | 0.28 | 19.1 | 12.26 | 24.72 | 7 | 1.61 | 0.73 | 252.7 | 483 | 1.93 |
| 4C | 5.23596 | 50.77905 | 12.89 | 31.91 | 20.74 | 0 | 12.09 | 22.37 | 160.12 | 6 | 1.61 | 0.65 | 190.42 | 576 | 2.28 |
| 2C | 5.23892 | 50.77182 | 4.89 | 44.76 | 30.22 | 0 | 9.55 | 10.58 | 324.9 | 6 | 1.12 | 0.67 | 202.1 | 335 | 2.28 |
| 12C | 5.23066 | 50.84962 | 15.41 | 11.92 | 31.26 | 0.03 | 21.14 | 20.25 | 90.45 | 7 | 1.48 | 0.8 | 236.59 | 402 | 1.83 |

**Table S3.2.** Correlation coefficients between all landscape variables, calculated at a spatial scale of 1000 m. AG = agricultural grassland cover, AL = arable land cover, OR = orchard cover, OT = cover of other land uses, U = urban land cover, SN = semi-natural habitat cover, DSN = distance to nearest semi-natural habitat, PR = patch richness, SHDI = Shannon landscape diversity index, SHEI = Shannon landscape evenness index, ED = landscape edge density, NP = number of patches, MPAR = mean perimeter to area ratio.

| | Agricultural grassland | Arable land | Orchards | Other land uses | Urban land | Semi-natural habitat | Distance to semi-natural habitat | Patch richness | Shannon diversity | Shannon evenness | Edge density | Number of patches | Mean perimeter to area ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AG | **1** | -0.22 | -0.24 | 0.03 | 0.11 | 0.03 | -0.18 | 0.46 | 0.13 | 0.40 | 0.57 | 0.51 | 0.03 |
| AL | -0.22 | **1** | -0.31 | 0.00 | -0.58 | -0.55 | 0.14 | -0.35 | -0.47 | -0.66 | -0.18 | -0.20 | 0.08 |
| OR | -0.24 | -0.31 | **1** | -0.31 | -0.32 | -0.25 | 0.29 | -0.03 | 0.34 | 0.07 | -0.15 | 0.00 | 0.07 |
| OT | 0.03 | 0.00 | -0.31 | **1** | 0.01 | 0.29 | -0.22 | 0.26 | 0.02 | 0.12 | 0.13 | -0.18 | -0.32 |
| U | 0.11 | -0.58 | -0.32 | 0.01 | **1** | 0.24 | -0.21 | 0.19 | 0.06 | 0.35 | 0.13 | 0.07 | -0.15 |
| SNH | 0.03 | -0.55 | -0.25 | 0.29 | 0.24 | **1** | -0.19 | 0.15 | 0.23 | 0.43 | 0.03 | 0.00 | -0.05 |
| DSNH | -0.18 | 0.14 | 0.29 | -0.22 | -0.21 | -0.19 | **1** | -0.15 | -0.17 | -0.28 | -0.21 | -0.05 | 0.09 |
| PR | 0.46 | -0.35 | -0.03 | 0.26 | 0.19 | 0.15 | -0.15 | **1** | 0.28 | 0.40 | 0.58 | 0.57 | -0.04 |
| SHDI | 0.13 | -0.47 | 0.34 | 0.02 | 0.06 | 0.23 | -0.17 | 0.28 | **1** | 0.44 | 0.06 | 0.12 | 0.07 |
| SHEI | 0.40 | -0.66 | 0.07 | 0.12 | 0.35 | 0.43 | -0.28 | 0.40 | 0.44 | **1** | 0.37 | 0.31 | -0.20 |
| ED | 0.57 | -0.18 | -0.15 | 0.13 | 0.13 | 0.03 | -0.21 | 0.58 | 0.06 | 0.37 | **1** | 0.62 | 0.17 |
| NP | 0.51 | -0.20 | 0.00 | -0.18 | 0.07 | 0.00 | -0.05 | 0.57 | 0.12 | 0.31 | 0.62 | **1** | 0.20 |
| MPAR | 0.03 | 0.08 | 0.07 | -0.32 | -0.15 | -0.05 | 0.09 | -0.04 | 0.07 | -0.20 | 0.17 | 0.20 | **1** |

**Table S3.3.** Results of the ANOVA analyses and post-hoc tests for differences in land use composition, compositional variables and configurational variables between management types. Test statistics (*F* for PERMANOVA and ANOVA and $X^2$ for Kruskal-Wallis) are given for the overall effect of management, as well as for the post-hoc tests (*F*-, *Z*-, or *T*- statistics). Post-hoc results for variables where no overall effect of management was detected, are displayed in grey. AG = agricultural grassland cover, AL = arable land cover, OR = orchard cover, OT = cover of other land uses, U = urban land cover, SN = semi-natural habitat cover, DSN = distance to nearest semi-natural habitat, PR = patch richness, SHDI = Shannon landscape diversity index, SHEI = Shannon landscape evenness index, ED = landscape edge density, NP = number of patches, MPAR = mean perimeter to area ratio.

| Explanatory var → Response var. ↓ | Overall effect | | Post-hoc test | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Management | | SN vs. Org | | SN vs. IPM | | Org vs. IPM | |
| Land use composition | | | | | | | | |
| (PERMANOVA) | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Composition | 1.701 | 0.130 | 1.190 | 0.825 | 3.501 | 0.084 | 0.454 | 0.718 |
| | | | | | | | | |
| Compositional variables | | | | | | | | |
| (Kruskal-Wallis) | $X^2$ | *P* | *Z* | *P* | *Z* | *P* | *Z* | *P* |
| SNH | 3.597 | 0.165 | 1.842 | 0.196 | -1.295 | 0.293 | -0.576 | 0.564 |
| (ANOVA) | *F* | *P* | *T* | *P* | *T* | *P* | *T* | *P* |
| AG | 2.211 | 0.126 | 1.189 | 0.807 | -2.678 | 0.331 | -3.867 | 0.119 |
| AL | 0.661 | 0.523 | -0.843 | 0.679 | -0.824 | 0.691 | 0.037 | 0.999 |
| OR | 7.233 | 0.003 | 1.962 | 0.138 | 3.537 | 0.001 | 2.076 | 0.058 |
| OT | 2.612 | 0.089 | -1.284 | 0.414 | -1.639 | 0.244 | -0.319 | 0.946 |
| U | 0.004 | 0.996 | -0.021 | 1.000 | 0.068 | 0.997 | 0.088 | 0.996 |
| | | | | | | | | |
| Configurational variables | | | | | | | | |
| (Kruskal-Wallis) | $X^2$ | *P* | *Z* | *P* | *Z* | *P* | *Z* | *P* |
| DSNH | 4.917 | 0.014 | 1.964 | 0.137 | 3.093 | 0.011 | 1.061 | 0.545 |
| (ANOVA) | *F* | *P* | *T* | *P* | *T* | *P* | *T* | *P* |
| PR | 0.167 | 0.847 | 0.571 | 0.836 | 0.357 | 0.932 | -0.222 | 0.973 |
| SHDI | 0.369 | 0.694 | 0.745 | 0.739 | -0.009 | 1.000 | -0.754 | 0.733 |
| SHEI | 0.340 | 0.714 | 0.654 | 0.791 | -0.118 | 0.992 | -0.770 | 0.724 |
| ED | 3.004 | 0.064 | 1.621 | 0.251 | -0.811 | 0.699 | -2.414 | 0.055 |
| NP | 2.426 | 0.105 | 2.202 | 0.086 | -1.142 | 0.496 | -1.380 | 0.057 |
| MPAR | 1.863 | 0.091 | 2.271 | 0.075 | -1.125 | 0.506 | -0.971 | 0.121 |
| | | | | | | | | |

**Table S3.4**. Overview of arthropod families collected during field sampling that qualify as possible predators of codling moth eggs based on literature survey and feeding strategy.

| ORDER | Family | Common name(s) | Feeding strategy |
|---|---|---|---|
| ARANEAE | Anyphaenidae | ghost spiders | chewing |
| ARANEAE | Clubionidae | sac spiders | chewing |
| ARANEAE | Philodromidae | running crab spiders | chewing |
| ARANEAE | Salticidae | jumping spiders | chewing |
| ARANEAE | Thomisidae | crab spiders | chewing |
| COLEOPTERA | Coccinellidae | ladybird beetles | chewing |
| DERMAPTERA | Forficulidae | earwigs | chewing |
| HETEROPTERA | Anthocoridae | minute pirate bugs / flower bugs | sucking |
| HETEROPTERA | Miridae | plant bugs / mirid bugs | sucking |
| HETEROPTERA | Nabidae | damsel bugs | sucking |
| NEUROPTERA | Chrysopidae | green lacewings / common lacewings | chewing |
| OPILIONES | Phalangiidae | harvestmen | chewing |
| TROMBIDIFORMES | Trombidiidae | red velvet mites | sucking |
| TROMBIDIFORMES | Anystidae | whirligig mites | sucking |

**Table S3.5.** Overview of the most predictive spatial scales for all landscape variables for each of the response variables. (Generalized) linear mixed models as well as the RDA model were constructed at each of the spatial scales with each of the landscape variables separately as fixed factor. These models (7 spatial scales x 4 landscape variables = 28 models for each response variable) were ranked based on AICc value and the scales of the models with the lowest AICc values are shown. Values between brackets represent the scales of models with ΔAICc < 2. The analysis was done for the models based on the entire dataset as well as for models included in the PSEM analysis which do not contain data of the semi-natural reference sites. Distance to nearest semi-natural habitat (DSNH) is independent of spatial scale and was therefore not included in the analysis.

| Explanatory variable → Response variable ↓ | Spatial scale proportion of orchards (m) | Spatial scale proportion of semi-natural habitat (m) | Spatial scale Shannon diversity index (m) | Spatial scale edge density (m) |
|---|---|---|---|---|
| Models including all data | | | | |
| Predator community composition | 1000 | 1500 | 1000 | 1000 |
| Predator abundance | 1000 | 1500 | 500 | 100 |
| Predator richness | 1000 | 500 | 100 (50) | 500 (250, 1000) |
| Predator energy use | 100 | 2000 | 50 | 50 |
| Sentinel egg predation | 50 (100) | 50 (100) | 50 (100) | 50 (100, 250, 500) |
| CV predation | 100 | 250 | 50 | 2000 |
| Yield damage | 1000 | 50 | 500 | 1000 (1500) |
| CV yield damage | 500 | 500 | 250 | 1500 |
| Models PSEM | | | | |
| Predator abundance | 1000 | 100 (50) | 1000 | 250 (50, 100) |
| Predator richness | 1000 (1500, 2000) | 100 (50) | 50 (100) | 1500 (2000) |
| Predator energy use | 1000 (1500, 2000) | 100 | 1500 (1000, 2000) | 250 |
| Sentinel egg predation | 100 (50) | 100 (50) | 50 (100) | 100 (50, 250, 500) |
| Yield damage | 1000 | 500 | 500 | 1500 (1000) |

**Table S3.6.** Results of the partial redundancy analysis (pRDA) on Hellinger-transformed predator community composition data. Degrees of freedom (Df), explained variance (var), test statistic (F) and adjusted p-value (P) are given for all retained variables after forward stepwise model selection. Adjusted $R^2$ values are given for the full model as well as for the unique and joint parts of variation explained by local and landscape variables as determined by variation partitioning. The bottom part of the table contains the results of the pairwise comparison between the management types (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references). Degrees of freedom (Df), sum of squares (SS), test statistic (F) and p-values are given for all pairwise comparisons.

| | *Df* | *var* | *F* | *Adj. P* | *Adj. $R^2$* |
|---|---|---|---|---|---|
| Full Model | 6 | 0.056 | 4.802 | 0.001 | 0.232 |
| Local variables | | | | | 0.153 |
| Management | 2 | 0.043 | 8.318 | 0.008 | |
| Location | - | - | - | - | |
| Landscape variables | | | | | 0.086 |
| Orchard cover (OR,%) | - | - | - | - | |
| Semi-natural habitat cover (SNH,%) | 1 | 0.050 | 3.545 | 0.008 | |
| Distance to semi-natural habitat (DSNH, m) | 1 | 0.062 | 2.389 | 0.039 | |
| Landscape Shannon diversity (SHDI) | 1 | 0.058 | 3.596 | 0.012 | |
| Landscape edge density (ED, m/ha) | 1 | 0.065 | 2.155 | 0.048 | |
| Joint variation | | | | | 0.012 |
| Residuals | | | | | 0.749 |

| Post-hoc Management | *Df* | *SS* | *F* | *P* |
|---|---|---|---|---|
| Org – SN == 0 | 5 | 0.053 | 3.576 | 0.001 |
| IPM – SN == 0 | 5 | 0.067 | 4.172 | 0.001 |
| IPM – Org == 0 | 5 | 0.054 | 4.277 | 0.001 |

**Table S3.7a.** Results of the final (generalized) linear mixed effects models for predator abundance, richness and standardized effect size (SES) of energy use, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic ($X^2$ for GLMMs and $F$ for LMMs), semi-partial $R^2_\beta$ and Variance Inflation Factor (*VIF*) are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Landscape variables were included at their most relevant spatial scale depending on the response variable (see Table S3.5). Test statistic (*Z*) and *P*-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Predator abundance $R^2_m$= 0.429 ; $R^2_c$ = 0.832 | | | Predator richness $R^2_m$= 0.413 ; $R^2_c$ = 0.522 | | | Predator energy use (SES) $R^2_m$= 0.062 ; $R^2_c$ = 0.802 | | |
|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* |
| Management | 6.148* | 0.028 | 1.693 | 17.853*** | 0.026 | 1.772 | 7.379* | 0.030 | 1.854 |
| Location | 2.353 | 0.004 | 1.576 | - | - | | - | - | |
| OR (%) | 9.217** | 0.006 | 2.096 | 9.319** | 0.012 | 2.026 | 0.020 | 0.001 | 2.097 |
| SNH (%) | 7.247** | 0.007 | 2.031 | 0.313 | 0.001 | 1.568 | 10.584** | 0.041 | 1.392 |
| DSNH (m) | 8.065** | 0.012 | 1.432 | 1.360 | 0.002 | 1.459 | 3.215 | 0.009 | 1.457 |
| SHDI | 0.039 | 0.002 | 2.285 | 0.302 | 0.004 | 1.993 | 3.662 | 0.007 | 1.813 |
| ED (m/ha) | 8.167** | 0.004 | 2.171 | 1.070 | 0.002 | 2.244 | 8.383** | 0.035 | 1.053 |
| MEM1 | - | - | | 10.701** | 0.032 | 1.548 | - | - | |
| MEM2 | - | - | | 4.433* | 0.017 | 1.692 | - | - | |
| MEM4 | 2.015 | 0.003 | 1.306 | 4.123* | 0.016 | 1.575 | - | - | |
| MEM5 | 4.709* | 0.025 | 1.419 | 20.026*** | 0.052 | 1.315 | - | - | |
| MEM6 | 0.132 | 0.001 | 1.277 | 5.633* | 0.017 | 1.316 | 2.414 | 0.025 | 1.171 |
| MEM9 | 0.738 | 0.005 | 1.191 | - | - | | - | - | |
| Management x Location | - | - | | - | - | | 3.852 | 0.010 | 1.728 |
| Management x OR | 2.880 | 0.001 | 1.942 | 2.618 | 0.003 | 1.955 | 4.336* | 0.017 | 2.012 |
| Management x SNH | 1.031 | 0.001 | 1.652 | - | - | | - | - | |
| Management x DSNH | 3.320 | 0.002 | 1.297 | - | - | | 0.625 | 0.001 | 1.299 |
| Management x SHDI | 7.260* | 0.010 | 1.712 | 7.191* | 0.011 | 1.519 | - | - | |
| Management x ED | 15.111*** | 0.012 | 1.576 | 8.237* | 0.022 | 1.633 | - | - | |

| Post-hoc Management | *Z* | *P* | *Z* | *P* | *Z* | *P* |
|---|---|---|---|---|---|---|
| Org – SN == 0 | -2.784 | 0.015* | -2.847 | 0.012* | 3.722 | 0.001*** |
| IPM – SN == 0 | -3.979 | <0.001*** | -5.192 | <0.001*** | 2.993 | 0.007** |
| IPM – Org == 0 | -2.385 | 0.041* | -3.384 | 0.002** | -1.445 | 0.307 |

**Table S3.7b.** Results of the sensitivity analysis for the (generalized) linear mixed effects models for predator abundance, richness and standardized effect size (SES) of energy use, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic ($X^2$ for GLMMs and $F$ for LMMs) and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Landscape variables were included at their most relevant spatial scale depending on the response variable (see Table S3.5). Test statistic ($Z$) and $P$-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Predator abundance $R^2_m$= 0.312 ; $R^2_c$ = 0.868 | | | Predator richness $R^2_m$= 0.343 ; $R^2_c$ = 0.483 | | | Predator energy use (SES) $R^2_m$= 0.072 ; $R^2_c$ = 0.751 | | |
|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* |
| Management | 8.071* | 0.017 | 1.932 | 25.492*** | 0.113 | 1.579 | 5.504** | 0.136 | 1.758 |
| Location | 2.638 | 0.003 | 1.165 | - | - | | - | - | |
| OR (%) | 5.076* | 0.008 | 2.003 | 4.199 | 0.032 | 1.880 | 0.003 | 0.003 | 2.037 |
| SNH (%) | 4.289* | 0.006 | 2.060 | 0.600 | 0.001 | 1.430 | 6.650** | 0.064 | 1.206 |
| DSNH (m) | 1.738 | 0.003 | 1.764 | 0.641 | 0.003 | 1.340 | 0.869 | 0.002 | 1.856 |
| SHDI | 0.040 | 0.001 | 1.991 | 1.387 | 0.010 | 1.779 | 1.238 | 0.004 | 1.841 |
| ED (m/ha) | 6.477* | 0.009 | 2.048 | 1.863 | 0.021 | 2.056 | 9.833** | 0.054 | 1.062 |
| Management x Location | - | - | | - | - | | 2.015 | 0.030 | 1.670 |
| Management x OR | 2.014 | 0.002 | 1.984 | 3.059 | 0.003 | 1.704 | 2.196 | 0.023 | 2.018 |
| Management x SNH | 0.091 | 0.001 | 1.578 | - | - | | - | - | |
| Management x DSNH | 0.706 | 0.001 | 1.665 | - | - | | 0.060 | 0.001 | 1.718 |
| Management x SHDI | 8.991* | 0.012 | 1.793 | 7.807* | 0.019 | 1.452 | - | - | |
| Management x ED | 23.386** | 0.050 | 1.697 | 11.444** | 0.046 | 1.564 | - | - | |

| Post-hoc Management | *Z* | *P* | *Z* | *P* | *Z* | *P* |
|---|---|---|---|---|---|---|
| Org – SN == 0 | -3.167 | 0.004** | -1.575 | 0.056 | 4.283 | <0.001*** |
| IPM – SN == 0 | -4.646 | <0.001*** | -3.348 | 0.002** | 3.309 | 0.002** |
| IPM – Org == 0 | -2.489 | 0.029* | -3.175 | 0.004** | -2.028 | 0.101 |

**Table S3.8.** Pairwise comparisons for all significant interaction terms between management and continuous explanatory variables in the (G)LMMs for predator abundance, family richness, energy use and sentinel egg predation reduction (OR = orchard cover, SHDI = Shannon landscape diversity index, ED = landscape edge density, SES = standardized effect size of energy use and IPM = Integrated Pest Management). Correlation coefficients and p-values are given for correlations between the response variable and continuous explanatory variables for each of the management types. Letters between brackets indicate significant differences between the levels of each interaction term.

| Response variable | Interaction term | Interaction term level | Correlation coefficient | P-value |
|---|---|---|---|---|
| Predator abundance | Management x SHDI | Semi-natural | 0.25 (a) | <0.001*** |
| | | Organic | -0.01 (b) | 0.810 |
| | | IPM | -0.05 (b) | 0.306 |
| | Management x ED | Semi-natural | -0.24 (a) | <0.001*** |
| | | Organic | -0.02 (b) | 0.310 |
| | | IPM | 0.01 (b) | 0.764 |
| Predator family richness | Management x SHDI | Semi-natural | 0.13 (a) | 0.044* |
| | | Organic | 0.04 (b) | 0.461 |
| | | IPM | 0.07 (b) | 0.157 |
| | Management x ED | Semi-natural | 0.35 (a) | <0.001*** |
| | | Organic | -0.13 (b) | 0.014* |
| | | IPM | 0.01 (c) | 0.830 |
| Predator energy use | Management x OR | Semi-natural | -0.11 (a) | 0.146 |
| | | Organic | 0.15 (b) | 0.012*** |
| | | IPM | -0.05 (ab) | 0.167 |
| Sentinel egg predation | Management x abundance | Semi-natural | 0.09 (a) | 0.169 |
| | | Organic | 0.24 (b) | <0.001*** |
| | | IPM | 0.13 (ab) | 0.009** |
| | Management x SES | Semi-natural | 0.05 (a) | 0.532 |
| | | Organic | 0.273 (b) | <0.001*** |
| | | IPM | 0.34 (b) | <0.001*** |
| | Management x SHDI | Semi-natural | 0.18 (a) | 0.010* |
| | | Organic | 0.04 (b) | 0.394 |
| | | IPM | 0.04 (b) | 0.373 |

**Table S3.9a.** Results of the final (generalized) linear mixed effects models for sentinel egg predation, pest infestation and their coefficients of variation (CV), showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic ($X^2$ for GLMMs and $F$ for LMMs) and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Landscape variables were included at their most relevant spatial scale depending on the response variable (see Table S3.5). Test statistic ($Z$) and $P$-values for post-hoc tests analyzing pairwise differences between management types (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references) are reported at the bottom of the table (except for pest infestation which was only quantified in organic and IPM orchards).

| Response variables → Explanatory variables ↓ | Sentinel egg predation $R^2_m$= 0.136 ; $R^2_c$ = 0.496 | | | CV Predation $R^2_m$= 0.341 ; $R^2_c$ = 0.376 | | | Pest infestation $R^2_m$= 0.647 ; $R^2_c$ = 0.951 | | | CV pest infestation $R^2_m$= 0.310 ; $R^2_c$ = 0.312 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* |
| Management [§] | 6.024* | 0.013 | 1.847 | 7.282* | 0.203 | 1.465 | 9.028** | 0.017 | 1.491 | 5.046* | 0.083 | 1.701 |
| Location | 5.464* | 0.008 | 1.611 | 7.135** | 0.048 | 1.103 | 3.044 | 0.006 | 2.371 | 2.650 | 0.039 | 1.035 |
| OR (%) | 0.008 | 0.001 | 1.939 | 7.308** | 0.157 | 1.577 | 20.937*** | 0.022 | 1.489 | 2.224 | 0.033 | 1.444 |
| SNH (%) | 4.744* | 0.009 | 2.176 | 0.008 | 0.005 | 1.709 | 30.008*** | 0.032 | 2.488 | 2.812 | 0.041 | 1.417 |
| DSNH (m) | 1.638 | 0.001 | 1.462 | 2.562 | 0.101 | 1.281 | 7.081* | 0.008 | 1.376 | 4.156* | 0.084 | 2.199 |
| SHDI | 5.075* | 0.009 | 2.389 | - | - | - | - | - | | 7.572** | 0.113 | 2.034 |
| ED (m/ha) | 0.616 | 0.001 | 2.317 | - | - | - | 27.022*** | 0.025 | 1.247 | 0.903 | 0.001 | 1.777 |
| Richness | 0.083 | 0.001 | 1.828 | - | - | - | 1.378 | 0.001 | 1.072 | - | - | - |
| Abundance | 5.582* | 0.008 | 1.789 | - | - | - | - | - | | - | - | - |
| Energy use (SES) | 4.737* | 0.005 | 1.531 | - | - | - | 17.520*** | 0.013 | 1.046 | - | - | - |
| Egg predation | - | - | | - | - | - | 1.672 | 0.002 | 1.049 | - | - | - |
| MEM1 | - | - | | 3.282 | 0.123 | 1.264 | - | - | | - | - | - |
| MEM2 | 2.069 | 0.001 | 1.196 | 8.580** | 0.316 | 1.398 | 0.303 | 0.001 | 1.348 | - | - | - |
| MEM4 | 0.260 | 0.001 | 1.353 | - | - | - | 3.328 | 0.002 | 1.221 | - | - | - |
| MEM6 | 3.348 | 0.002 | 1.295 | - | - | - | - | - | | - | - | - |
| MEM7 | 0.763 | 0.001 | 1.418 | - | - | - | - | - | | - | - | - |
| Mana x Location | 2.712 | 0.003 | 1.734 | - | - | - | 3.709 | 0.005 | 2.439 | - | - | - |
| Mana x OR | 1.828 | 0.002 | 1.942 | - | - | - | 1.490 | 0.001 | 1.326 | - | - | - |
| Mana x SNH | 3.929 | 0.003 | 1.288 | 4.602 | 0.158 | 1.378 | 2.337 | 0.007 | 2.532 | - | - | - |
| Mana x DSNH | - | - | - | - | - | - | - | - | | 1.810 | 0.027 | 2.358 |
| Mana x SHDI | 6.747* | 0.011 | 1.652 | - | - | - | 2.810 | 0.003 | 1.489 | - | - | - |
| Mana x ED | 2.055 | 0.004 | 2.075 | - | - | - | - | - | | 5.921* | 0.083 | 2.014 |
| Mana x Richness | 0.148 | 0.002 | 1.885 | - | - | - | - | - | | - | - | - |
| Mana x Abundance | 6.171* | 0.014 | 1.654 | - | - | - | - | - | | - | - | - |
| Mana x SES | 7.877* | 0.016 | 1.774 | - | - | - | - | - | | - | - | - |

| Post-hoc Management | Z | P | Z | P | Z | P | Z | P |
|---|---|---|---|---|---|---|---|---|
| Org – SN == 0 | -2.847 | 0.012* | 2.682 | 0.019* | - | - | - | - |
| IPM – SN == 0 | -2.631 | 0.023* | 5.264 | <0.001*** | - | - | - | - |
| IPM – Org == 0 | 0.276 | 0.959 | 2.762 | 0.016* | - | - | - | - |

[§] Models for pest infestation and CV pest infestation only contain data from the organic and IPM orchards

**Table S3.9b**. Results of the sensitivity analysis for the (generalized) linear mixed effects models for sentinel egg predation, pest infestation and their coefficients of variation (CV), showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic ($X^2$ for GLMMs and $F$ for LMMs) and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Landscape variables were included at their most relevant spatial scale depending on the response variable (see Table S3.5). Test statistic ($Z$) and $P$-values for post-hoc tests analyzing pairwise differences between management types (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references) are reported at the bottom of the table (except for pest infestation which was only quantified in organic and IPM orchards).

| Response variables → Explanatory variables ↓ | Sentinel egg predation $R^2_m$= 0.109 ; $R^2_c$ = 0.553 | | | CV Predation $R^2_m$= 0.262 ; $R^2_c$ = 0.324 | | | Pest infestation $R^2_m$= 0.462 ; $R^2_c$ = 0.560 | | | CV pest infestation $R^2_m$= 0.226 ; $R^2_c$ = 0.346 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* |
| Management [§] | 7.255* | 0.017 | 2.021 | 4.744* | 0.070 | 1.465 | 6.260* | 0.007 | 1.685 | 13.309** | 0.098 | 1.546 |
| Location | 2.003 | 0.002 | 1.977 | 5.063* | 0.092 | 1.103 | 0.025 | 0.001 | 1.911 | 1.591 | 0.017 | 1.031 |
| OR (%) | 0.903 | 0.001 | 1.924 | 4.090* | 0.082 | 1.577 | 8.836** | 0.018 | 1.553 | 1.955 | 0.033 | 1.499 |
| SNH (%) | 4.392* | 0.011 | 2.166 | 0.256 | 0.012 | 1.709 | 4.949* | 0.003 | 1.890 | 1.979 | 0.018 | 1.317 |
| DSNH (m) | 2.305 | 0.004 | 1.556 | 1.011 | 0.036 | 1.281 | 11.712** | 0.007 | 1.796 | 1.467 | 0.005 | 2.184 |
| SHDI | 2.668 | 0.003 | 2.279 | - | - | - | - | - | - | 3.856* | 0.038 | 1.849 |
| ED (m/ha) | 0.221 | 0.001 | 1.741 | - | - | - | 7.956** | 0.022 | 1.668 | 9.260** | 0.071 | 1.317 |
| Richness | 0.521 | 0.001 | 1.602 | - | - | - | 0.016 | 0.001 | 1.633 | - | - | - |
| Abundance | 4.248* | 0.008 | 1.578 | - | - | - | - | - | - | - | - | - |
| Energy use (SES) | 1.526 | 0.002 | 1.085 | - | - | - | 4.456* | 0.017 | 1.075 | - | - | - |
| Egg predation | - | - | | - | - | - | 1.279 | 0.001 | 1.150 | - | - | - |
| Mana x Location | 1.916 | 0.001 | 1.752 | - | - | - | 1.277 | 0.001 | 1.703 | - | - | - |
| Mana x OR | 0.341 | 0.001 | 1.955 | - | - | - | 0.230 | 0.001 | 1.230 | - | - | - |
| Mana x SNH | 2.147 | 0.002 | 2.142 | 1.211 | 0.021 | 1.378 | 2.690 | 0.002 | 2.203 | - | - | - |
| Mana x DSNH | - | - | - | - | - | - | - | - | - | 1.095 | 0.015 | 1.361 |
| Mana x SHDI | 2.232 | 0.008 | 1.579 | - | - | - | 0.871 | 0.001 | 1.404 | - | - | - |
| Mana x ED | 0.159 | 0.002 | 2.044 | - | - | - | - | - | | 1.013 | 0.024 | 2.141 |
| Mana x Richness | 0.381 | 0.001 | 1.831 | - | - | - | - | - | | - | - | - |
| Mana x Abundance | 3.958* | 0.014 | 1.514 | - | - | - | - | - | | - | - | - |
| Mana x SES | 3.655* | 0.011 | 1.648 | - | - | - | - | - | | - | - | - |

| Post-hoc Management | Z | P | Z | P | Z | P | Z | P |
|---|---|---|---|---|---|---|---|---|
| Org – SN == 0 | -3.362 | 0.002** | 1.634 | 0.079 | - | - | - | - |
| IPM – SN == 0 | -2.196 | 0.063 | 2.167 | 0.007** | - | - | - | - |
| IPM – Org == 0 | 0.145 | 0.426 | 1.834 | 0.046* | - | - | - | - |

[§] Models for pest infestation and CV pest infestation only contain data from the organic and IPM orchards

**Table S3.10.** Results of the initial (generalized) linear mixed effects models for the response variables included in PSEM analysis, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Models were exclusively fitted to the data of the organic and IPM orchards. Test statistic ($X^2$ for GLMMs and $F$ for LMMs) and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Landscape variables were included at their most relevant spatial scale depending on the response variable (see Table S3.5). To reduce the number of variables, only significant factors were entered in the PSEM model.

| Response variables → Explanatory variables ↓ | Predator abundance $R^2_m$= 0.291 ; $R^2_c$ = 0.716 | | | Predator richness $R^2_m$= 0.324 ; $R^2_c$ = 0.429 | | | Predator energy use $R^2_m$= 0.061 ; $R^2_c$ = 0.620 | | | Sentinel egg predation $R^2_m$= 0.085 ; $R^2_c$ = 0.318 | | | Pest infestation $R^2_m$= 0.647 ; $R^2_c$ = 0.951 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | *F* | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* | $X^2$ | $R^2_\beta$ | *VIF* |
| Management | 7.935* | 0.047 | 1.182 | 17.200*** | 0.130 | 1.300 | 4.712* | 0.025 | 1.243 | 4.953* | 0.008 | 1.086 | 9.028** | 0.017 | 1.727 |
| Location | 2.093 | 0.002 | 1.560 | 2.599 | 0.004 | 1.242 | 2.754 | 0.001 | 1.579 | 23.967*** | 0.015 | 1.613 | 3.044 | 0.006 | 1.026 |
| OR (%) | 12.596*** | 0.064 | 1.295 | 4.756* | 0.028 | 1.386 | - | - | - | 1.180 | 0.001 | 1.848 | 20.937*** | 0.022 | 2.047 |
| SNH (%) | 21.983*** | 0.077 | 1.081 | 6.384* | 0.014 | 1.228 | 20.343*** | 0.053 | 1.236 | 21.454*** | 0.012 | 1.444 | 30.008*** | 0.032 | 1.878 |
| DSNH (m) | 12.035*** | 0.059 | 1.142 | 6.750* | 0.020 | 1.287 | 6.221* | 0.089 | 1.247 | 0.304 | 0.001 | 1.346 | 7.081* | 0.008 | 1.922 |
| SHDI | 2.503 | 0.008 | 1.052 | 1.982 | 0.002 | 1.324 | 2.521 | 0.034 | 1.101 | 1.524 | 0.001 | 2.140 | - | - | - |
| ED (m/ha) | - | - | - | - | - | - | 7.750** | 0.107 | 1.068 | 11.596*** | 0.007 | 1.101 | 27.022*** | 0.025 | 1.835 |
| Richness | - | - | - | - | - | - | - | - | - | - | - | - | 1.378 | 0.001 | 1.628 |
| Abundance | - | - | - | - | - | - | - | - | - | 16.178*** | 0.009 | 1.082 | - | - | - |
| Energy use (SES) | - | - | - | - | - | - | - | - | - | 2.636 | 0.002 | 1.089 | 17.520*** | 0.013 | 1.321 |
| Egg predation | - | - | - | - | - | - | - | - | - | - | - | - | 1.672 | 0.002 | 1.160 |
| MEM2 | - | - | - | - | - | - | - | - | - | - | - | - | 0.303 | 0.001 | 1.242 |
| MEM4 | - | - | - | 0.166 | 0.001 | 1.135 | - | - | - | - | - | - | 3.328 | 0.002 | 1.659 |
| Management x Location | 3.309 | 0.007 | 1.560 | - | - | - | 2.257 | 0.018 | 1.601 | - | - | - | 3.709 | 0.005 | 2.099 |
| Management x ED | - | - | - | 2.321 | 0.003 | 1.108 | - | - | - | - | - | - | - | - | - |
| Management x OR | - | - | - | - | - | - | - | - | - | - | - | - | 1.490 | 0.001 | 1.545 |
| Management x SNH | - | - | - | - | - | - | - | - | - | - | - | - | 2.337 | 0.007 | 1.711 |
| Management x SHDI | - | - | - | - | - | - | - | - | - | - | - | - | 2.810 | 0.003 | 1.287 |
| | | | | | | | | | | | | | | | |

**Table S3.11.** Summary statistics of the piecewise structural equation model (PSEM) explaining the direct and indirect, predator-mediated effects of local and landscape factors on pest infestation as the final response variable. Each row represents a path in the PSEM for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fit was assessed using Fischer's C statistic and significant paths are shown in Figure 3.5.

| **Response variable** | **Predictor variable** | ***Estimate*** | ***SE*** | ***P*** |
|---|---|---|---|---|
| Predator abundance | Orchard cover | -0,289 | 0,089 | 0,001 |
| | SN-habitat cover | 0,062 | 0,020 | 0,002 |
| | Organic management (vs. IPM) | 0,224 | 0,092 | 0,015 |
| | Distance to SN-habitat | -0,082 | 0,015 | 0,025 |
| | Orchard edge (vs. center) | -0,035 | 0,024 | 0,056 |
| | Edge density | -0,081 | 0,052 | 0,122 |
| Predator richness | Organic management (vs. IPM) | 0,207 | 0,064 | 0,001 |
| | Orchard cover | -0,129 | 0,063 | 0,039 |
| | SN-habitat cover | 0,086 | 0,026 | 0,041 |
| | Orchard edge (vs. center) | -0,009 | 0,019 | 0,635 |
| | Distance to SN-habitat | 0,013 | 0,048 | 0,793 |
| Predator energy use | SN-habitat cover | 0,131 | 0,039 | <0,001 |
| | Edge density | 0,208 | 0,070 | 0,003 |
| | Distance to SN-habitat | 0,096 | 0,054 | 0,086 |
| | Organic management (vs. IPM) | 0,045 | 0,058 | 0,439 |
| | Orchard edge (vs. center) | -0,017 | 0,030 | 0,562 |
| Sentinel egg predation | Orchard edge (vs. center) | 0,186 | 0,034 | <0,001 |
| | SN-habitat cover | 0,271 | 0,051 | <0,001 |
| | Predator abundance | 0,140 | 0,010 | <0,001 |
| | Edge density | 0,254 | 0,073 | <0,001 |
| | Organic management (vs. IPM) | -0,238 | 0,123 | 0,052 |
| | Predator energy use | 0,083 | 0,050 | 0,098 |
| | Distance to SN-habitat | 0,015 | 0,087 | 0,860 |
| Pest infestation | Predator energy use | 0,290 | 0,050 | <0,001 |
| | SN-habitat cover | 0,916 | 0,174 | <0,001 |
| | Orchard edge (vs. center) | -0,139 | 0,029 | <0,001 |
| | Edge density | 0,686 | 0,148 | <0,001 |
| | Organic management (vs. IPM) | 0,595 | 0,222 | 0,007 |
| | Predator richness | 0,056 | 0,025 | 0,026 |
| | Orchard cover | -0,170 | 0,840 | 0,046 |
| | Distance to SN-habitat | 0,169 | 0,134 | 0,206 |
| | Predator abundance | -0,007 | 0,010 | 0,475 |

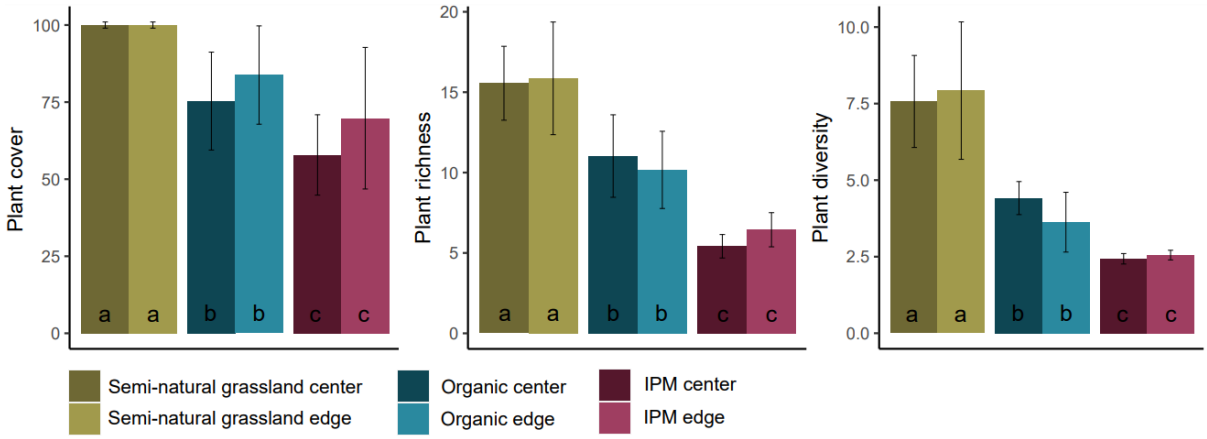



**Figure S4.1.** Average plant cover (left), plant richness (center) and plant diversity (right) per sampling plot in the semi-natural grasslands, organic orchards and IPM orchards. Average values with standard error are shown for both center and edge plots and significant differences are indicated by different letters. Vegetation surveys of the herb layer were done using quadrants (3x1 m) covering both the drive rows and crop rows in the orchards. High standard errors reflect high variability between study sites and might be caused by different timing and methods of weed removal (herbicides in the IPM orchards and mechanical removal in the organic orchards).

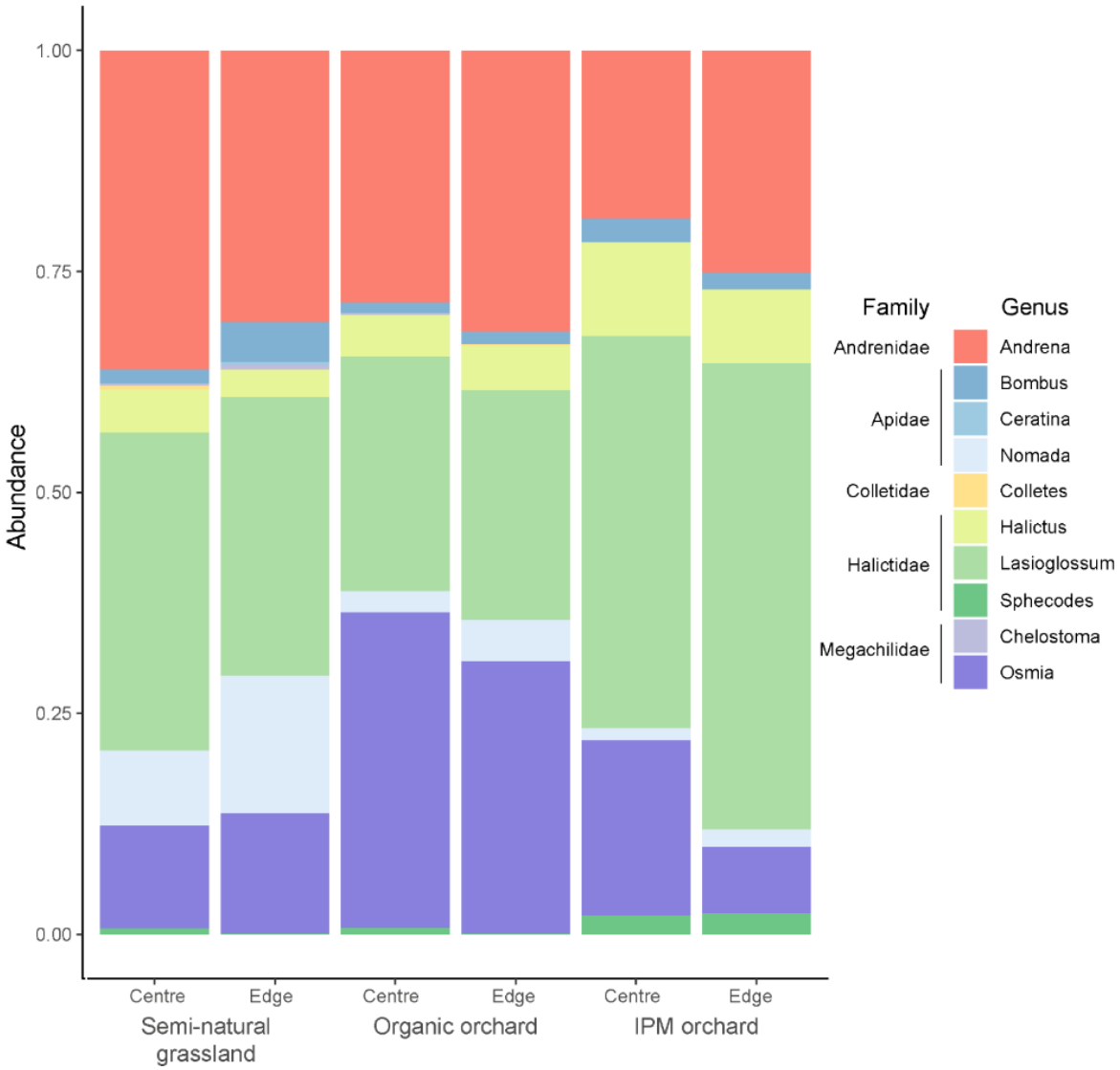



**Figure S4.2**. Relative abundance of wild bee genera and families in the center and edge of IPM and organic orchards and semi-natural grasslands.

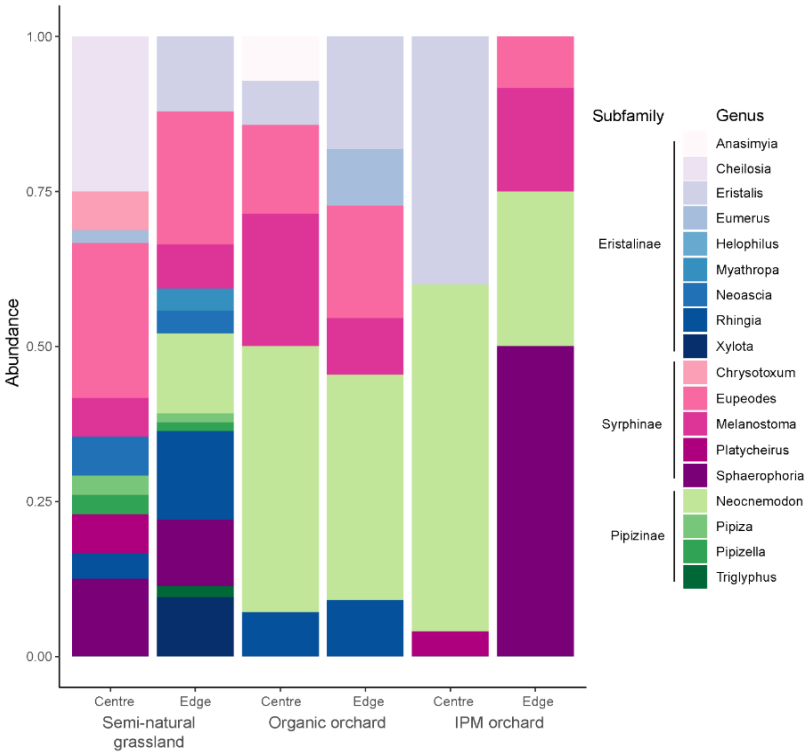



**Figure S4.3**. Relative abundance of hoverfly genera and families in the center and edge of IPM and organic orchards and semi-natural grasslands.

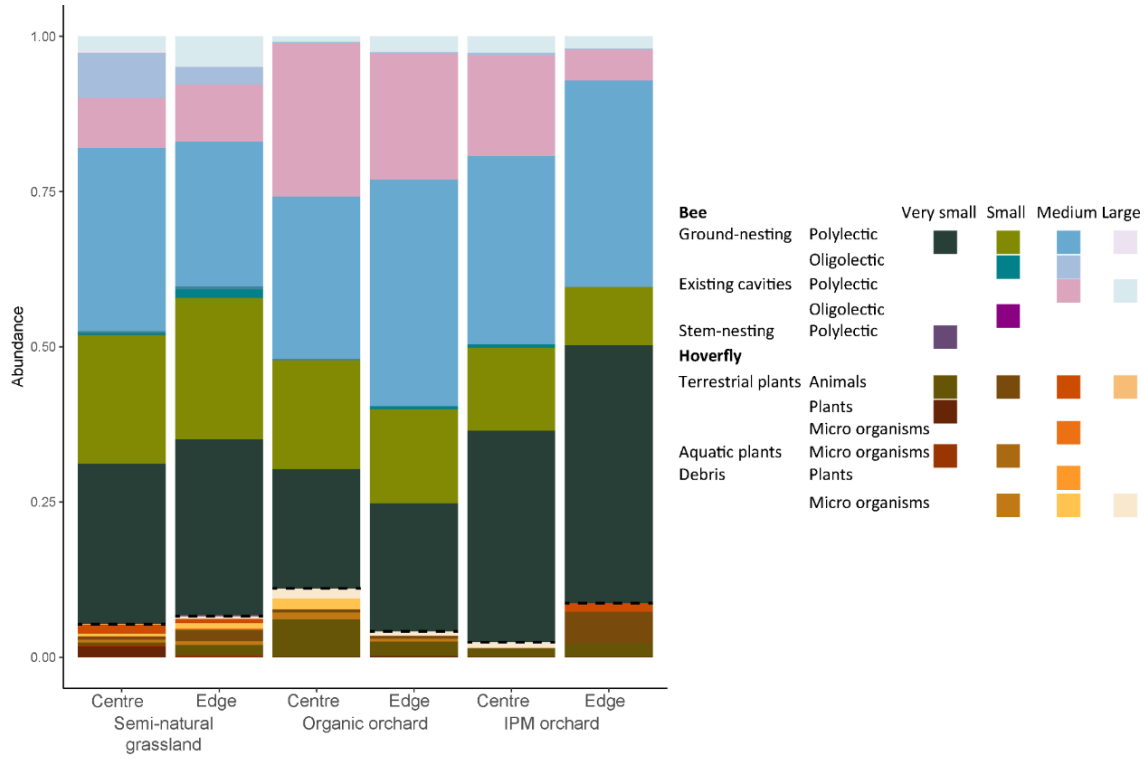



**Figure S4.4.** Relative abundance of functional groups in the center and edge of IPM and organic orchards and semi-natural grasslands. Functional groups were based on clusters of functional traits relating to larval micro-habitat, larval food source and body size for bees and hoverflies separately. Combinations of functional traits without representatives in the study were not assigned a color code. A dashed line marks the boundary between bee and hoverfly relative abundances.

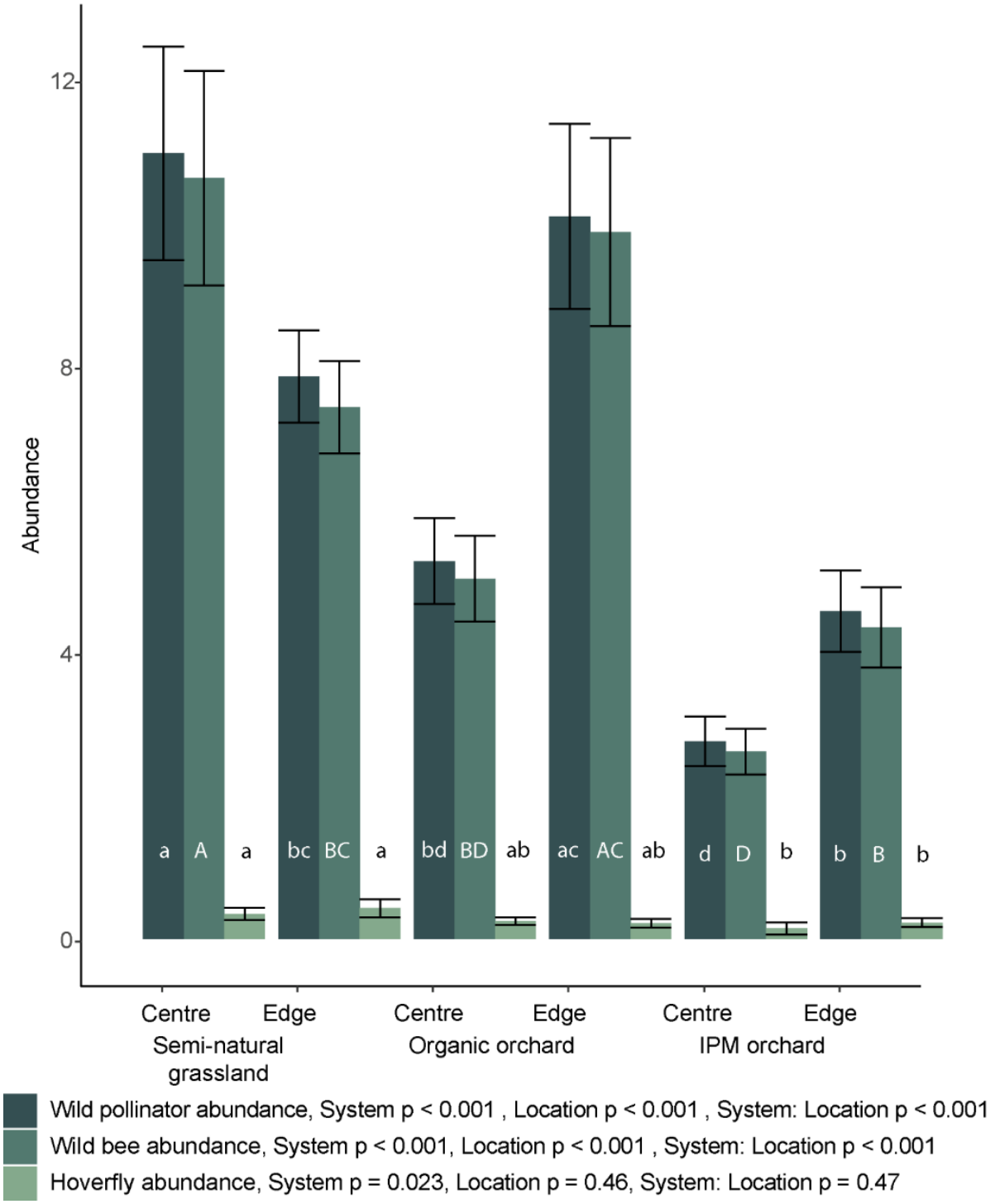



**Figure 4.5.** Pollinator abundance in IPM and organic orchards with a semi-natural reference. Mean values ±1SE of total wild pollinator abundance, wild bee abundance and hoverfly abundance across management systems and within-site sampling locations. Same color lowercase or uppercase letters indicate no statistically significant difference ($p < 0.05$) after post hoc testing.

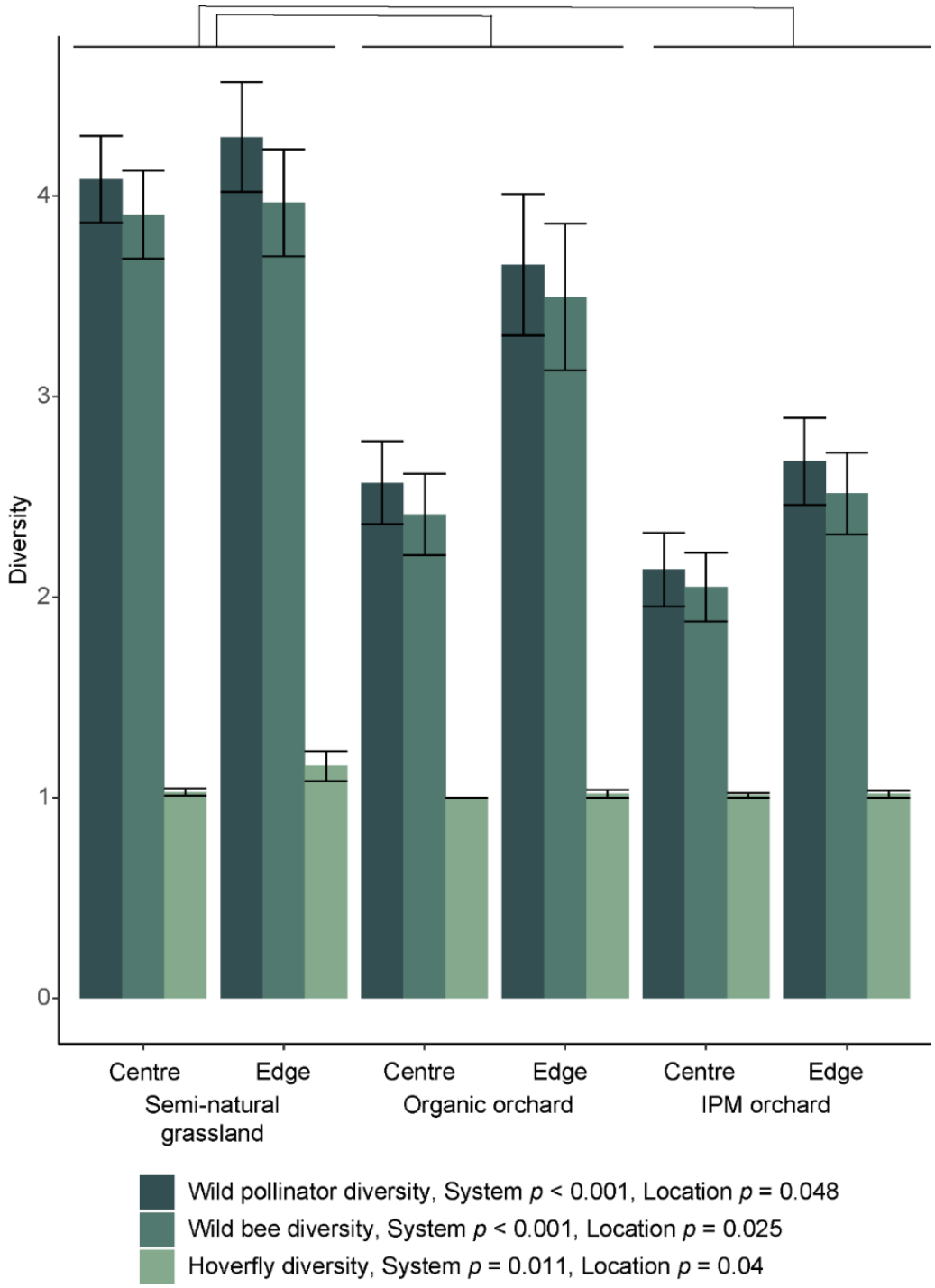



**Figure S4.6.** Pollinator diversity in IPM and organic orchards with a semi-natural reference. Mean values ±1SE of total wild pollinator diversity, wild bee diversity and hoverfly diversity across management systems and within-site sampling locations. Statistically significant differences between systems revealed by post hoc testing are indicated using brackets.

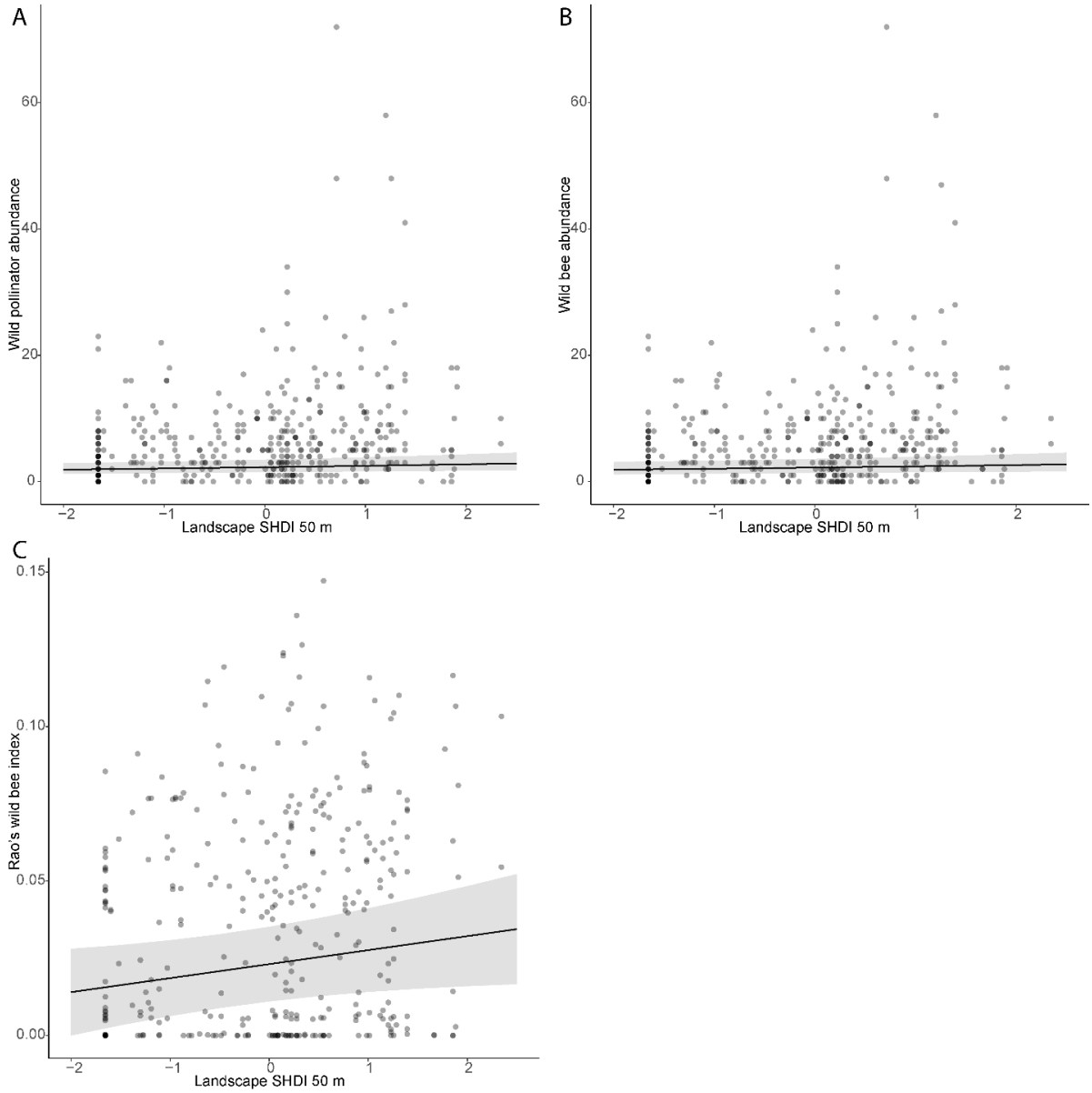



**Figure S4.7.** Effect plots with raw data points of the effect of landscape variables on biodiversity variables in IPM and organic orchards and semi-natural grasslands. Effect of landscape Shannon diversity at the 50 m scale on wild pollinator abundance (A) and wild bee abundance (B). Effect of landscape Shannon diversity at the 50 m scale on Rao's wild bee index (C).

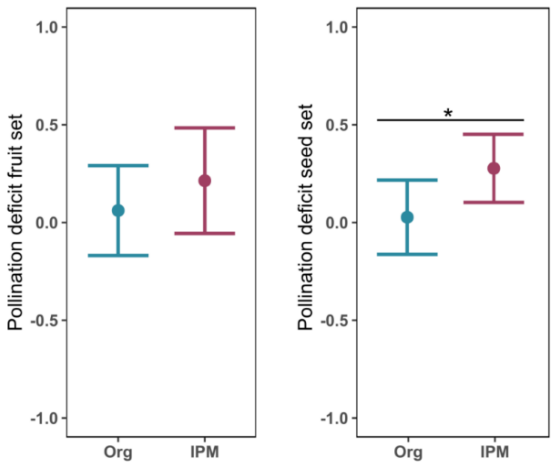



**Figure S4.8.** Mean ± 1SE for pollination deficits calculated based on fruit set (left) and seed set (right) in both the organic and IPM orchards. Deficits were calculated as the percentage difference between the number of fruits/seeds resulting from the open pollination treatment and the number resulting from hand pollination. Positive deficits indicate that the number of fruits/seeds is greater under supplementary hand pollination, while negative deficits indicate that the number of fruits/seeds is greater under open pollination. *P < 0.05, **P < 0.01, ***P < 0.001.

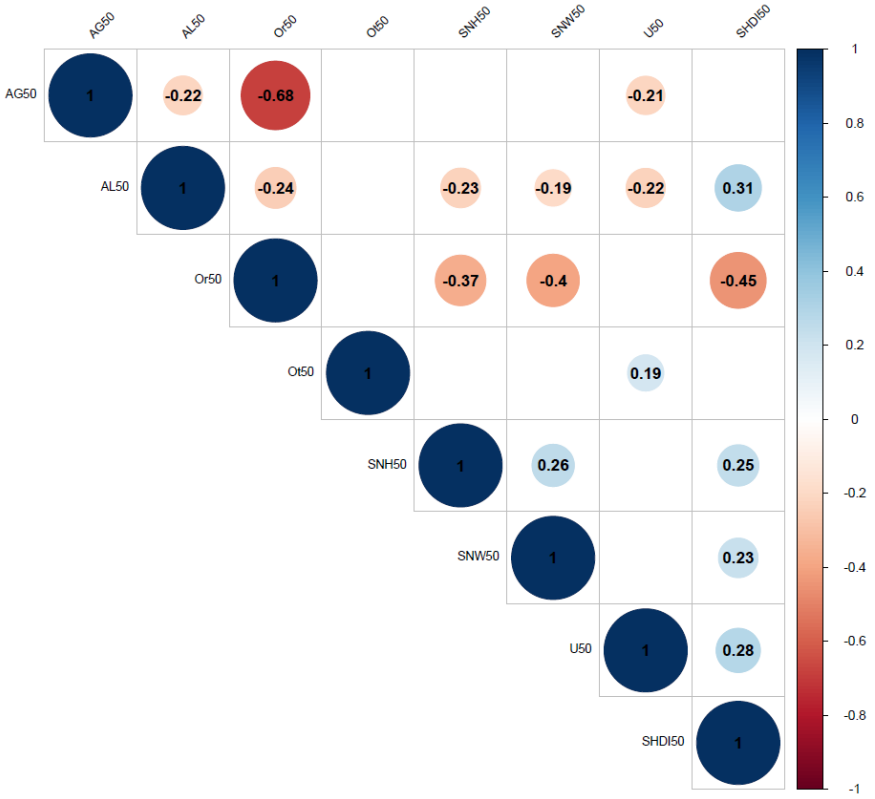



**Figure S4.9**. Pairwise Pearson's correlations between the Shannon landscape diversity index (SHDI) and the seven land use classes included in the calculation of SHDI. AG = agricultural grassland cover, AL = arable land cover, OR = orchard cover, OT = cover of other land uses, U = urban land cover, SNH = herbaceous semi-natural habitat cover, SNW = wooded semi-natural habitat cover. Blue dots indicate positive correlations and red dots indicate negative correlations. Only significant correlations are shown (P < 0.05).

**Table S4.1.** Bee and hoverfly functional traits used for the calculation of functional group richness (*) and Rao's wild bee index (1). All categorical bee traits were taken from Falk and Lewington (2017), while ITD measurements were retrieved from the R package pollimetry (Kendall et al., 2019) and Duchenne et al. (2020). All hoverfly traits were sourced from the Syrph the Net database (Speight et al., 2020).

| Trait | Levels | Definition |
|---|---|---|
| **Bees** | | |
| Tongue length[1] | Short | Short proboscis or tongue length. |
| | Long | Long proboscis or tongue length. |
| Diet*[1] | Polylectic | Pollen sourced from multiple plant families. Generalists. |
| | Oligolectic | Pollen source restricted to one plant family. Specialists. |
| Intertegular distance (ITD)[1] | Continuous (mm) | Distance between the tegulae of female specimens. Established proxy for body size and dispersion capacity. |
| Size class* | Very small | ITD lower than 1.5 mm |
| | Small | ITD between 1.5 and 2.25 mm |
| | Medium | ITD between 2.25 and 3.25 mm |
| | Large | ITD larger than 3.25 mm |
| Nesting type*[1] | Ground | Excavates nests in the ground. |
| | Existing cavities | Nesting in existing cavities, such as old rodent nests or existing tunnels in dead wood. |
| | Stems | Nesting in pithy stems. |
| Sociality[1] | Eusocial | Fixed roles and task division. |
| | Primitively eusocial | Flexible roles and task division. |
| | Communal | Females nest and provide resources alone, yet nest entrance may be shared. |
| | Solitary | Females nest and provide resources alone. |
| | Cleptoparasitic | Cuckoo bees. Females lay eggs in host species nests. |
| Season[1] | Year | At least some individuals hibernate as adults. *Apis melifera* and *Bombus* spp. |
| | Spring and Summer | Adults in Spring and Summer. |
| | Spring | Adults only in Spring. |
| Pollen carrying structure[1] | Scopa | Pollen is carried in a scopa, modified hairs on legs or the underside of the abdomen. |
| | Corbicula | Pollen is carried in a corbicula or pollen basket, which is more highly-developed than a scopa. *Apis melifera* and *Bombus* spp. |
| | Accidental | Parasitic species which do not have specialized pollen carrying structures. |
| **Hoverflies** | | |
| Larval food* | Animals | Predatory larvae feeding on animals. |
| | Plants | Larvae feeding on living, non-woody plants. |
| | Microorganisms | Larvae feeding on microorganisms associated with decomposing organic matter. |
| Size class* | Very small | Adult body length, measured from the tip of the head (exclusing antennae) to the end of the abdomen, smaller than 8 mm. |
| | Small | Body length between 8 and 10 mm. |
| | Medium | Body length between 10 and 13 mm. |
| | Large | Body length longer than 13 mm. |
| Larval microhabitat* | Terrestrial plants | Larval activity zone on or in living terrestrial plants. |
| | Aquatic plants | Larval activity zone on or in living aquatic plants. |
| | Debris | Larval activity zone in debris. |

**Table S4.2.** Overview of the landscape metrics calculated at a spatial scale of 50 m, averaged per study site. The last letter of the site name indicates the respective management (N = semi-natural reference, O = organic orchard and C = IPM orchard). AG = agricultural grassland cover, AL = arable land cover, OR = orchard cover, OT = cover of other land uses, U = urban land cover, SNH = herbaceous semi-natural habitat cover, SNW = wooded semi-natural habitat cover, DSN = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index.

| Site | Longitude | Latitude | AG | AL | OR | OT | U | SNH | SNW | DSN | SHDI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2C | 5.23892 | 50.77182 | 4,97 | 29,88 | 65,16 | 0,00 | 0,00 | 0,00 | 0,00 | 317,85 | 0,61 |
| 4C | 5.23596 | 50.77905 | 5,51 | 38,48 | 51,10 | 0,00 | 0,00 | 0,00 | 4,91 | 8,73 | 0,88 |
| 5C | 5.15041 | 50.78554 | 0,00 | 17,71 | 82,29 | 0,00 | 0,00 | 0,00 | 0,00 | 396,06 | 0,28 |
| 9C | 5.14716 | 50.9336 | 9,09 | 63,91 | 26,98 | 0,00 | 0,02 | 0,00 | 0,00 | 63,23 | 0,77 |
| 11C | 5.14584 | 50.93979 | 0,00 | 73,99 | 26,01 | 0,00 | 0,00 | 0,00 | 0,00 | 80,28 | 0,56 |
| 12C | 5.23066 | 50.84962 | 0,00 | 0,00 | 69,77 | 0,00 | 27,20 | 3,04 | 0,00 | 40,92 | 0,62 |
| 15C | 5.16993 | 50.79227 | 14,93 | 19,23 | 63,61 | 0,00 | 2,24 | 0,00 | 0,00 | 94,70 | 0,68 |
| 17C | 5.1802 | 50.84799 | 15,75 | 0,04 | 74,39 | 0,00 | 0,00 | 9,83 | 0,00 | 41,66 | 0,43 |
| 19C | 5.23631 | 50.8459 | 0,00 | 0,00 | 77,33 | 0,00 | 17,23 | 5,44 | 0,00 | 44,21 | 0,54 |
| 23C | 5.23682 | 50.86415 | 0,00 | 5,30 | 91,70 | 0,00 | 3,01 | 0,00 | 0,00 | 158,34 | 0,27 |
| 24C | 4.90508 | 50.87777 | 0,00 | 13,14 | 75,43 | 0,00 | 0,00 | 0,00 | 11,43 | 43,55 | 0,52 |
| 25C | 4.89168 | 50.87483 | 6,22 | 2,57 | 77,34 | 0,00 | 3,81 | 10,06 | 0,00 | 34,03 | 0,55 |
| 4N | 4.86391 | 50.77304 | 50,60 | 43,52 | 0,00 | 0,00 | 0,00 | 1,23 | 4,65 | 0,00 | 0,86 |
| 7N | 4.8511743 | 50.82234 | 26,60 | 44,94 | 0,00 | 0,00 | 0,00 | 4,27 | 24,19 | 0,00 | 1,15 |
| 9N | 4.519408 | 50.93599 | 66,47 | 19,88 | 0,00 | 0,00 | 0,00 | 1,98 | 11,68 | 0,00 | 0,63 |
| 11N | 3.6541 | 50.93691 | 62,20 | 24,13 | 0,07 | 0,00 | 0,00 | 6,45 | 7,16 | 0,00 | 0,80 |
| 12N | 5.41397 | 51.15256 | 82,69 | 0,00 | 0,00 | 0,00 | 8,61 | 8,70 | 0,00 | 0,00 | 0,44 |
| 13N | 4.8603017 | 50.7994 | 44,48 | 32,87 | 0,00 | 0,00 | 0,00 | 10,33 | 12,31 | 0,00 | 0,98 |
| 15N | 4.53601 | 50.92538 | 20,41 | 32,44 | 0,00 | 0,00 | 3,82 | 39,52 | 3,82 | 0,00 | 1,20 |
| 18N | 5.2670589 | 50.76203 | 94,97 | 0,00 | 0,00 | 0,00 | 0,00 | 5,03 | 0,00 | 0,00 | 0,18 |
| 25N | 4.8584759 | 50.8953 | 63,28 | 11,02 | 0,00 | 0,00 | 0,00 | 22,67 | 3,03 | 0,00 | 0,84 |
| 26N | 4.91728 | 50.88512 | 0,00 | 0,67 | 0,20 | 0,00 | 0,00 | 59,33 | 39,81 | 0,00 | 0,68 |
| 27N | 4.7781528 | 50.91272 | 40,36 | 0,00 | 0,00 | 0,00 | 0,00 | 6,66 | 52,98 | 0,00 | 0,85 |
| 30N | 4.2121653 | 50.95811 | 69,94 | 14,55 | 0,00 | 0,00 | 0,00 | 15,51 | 0,00 | 0,00 | 0,77 |
| 1O | 4.91326 | 50.91381 | 0,00 | 23,30 | 49,09 | 0,00 | 1,21 | 15,05 | 11,35 | 44,10 | 0,87 |
| 4O | 4.61912 | 50.8028 | 1,71 | 16,77 | 81,10 | 0,00 | 0,41 | 0,00 | 0,00 | 77,12 | 0,32 |
| 5O | 4.9182 | 50.92098 | 0,00 | 32,29 | 46,01 | 0,00 | 11,28 | 10,43 | 0,00 | 27,49 | 0,91 |
| 9O | 5.12864 | 50.94523 | 0,00 | 19,78 | 58,23 | 2,17 | 15,69 | 2,63 | 1,49 | 47,66 | 1,08 |
| 10O | 5.1393444 | 50.92353 | 4,40 | 28,80 | 53,77 | 0,00 | 5,33 | 7,69 | 0,00 | 41,33 | 0,96 |
| 12O | 5.34184 | 50.90284 | 28,70 | 21,03 | 48,79 | 0,00 | 1,48 | 0,00 | 0,00 | 90,05 | 0,87 |
| 13O | 4.07894 | 50.76953 | 0,00 | 23,60 | 75,73 | 0,00 | 0,66 | 0,00 | 0,00 | 70,01 | 0,50 |
| 14O | 5.07678 | 50.93709 | 8,26 | 19,04 | 44,48 | 0,00 | 18,37 | 5,47 | 4,38 | 28,49 | 1,21 |
| 15O | 5.08162 | 50.92705 | 17,26 | 19,69 | 57,97 | 0,00 | 5,08 | 0,00 | 0,00 | 72,29 | 0,93 |
| 19O | 4.9351 | 50.92462 | 8,34 | 24,83 | 64,46 | 0,00 | 0,00 | 2,36 | 0,00 | 49,24 | 0,78 |
| 20O | 4.9459 | 50.92608 | 29,94 | 10,81 | 49,29 | 0,00 | 4,40 | 0,00 | 5,56 | 31,04 | 0,92 |
| 26O | 5.02499 | 50.93227 | 0,00 | 26,04 | 73,96 | 0,00 | 0,00 | 0,00 | 0,00 | 141,39 | 0,43 |

**Table S4.3.** Overview of the most predictive spatial scales for the landscape variables. (Generalized) linear models were fitted for each response variable at each of the six spatial scales. We then used model selection based on the small sample–corrected Akaike information criterion (AICc) to identify the most predictive model and scale and applied that scale in all subsequent analyses. This analysis was performed both for the models based on the entire dataset (semi-natural grassland vs. organic orchard vs. IPM orchard) and for the models used in the pSEM (organic orchard vs. IPM orchard).

| Response | Selected scale of models including all data | Selected scale of models in pSEM |
|---|---|---|
| Wild pollinator abundance | 50 m | 50 m |
| Wild bee abundance | 50 m | |
| Hoverfly abundance | 100 m | |
| Wild pollinator diversity | 50 m | 50 m |
| Wild bee diversity | 50 m | |
| Hoverfly diversity | 100 m | |
| Rao's wild bee index | 50 m | 100 m |
| Functional group richness | 2000 m | 2000 m |
| Honeybee abundance | | 50 m |
| Seed set | | 500 m |
| Fruit set | | 250 m |
| Yield | | 250 m |

**Table S4.4.** Full list of observed wild bee and hoverfly species with their attributed functional traits used for the categorization into functional groups.

| Species | Body size | Food source | Habitat |
|---|---|---|---|
| Bees | | | |
| *Apis mellifera* | Medium | Polylectic | Ground |
| *Andrena angustior* | Small | Polylectic | Ground |
| *Andrena barbilabris* | Medium | Polylectic | Ground |
| *Andrena bicolor* | Small | Polylectic | Ground |
| *Andrena bimaculata* | Medium | Polylectic | Ground |
| *Andrena chrysosceles* | Small | Polylectic | Ground |
| *Andrena cineraria* | Medium | Polylectic | Ground |
| *Andrena dorsata* | Small | Polylectic | Ground |
| *Andrena flavipes* | Medium | Polylectic | Ground |
| *Andrena fulva* | Medium | Polylectic | Ground |
| *Andrena fulvago* | Small | Oligolectic | Ground |
| *Andrena gravida* | Medium | Polylectic | Ground |
| *Andrena haemorrhoa* | Medium | Polylectic | Ground |
| *Andrena helvola* | Medium | Polylectic | Ground |
| *Andrena humilis* | Small | Oligolectic | Ground |
| *Andrena labiata* | Small | Polylectic | Ground |
| *Andrena minutula* | Very small | Polylectic | Ground |
| *Andrena mitis* | Medium | Oligolectic | Ground |
| *Andrena nigroaenea* | Medium | Polylectic | Ground |
| *Andrena nitida* | Medium | Polylectic | Ground |
| *Andrena ovatula* | Small | Polylectic | Ground |
| *Andrena proxima* | Small | Oligolectic | Ground |
| *Andrena scotica* | Medium | Polylectic | Ground |
| *Andrena subopaca* | Very small | Polylectic | Ground |
| *Andrena vaga* | Medium | Oligolectic | Ground |
| *Andrena ventralis* | Small | Oligolectic | Ground |
| *Andrena wilkella* | Small | Polylectic | Ground |
| *Bombus hortorum* | Large | Polylectic | Existing cavities |
| *Bombus hypnorum* | Large | Polylectic | Existing cavities |
| *Bombus lapidarius* | Large | Polylectic | Existing cavities |
| *Bombus pascuorum* | Large | Polylectic | Existing cavities |
| *Bombus pratorum* | Large | Polylectic | Existing cavities |
| *Bombus terrestris* | Large | Polylectic | Existing cavities |
| *Ceratina cyanea* | Very small | Polylectic | Stems |
| *Chelostoma florisomne* | Small | Oligolectic | Existing cavities |
| *Halictus maculatus* | Very small | Polylectic | Ground |
| *Halictus quadricinctus* | Medium | Polylectic | Ground |
| *Halictus rubicundus* | Small | Polylectic | Ground |
| *Halictus scabiosae* | Medium | Oligolectic | Ground |
| *Halictus tumulorum* | Very small | Polylectic | Ground |
| *Lasioglossum calceatum* | Small | Polylectic | Ground |
| *Lasioglossum fulvicorne* | Very small | Polylectic | Ground |

| Species | Body size | Food source | Habitat |
|---|---|---|---|
| *Lasioglossum lativentre* | Small | Polylectic | Ground |
| *Lasioglossum leucopus* | Very small | Polylectic | Ground |
| *Lasioglossum leucozonium* | Small | Polylectic | Ground |
| *Lasioglossum malachurum* | Small | Polylectic | Ground |
| *Lasioglossum minutissimum* | Very small | Polylectic | Ground |
| *Lasioglossum morio* | Very small | Polylectic | Ground |
| *Lasioglossum nitidiusculum* | Very small | Polylectic | Ground |
| *Lasioglossum nitidulum* | Very small | Polylectic | Ground |
| *Lasioglossum parvulum* | Very small | Polylectic | Ground |
| *Lasioglossum pauxillum* | Very small | Polylectic | Ground |
| *Lasioglossum punctatissimum* | Very small | Polylectic | Ground |
| *Lasioglossum quadrinotatum* | Small | Polylectic | Ground |
| *Lasioglossum semilucens* | Very small | Polylectic | Ground |
| *Lasioglossum sexnotatum* | Small | Polylectic | Ground |
| *Lasioglossum sexstrigatum* | Medium | Polylectic | Ground |
| *Lasioglossum villosulum* | Very small | Polylectic | Ground |
| *Lasioglossum zonulum* | Small | Polylectic | Ground |
| *Nomada bifasciata* | Small | Polylectic | Ground |
| *Nomada fabriciana* | Small | Polylectic | Ground |
| *Nomada ferruginata* | Very small | Polylectic | Ground |
| *Nomada flava* | Small | Polylectic | Ground |
| *Nomada flavoguttata* | Very small | Polylectic | Ground |
| *Nomada fucata* | Small | Polylectic | Ground |
| *Nomada fulvicornis* | Small | Polylectic | Ground |
| *Nomada fuscicornis* | Small | Polylectic | Ground |
| *Nomada goodeniana* | Small | Polylectic | Ground |
| *Nomada lathburiana* | Small | Polylectic | Ground |
| *Nomada marshamella* | Small | Polylectic | Ground |
| *Nomada panzeri* | Small | Polylectic | Ground |
| *Nomada ruficornis* | Small | Polylectic | Ground |
| *Nomada sheppardana* | Very small | Polylectic | Ground |
| *Nomada signata* | Small | Polylectic | Ground |
| *Nomada zonata* | Small | Polylectic | Ground |
| *Osmia bicornis* | Medium | Polylectic | Existing cavities |
| *Osmia caerulescens* | Medium | Polylectic | Existing cavities |
| *Osmia cornuta* | Large | Polylectic | Existing cavities |
| *Sphecodes crassus* | Very small | Polylectic | Ground |
| *Sphecodes ephippius* | Very small | Polylectic | Ground |
| *Sphecodes monilicornis* | Very small | Polylectic | Ground |
| *Sphecodes niger* | Very small | Polylectic | Ground |
| *Sphecodes puncticeps* | Very small | Polylectic | Ground |
| *Sphecodes scabricollis* | Very small | Polylectic | Ground |
| Hoverflies | | | |
| *Anasimyia interpuncta* | Small | Micro-organisms | Aquatic Plants |
| *Cheilosia vernalis* | Very small | Plants | Terrestrial Plants |
| *Chrysotoxum cautum* | Large | Animals | Terrestrial Plants |
| *Eristalis nemorum* | Medium | Micro-organisms | Debris |

| Species | Body size | Food source | Habitat |
|---|---|---|---|
| *Eristalinus sepulchralis* | Small | Micro-organisms | Debris |
| *Eristalis similis* | Large | Micro-organisms | Debris |
| *Eristalis tenax* | Large | Micro-organisms | Debris |
| *Eumerus strigatus sogdianus* | Very small | Plants | Terrestrial Plants |
| *Eupeodes corollae* | Small | Animals | Terrestrial Plants |
| *Eupeodes luniger* | Small | Animals | Terrestrial Plants |
| *Helophilus pendulus* | Medium | Micro-organisms | Debris |
| *Melanostoma mellinum* | Very small | Animals | Terrestrial Plants |
| *Melanostoma scalare* | Medium | Plants | Debris |
| *Myatropa florea* | Medium | Micro-organisms | Debris |
| *Neoascia meticulosa* | Very small | Micro-organisms | Aquatic Plants |
| *Neoascia tenur* | Very small | Micro-organisms | Aquatic Plants |
| *Neocnemodon latitarsis* | Very small | Animals | Terrestrial Plants |
| *Neocnemodon pubescens* | Very small | Animals | Terrestrial Plants |
| *Neocnemodon sp* | Very small | Animals | Terrestrial Plants |
| *Neocnemodon vitripennis* | Very small | Animals | Terrestrial Plants |
| *Pipiza noctiluca notata* | Very small | Animals | Terrestrial Plants |
| *Pipizella viduata* | Very small | Animals | Terrestrial Plants |
| *Platycheirus albimanus* | Small | Animals | Terrestrial Plants |
| *Rhingia campestris* | Small | Micro-organisms | Debris |
| *Sphaerophoria fatarum* | Small | Animals | Terrestrial Plants |
| *Sphaerophoria scripta* | Medium | Animals | Terrestrial Plants |
| *Triglyphus primus* | Very small | Animals | Terrestrial Plants |
| *Xylota segnis* | Medium | Micro-organisms | Terrestrial Plants |

**Table S4.5.** Overall Permutational Multivariate Analysis of Variance (PERMANOVA) and pairwise comparisons based on Bray-Curtis dissimilarities of wild pollinator communities in the center and edge of IPM and organic orchards and semi-natural grasslands. Test statistics (F), $R^2$-values ($R^2$) and p-values (*p*) are reported for management system and within-site location, as well as their interaction.

| | Predictor | F | $R^2$ | *p* |
|---|---|---|---|---|
| PERMANOVA | System | 7.64 | 0.043 | 0.001 |
| | Location | 2.49 | 0.0071 | 0.001 |
| | System:Location | 0.89 | 0.005 | 0.38 |
| IPM vs. semi-natural grasslands | System | 9.79 | 0.041 | 0.019 |
| | Location | 1.53 | 0.0064 | 0.019 |
| IPM vs. organic | System | 6.91 | 0.033 | 0.001 |
| | Location | 2.86 | 0.014 | 0.001 |
| Organic vs. semi-natural grasslands | System | 6.14 | 0.025 | 0.016 |
| | Location | 1.52 | 0.0061 | 0.016 |

**Table S4.6.** Scaled path coefficients for the pSEM explaining management, location and landscape effects on pollinator biodiversity, pollination and fruit production. No causal relationship is assumed between functional group richness and Rao's wild bee index (indicated by ~~). Estimates of path coefficients (±SE) and p-values (*p*) are given for each predictor.

| Response | Predictor | Estimate ± se | *p* |
|---|---|---|---|
| Wild pollinator abundance | Edge | 0.24 ± 0.04 | <0.001 |
| | Organic management | 0.34 ± 0.11 | 0.0017 |
| | Agriculture proportion 50 m | 0.08 ± 0.05 | 0.13 |
| | Landscape SHDI 50 m | 0.05 ± 0.05 | 0.35 |
| | Distance to SNH | -0.06 ± 0.07 | 0.38 |
| Wild pollinator diversity | Edge | 0.16 ± 0.06 | 0.013 |
| | Organic management | 0.16 ± 0.09 | 0.081 |
| | Landscape SHDI | 0.09 ± 0.09 | 0.32 |
| | Organic management:Edge | 0.05 ± 0.06 | 0.39 |
| | Agriculture proportion 50 m | 0.03 ± 0.09 | 0.75 |
| | Distance to SNH | -0.03 ± 0.08 | 0.76 |
| Honeybee abundance | Edge | 0.49 ± 0.07 | <0.001 |
| | Agriculture proportion 50 m | 0.22 ± 0.1 | 0.030 |
| | Organic management | 0.27 ± 0.16 | 0.094 |
| | Landscape SHDI 50 m | -0.07 ± 0.09 | 0.43 |
| | Distance to SNH | 0.05 ± 0.11 | 0.62 |
| Rao's wild bee index | Edge | 0.15 ± 0.08 | 0.058 |
| | Landscape SHDI 100 m | -0.15 ± 0.11 | 0.19 |
| | Agriculture proportion 100 m | 0.07 ± 0.11 | 0.53 |
| | Organic management | -0.05 ± 0.11 | 0.62 |
| Functional group richness | ~~ Rao's wild bee index | 0.39 | <0.001 |
| | Agriculture proportion 2000 m | -0.23 ± 0.1 | 0.017 |
| | Edge | 0.16 ± 0.07 | 0.024 |
| | Organic management | -0.06 ± 0.08 | 0.47 |
| | Landscape SHDI 2000 m | -0.02 ± 0.09 | 0.85 |
| Seed set | Organic management | 0.53 ± 0.18 | 0.0029 |
| | Edge | -0.31 ± 0.18 | 0.079 |
| | Honeybee abundance | -0.11 ± 0.07 | 0.12 |
| | Functional group richness | -0.26 ± 0.18 | 0.15 |
| | Wild pollinator diversity | 0.27 ± 0.21 | 0.19 |
| | Wild pollinator abundance | 0.03 ± 0.03 | 0.38 |
| Fruit set | Wild pollinator diversity | 0.42 ± 0.24 | 0.08 |
| | Seed set | 1.67 ± 1.16 | 0.15 |
| | Rao's wild bee index | -0.24 ± 0.21 | 0.27 |
| | Wild pollinator abundance | -0.02 ± 0.03 | 0.57 |
| Yield | Organic management | -0.20 ± 0.07 | 0.0061 |
| | Edge | 0.14 ± 0.06 | 0.029 |
| | Seed set | 0.56 ± 0.38 | 0.15 |

**Methods S5.1.** Indicators of soil bacterial and fungal diversity.

Indicators of soil bacterial and fungal diversity were obtained from Hulsmans et al. (2022). Similar to the sampling of the soil-based ES, soil samples from the top layer (0-10 cm) were taken in the center plots of all study sites, with separate subsamples for the drive rows and crop rows in the orchards. Genomic DNA was extracted using the soil DNA Isolation Plus Kit (Norgen Biotek Crop., Thorold, ON, Canada) and PCR amplification was conducted using ALLin HiFi DNA Polymerase (HighQu, Kraichtal, Germany) with the fungal primers ITS86F and ITS4 and the bacterial 515F/806R primer pair (Waud et al., 2014; Caporaso et al., 2011). After purification, amplicons were sequenced on an Illumina Miseq platform (Illumina, San Diego, CA, United States) and sequences were clustered into operational taxonomic units (OTUs) in USEARCH v. 11 (Edgar, 2013). Based on these OTUs, taxonomic richness and diversity of fungi and bacteria were calculated (hill numbers 0 and 1, respectively; Hill, 1973).

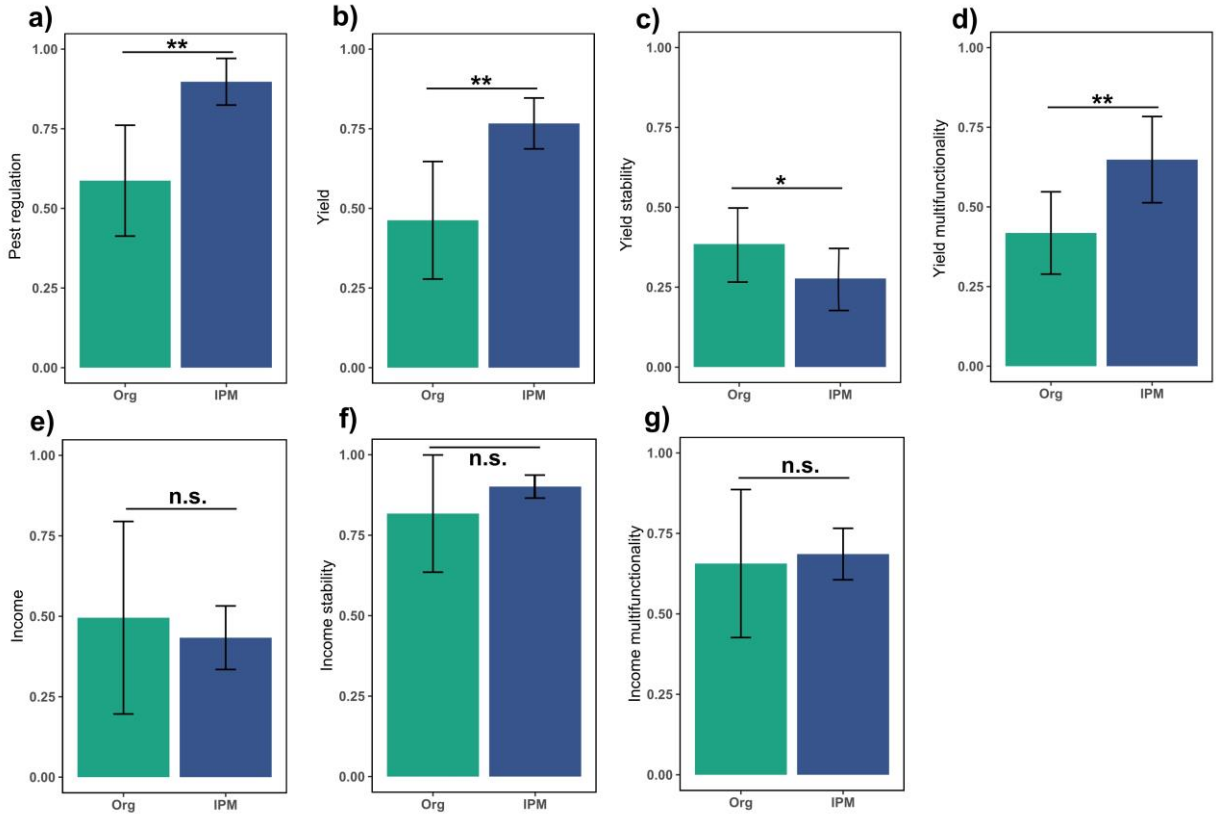



**Figure S5.1.** Pairwise comparison of (a) pest regulation, (b) yield, (c) yield stability, (d) yield multifunctionality, (e) income, (f) income stability, (g) income multifunctionality levels between the organic and IPM orchards. (*$P$ < 0.05, **$P$ < 0.01, n.s. = non-significant).

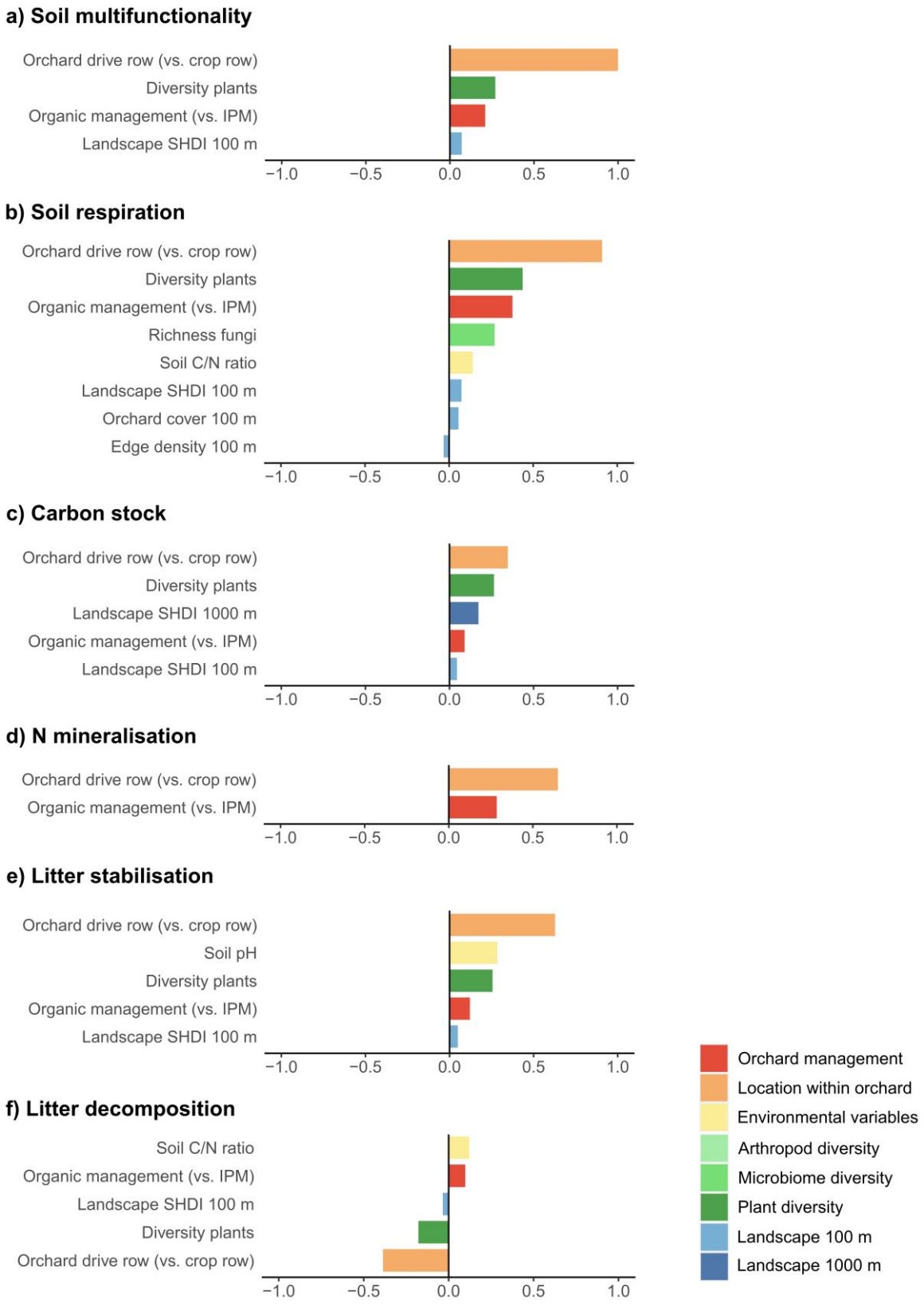



**Figure S5.2.** Relative importance of different drivers of soil multifunctionality (a) and soil ES indicators (b-f). For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Individual path coefficient for each PSEM can be found in Table S5.6.

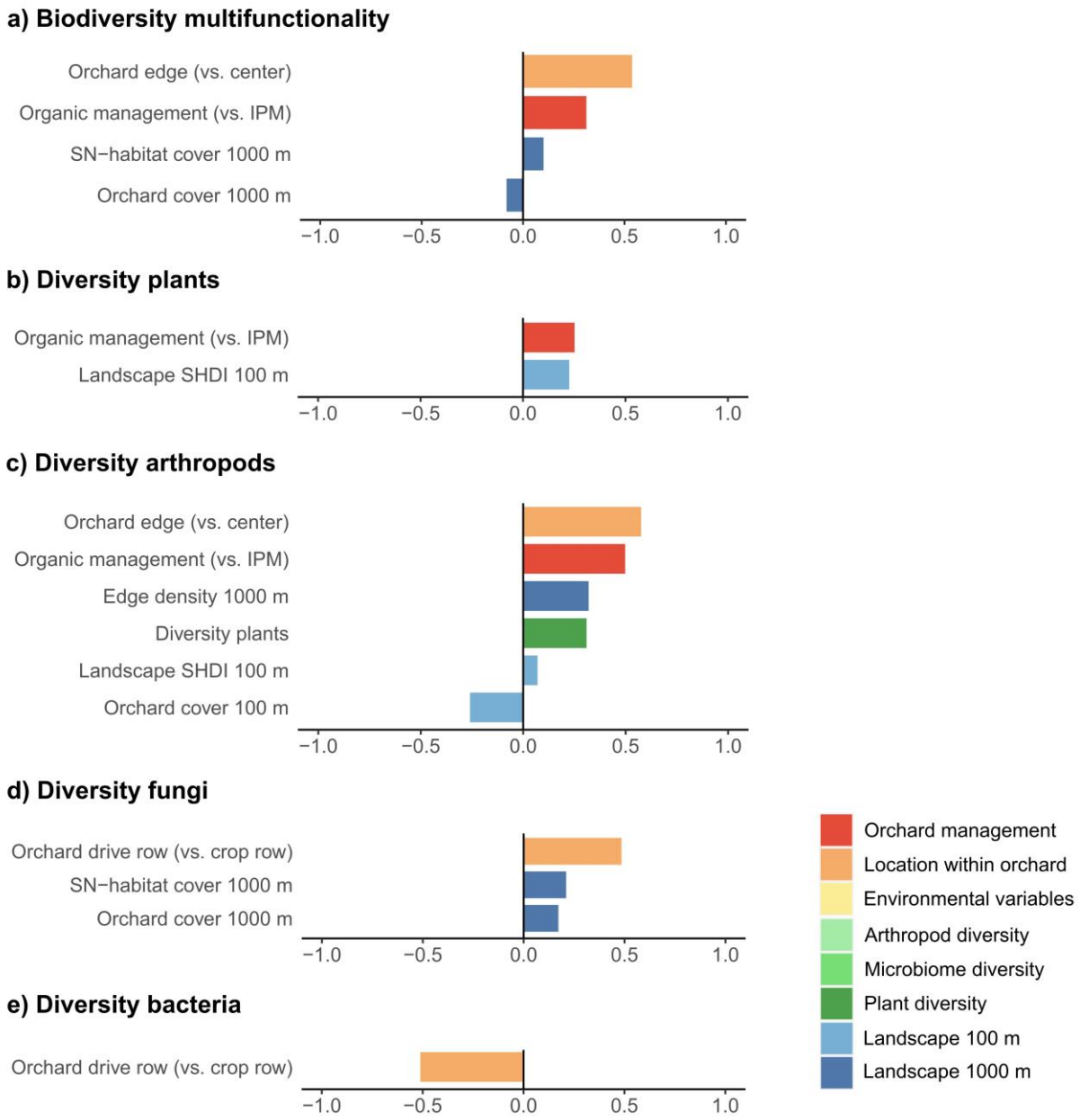



**Figure S5.3.** Relative importance of different drivers of biodiversity multifunctionality (a) and biodiversity ES indicators (b-e). For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Individual path coefficient for each PSEM can be found in Table S5.7.

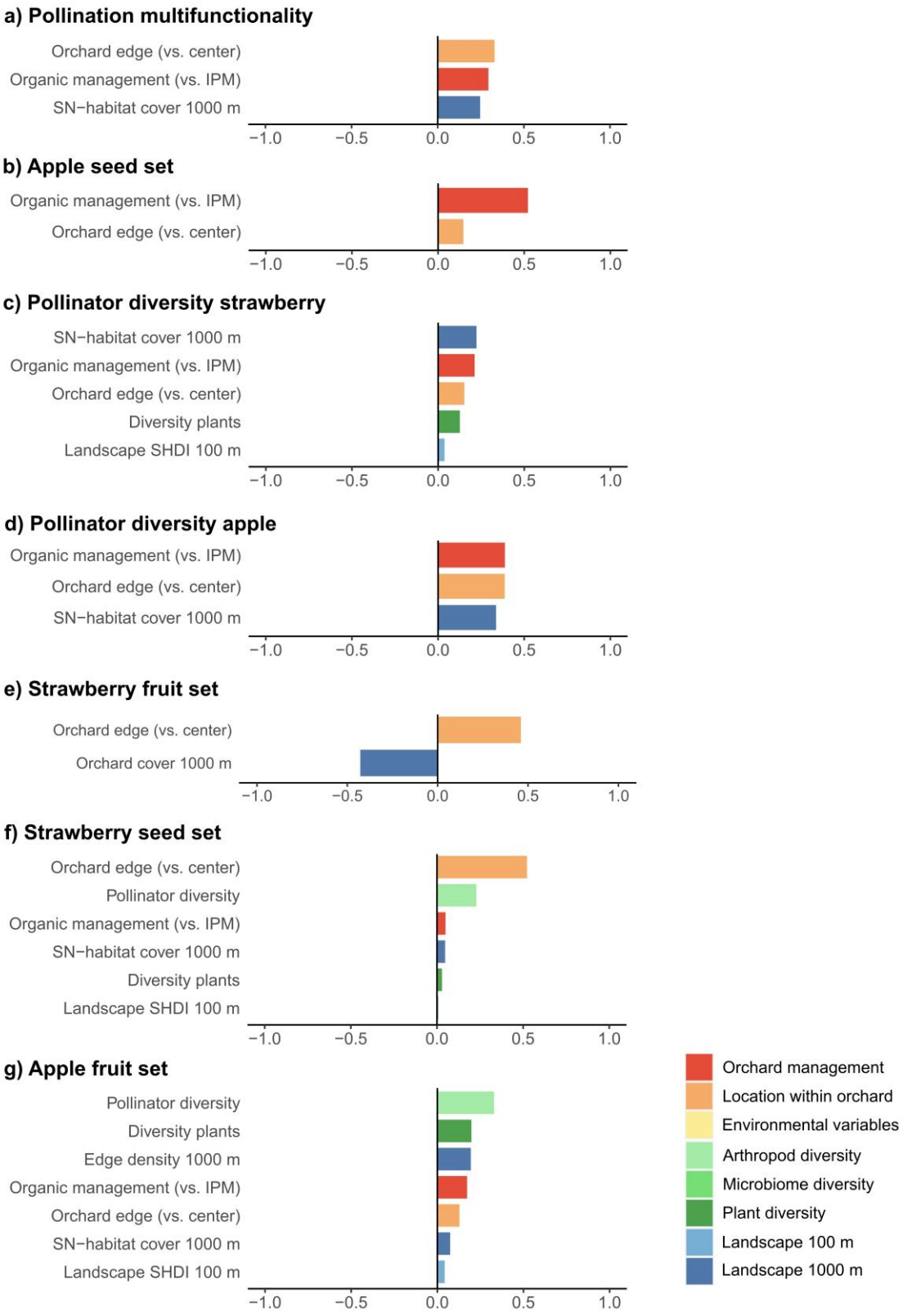



**Figure S5.4.** Relative importance of different drivers of pollination multifunctionality (a) and pollination ES indicators (b-g). For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Individual path coefficient for each PSEM can be found in Table S5.8.

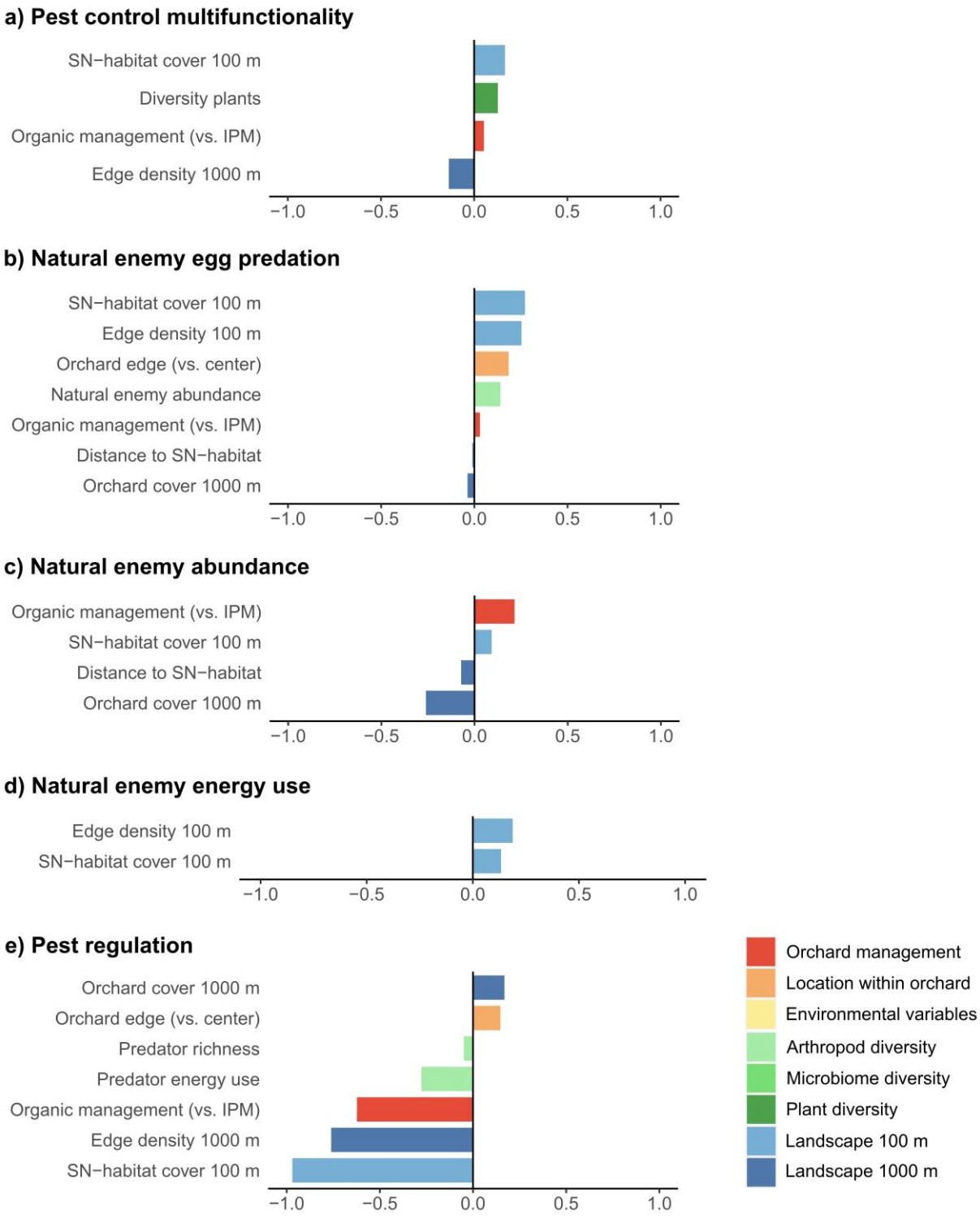



**Figure S5.5.** Relative importance of different drivers of pest control multifunctionality (a) and pest control ES indicators (b-e). For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Individual path coefficient for each PSEM can be found in Table S5.9.

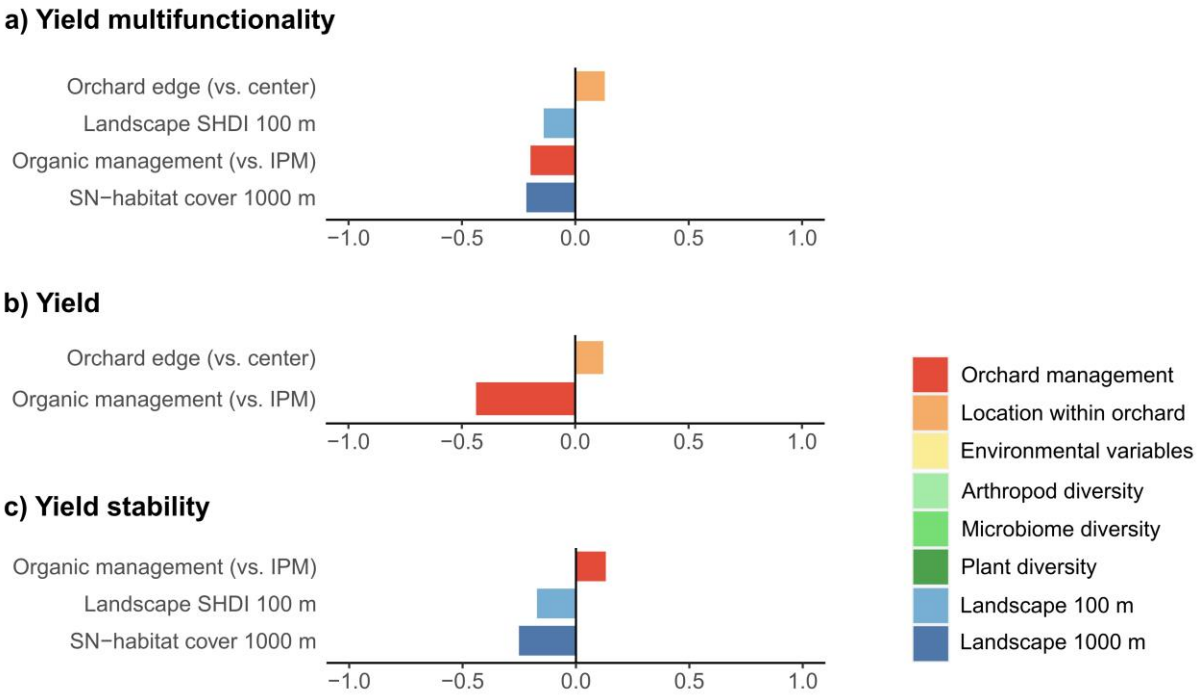



**Figure S5.6.** Relative importance of different drivers of yield multifunctionality (a) and yield ES indicators (b-c). For each response variable, the relative effect of each driver was determined by constructing a PSEM, considering both direct and indirect relationships between drivers and response variables. Individual path coefficient for each PSEM can be found in Table S5.10.

**Table S5.1**. Additional information on the conceptual framework illustrating the hypothesized direct and indirect relationships between the fundamental predictors (landscape, management and environment), the intermediate variables (biodiversity indicators) and the ultimate response variables (pollination, pest control, soil-based services, production services and farmer income) that were tested using a series of piecewise SEMs.

| **Hypothesized pathways** | **Additional information** |
|---|---|
| Direct and indirect effects of landscape | From 10 original landscape variables (seven land use classes, Shannon diversity, edge density and distance to nearest semi-natural habitat), five variables were retained for further analysis as to not make the models unnecessarily complicated. The five landscape variables were chosen bases on several criteria: (i) minimal correlation between variables over all spatial scales, (ii) importance as predictors of biodiversity and ecosystem services based on literature and (iii) relating to the composition, the compositional heterogeneity as well as the configuration and configurational complexity of the landscape. Landscape variables were hypothesized to directly affect biodiversity, and both directly and indirectly affect ecosystem service measures. Landscape effects on biodiversity mostly include the provisioning of suitable habitat and resources for organisms. As most ecosystem services are biodiversity based, the effect of the landscape on biodiversity also provides an indirect pathway from landscape to ecosystem services. Direct effects of landscape on ecosystem services can for instance result from an input of agrochemicals from neighboring fields, or can reflect that our sampling methodology resulted in undersampling of some groups of service providers. |
| Direct and indirect effects of management | The management types considered in the PSEM were organic farming and Integrated Pest Management (IPM), which were expected to directly affect biodiversity, and both directly and indirectly affect ecosystem services and economic performance. Direct effects of management on biodiversity can for instance be due to the quantities and types of pesticides and herbicides used in organic and IPM orchards, and can thus also indirectly affect ecosystem services through the impact on service providing organisms. Direct effects of management on ecosystem services and economic performance can for instance reflect local management practices such as manual of chemical thinning of (developing) fruits, or can result from different policy and market dynamics for organic and IPM farming (for instance affecting farmer income). |

| | |
|---|---|
| Direct and indirect effects of environmental variables | As environmental variables, we selected the soil C:N ratio and soil pH as those metrics showed to be significant predictors of soil-based ES in a previous study (Daelemans et al. 2022b). Also soil texture was added as an explanatory variable because orchards were located both on sandy loam and loam soil types. C:N ratio, pH and soil texture did not significantly differ between organic and IPM orchards, so to keep the conceptual model concise we did not include additional pathways from Management > environmental variables. Although being a potentially important predictor for soil-based services, soil biodiversity and plant diversity, soil water content was not included as an environmental variable. Soil water content was only determined at two moments (autumn 2018 and spring 2020) and showed high variability. Because the ES indicators were determined at various moments, there were no reliable measurements of soil water content available for all the different response variables. Environmental variables were hypothesized to directly affect biodiversity measures through affecting habitat quality and resource availability, and to affect ecosystem services both indirectly (through the relationships with biodiversity) and directly (for instance by directly affecting nutrient availability for the apple trees). A feedback loop from biodiversity metrics on environmental variables might also be present, but was not included in the analysis due to the analytical constraints of piecewise structural equation modelling (overall model fit cannot be evaluated when feedback loops are integrated) and because it was beyond the scope of our study. |

**Table S5.2.** Results of the linear mixed effects models for the **soil-based ecosystem service indicators and soil multifunctionality**, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Test statistic ($Z$) and $P$-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Soil multifunctionality $R^2_m$= 0.583 $R^2_c$ = 0.825 | | Soil respiration $R^2_m$= 0.694 $R^2_c$ = 0.818 | | Carbon stock $R^2_m$= 0.092 $R^2_c$ = 0.824 | | N mineralisation $R^2_m$= 0.316 $R^2_c$ = 0.847 | | Litter stabilisation $R^2_m$= 0.387 $R^2_c$ = 0.658 | | Litter decomposition $R^2_m$= 0.355 $R^2_c$ = 0.587 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ |
| Management | 2.868 | 0.049 | 6.133* | 0.067 | 0.136 | 0.004 | 1.135 | 0.064 | 1.505 | 0.032 | 4.114* | 0.095 |
| Location | 13.173*** | 0.109 | 37.032*** | 0.450 | 1.785 | 0.047 | 13.914** | 0.192 | 2.411 | 0.054 | 7.466** | 0.141 |
| OR (%) | 0.596 | 0.018 | 2.141 | 0.040 | - | - | 0.236 | 0.017 | - | - | - | - |
| C/N ratio | 0.469 | 0.005 | 5.208* | 0.049 | - | - | 0.288 | 0.003 | - | - | 3.712* | 0.035 |
| pH | 6.987** | 0.066 | 0.736 | 0.003 | - | - | - | - | 10.071** | 0.159 | 2.719 | 0.038 |
| SOC (%) | 2.249 | 0.019 | - | - | - | - | 1.497 | 0.012 | - | - | - | - |
| SNH (%) | 2.969 | 0.037 | 0.004 | 0.001 | - | - | - | - | - | - | 3.218 | 0.033 |
| DSNH (m) | - | - | 0.103 | 0.008 | - | - | - | - | - | - | - | - |
| SHDI | 0.446 | 0.004 | 1.184 | 0.004 | - | - | - | - | - | - | 0.482 | 0.009 |
| ED (m/ha) | - | - | 0.113 | 0.005 | 0.288 | 0.007 | - | - | 6.347* | 0.073 | - | - |
| Diversity plants | 9.601** | 0.083 | 10.343** | 0.089 | 7.132* | 0.106 | - | - | 5.860* | 0.082 | - | - |
| Diversity fungi | 4.560* | 0.038 | - | - | - | - | - | - | - | - | - | - |
| Richness fungi | 0.688 | 0.005 | 6.034* | 0.052 | - | - | - | - | 3.860 | 0.048 | - | - |
| Richness plants | - | - | - | - | - | - | 1.498 | 0.012 | - | - | - | - |
| Mana x Location | 1.211 | 0.012 | 3.020 | 0.022 | - | - | 14.652** | 0.220 | 2.178 | 0.018 | 3.617* | 0.041 |
| Mana x Richness bacteria | 9.385** | 0.044 | - | - | - | - | - | - | 3.697 | 0.027 | - | - |
| Mana x Diversity bacteria | 6.806* | 0.031 | - | - | - | - | - | - | - | - | - | - |
| Mana x Richness fungi | - | - | 0.388 | 0.003 | - | - | - | - | - | - | - | - |
| Mana x SHDI | - | - | 2.966 | 0.027 | - | - | - | - | - | - | - | - |
| Mana x SN | - | - | 1.659 | 0.007 | - | - | - | - | - | - | - | - |
| Mana x DSNH | - | - | - | - | - | - | - | - | 0.237 | 0.004 | - | - |
| | | | | | | | | | | | | |
| Post-hoc Management | - | - | Z | P | - | - | - | - | - | - | Z | P |
| Org – SN == 0 | - | - | -2.249 | 0.014* | - | - | - | - | - | - | 1.554 | 0.048* |
| IPM – SN == 0 | - | - | -3.541 | 0.008** | - | - | - | - | - | - | 0.021 | 1.000 |
| IPM – Org == 0 | - | - | -1.900 | 0.037* | - | - | - | - | - | - | -0.682 | 0.773 |
| | | | | | | | | | | | | |

**Table S5.3.** Results of the initial linear mixed effects models for the **biodiversity ecosystem service indicators and biodiversity multifunctionality**, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, SHDI = Shannon landscape diversity index, ED = landscape edge density). Test statistic (Z) and P-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Biodiversity multifunctionality $R^2_m$= 0.231 $R^2_c$ = 0.565 | | Diversity plants $R^2_m$= 0.612 $R^2_c$ = 0.683 | | Diversity arthropods $R^2_m$= 0.352 $R^2_c$ = 0.447 | | Diversity fungi $R^2_m$= 0.061 $R^2_c$ = 0.197 | | Diversity bacteria $R^2_m$= 0.591 $R^2_c$ = 0.804 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ |
| Management | 4.889* | 0.031 | 70.731*** | 0.132 | 3.842* | 0.026 | 2.379 | 0.014 | 23.301*** | 0.245 |
| Location | 16.641*** | 0.064 | 4.926* | 0.032 | 4.359* | 0.072 | 20.933*** | 0.065 | 5.037* | 0.041 |
| OR (%) | 0.596 | 0.005 | - | - | - | - | - | - | 0.490 | 0.006 |
| SNH (%) | 2.628 | 0.021 | - | - | - | - | - | - | 0.395 | 0.006 |
| ED (m/ha) | 1.246 | 0.006 | 1.671 | 0.11 | - | - | - | - | - | - |
| MEM1 | - | - | 1.658 | 0.009 | - | - | - | - | - | - |
| MEM3 | - | - | - | - | 1.575 | 0.004 | - | - | 1.838 | 0.023 |
| MEM6 | - | - | - | - | 4.951* | 0.085 | - | - | 0.385 | 0.010 |
| MEM13 | - | - | - | - | - | - | - | - | 6.786* | 0.120 |
| Ground drainage class | - | - | - | - | - | - | - | - | 2.325 | 0.030 |
| Diversity plants | - | - | - | - | 5.305* | 0.081 | - | - | - | - |
| Mana x Location | 16.176*** | 0.052 | 18.453*** | 0.83 | 9.078** | 0.052 | - | - | 3.185 | 0.015 |
| Mana x ED | 5.684* | 0.027 | - | - | - | - | - | - | - | - |
| Mana x Diversity plants | - | - | - | - | 5.931* | 0.041 | - | - | - | - |
| Mana x SHDI | - | - | - | - | 2.620 | 0.024 | - | - | - | - |
| | | | | | | | | | | |
| Post-hoc Management | Z | P | Z | P | Z | P | - | - | Z | P |
| Org – SN == 0 | -0.703 | 0.762 | -2.660 | 0.008** | -1.195 | 0.443 | - | - | 4.286 | <0.001*** |
| IPM – SN == 0 | -1.908 | 0.035* | -2.640 | 0.002** | -1.885 | 0.046* | - | - | 4.643 | <0.001*** |
| IPM – Org == 0 | -1.331 | 0.071 | -1.961 | 0.047* | -1.599 | 0.053 | - | - | 0.488 | 0.876 |
| | | | | | | | | | | |

**Table S5.4.** Results of the linear mixed effects models for the **pollination ecosystem service indicators and pollination multifunctionality**, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Test statistic (*Z*) and *P*-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Pollination multifunct. $R^2_m$= 0.221 $R^2_c$ = 0.224 | | Seed set apple $R^2_m$= 0.125 $R^2_c$ = 0.335 | | Pollinator div. strawberry $R^2_m$= 0.153 $R^2_c$ = 0.210 | | Pollinator div. apple $R^2_m$= 0.107 $R^2_c$ = 0.369 | | Fruit set strawberry $R^2_m$= 0.337 $R^2_c$ = 0.382 | | Seed set strawberry $R^2_m$= 0.159 $R^2_c$ = 0.438 | | Fruit set apple $R^2_m$= 0.084 $R^2_c$ = 0.172 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ |
| Management | 4.715* | 0.042 | 9.359** | 0.076 | 11.055** | 0.075 | 5.436* | 0.046 | 21.282*** | 0.117 | 8.852* | 0.073 | 0.298 | 0.006 |
| Location | 5.947* | 0.38 | 0.596 | 0.001 | 3.227 | 0.014 | 6.153* | 0.023 | 17.992** | 0.131 | 0.806 | 0.010 | 1.080 | 0.008 |
| OR (%) | - | - | - | - | 0.243 | 0.002 | 0.119 | 0.001 | - | - | - | - | - | - |
| SNH (%) | 1.269 | 0.009 | - | - | 0.496 | 0.003 | 5.862* | 0.035 | - | - | - | - | - | - |
| DSNH (m) | - | - | 0.006 | 0.002 | 0.276 | 0.002 | 0.107 | 0.001 | - | - | 0.107 | 0.001 | 0.121 | 0.001 |
| SHDI | 0.025 | 0.003 | - | - | - | - | 3.896* | 0.023 | 6.664* | 0.073 | 3.895* | 0.047 | - | - |
| ED (m/ha) | 3.845* | 0.029 | 1.829 | 0.010 | 0.176 | 0.002 | 0.482 | 0.003 | - | - | - | - | 5.591* | 0.032 |
| Diversity plants | 1.408 | 0.005 | 2.477 | 0.003 | - | - | 0.007 | 0.001 | - | - | - | - | 13.112*** | 0.122 |
| Richness plants | 0.051 | 0.001 | - | - | 1.470 | 0.007 | 1.933 | 0.009 | 0.065 | 0.002 | - | - | - | - |
| Pollinator diversity | - | - | 0.004 | 0.001 | - | - | - | - | - | - | 1.670 | 0.021 | 0.367 | 0.009 |
| Mana x Location | - | - | - | - | - | - | 3.827 | 0.018 | 4.188* | 0.053 | 5.235* | 0.033 | - | - |
| Mana x Richness plants | 1.281 | 0.011 | - | - | 5.057* | 0.019 | - | - | 1.649 | 0.031 | - | - | - | - |
| Mana x Pollinator diversity | - | - | 0.112 | 0.001 | - | - | - | - | 6.511** | 0.094 | - | - | - | - |
| Mana x DNSH | - | - | - | - | - | - | - | - | - | - | 4.926* | 0.058 | - | - |
| Mana x SHDI | 7.685* | 0.043 | - | - | - | - | - | - | - | - | - | - | - | - |
| Mana x SN | 9.616** | 0.055 | - | - | 9.759** | 0.034 | - | - | - | - | - | - | - | - |
| Mana x ED | - | - | - | - | 3.908 | 0.024 | - | - | 2.495 | 0.046 | - | - | - | - |
| | | | | | | | | | | | | | | |
| Post-hoc Management | Z | P | Z | P | Z | P | Z | P | Z | P | Z | P | Z | P |
| Org – SN == 0 | -1.651 | 0.220 | -0.862 | 0.650 | -1.970 | 0.046* | -0.130 | 0.990 | -0.675 | 0.929 | -2.787 | 0.015* | - | - |
| IPM – SN == 0 | -2.819 | 0.013* | -2.377 | 0.043* | -2.600 | 0.024* | -2.101 | 0.037* | -3.440 | 0.002** | -2.513 | 0.032* | - | - |
| IPM – Org == 0 | -1.932 | 0.032* | -2.911 | 0.009** | -2.597 | 0.024* | -1.635 | 0.058 | -1.363 | 0.082 | 0.063 | 0.998 | - | - |
| | | | | | | | | | | | | | | |

**Table S5.5.** Results of the linear mixed effects models for the **pest control ecosystem service indicators and pest control multifunctionality**, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, DSNH = distance to nearest semi-natural habitat, SHDI = Shannon landscape diversity index, ED = landscape edge density). Test statistic (*Z*) and *P*-values for post-hoc tests analyzing pairwise differences between management types are reported at the bottom of the table (Org = organic orchards, IPM = Integrated Pest Management orchards, SN = semi-natural references).

| Response variables → Explanatory variables ↓ | Pest control multifunctionality $R^2_m$= 0.065 $R^2_c$ = 0.608 | | Natural enemy egg predation $R^2_m$= 0.128 $R^2_c$ = 0.517 | | Natural enemy abundance $R^2_m$= 0.433 $R^2_c$ = 0.823 | | Natural enemy energy use $R^2_m$= 0.061 $R^2_c$ = 0.802 | | Pest regulation $R^2_m$= 0.668 $R^2_c$ = 0.941 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ |
| Management[§] | 2.848 | 0.014 | 6.058* | 0.012 | 5.711* | 0.025 | 7.399* | 0.029 | 9.201** | 0.017 |
| Location | 3.988* | 0.031 | 5.648* | 0.011 | 2.470 | 0.006 | - | - | 2.924 | 0.002 |
| OR (%) | 2.145 | 0.019 | 0.014 | 0.001 | 9.015** | 0.005 | 0.015 | 0.001 | 20.655*** | 0.023 |
| SNH (%) | 2.391 | 0.021 | 5.128* | 0.010 | 8.145** | 0.009 | 10.285** | 0.040 | 29.221*** | 0.036 |
| DSNH (m) | - | - | 1.364 | 0.002 | 5.285* | 0.003 | 3.158 | 0.009 | 7.013* | 0.007 |
| SHDI | - | - | 4.925* | 0.009 | - | - | 3.563 | 0.007 | - | - |
| ED (m/ha) | 0.269 | 0.002 | 0.168 | 0.001 | 8.317* | 0.010 | 8.402** | 0.033 | 27.814*** | 0.024 |
| Diversity plants | 5.676* | 0.037 | - | - | - | - | - | - | - | - |
| Predator abundance | - | - | 5.691* | 0.011 | - | - | - | - | - | - |
| Predator energy use | - | - | 4.822* | 0.009 | - | - | - | - | 16.228*** | 0.017 |
| Predator egg predation | - | - | - | - | - | - | - | - | 0.981 | 0.001 |
| MEM2 | - | - | 2.061 | 0.002 | 1.250 | 0.002 | - | - | 0.054 | 0.001 |
| MEM3 | - | - | - | - | 2.015 | 0.002 | - | - | 2.888 | 0.003 |
| MEM6 | - | - | 3.211 | 0.005 | 4.902* | 0.018 | 1.921 | 0.006 | - | - |
| Mana x Location | - | - | 2.885 | 0.003 | - | - | 3.965 | 0.007 | 3.629 | 0.003 |
| Mana x Predator abundance | - | - | 6.344* | 0.016 | - | - | - | - | - | - |
| Mana x Predator energy use | - | - | 7.692* | 0.021 | - | - | - | - | - | - |
| Mana x SHDI | - | - | 6.525* | 0.011 | 6.474* | 0.008 | - | - | - | - |
| Mana x OR | 2.871 | 0.016 | 1.922 | 0.002 | 1.958 | 0.001 | 4.833* | 0.017 | 1.299 | 0.002 |
| Mana x SN | 4.983* | 0.066 | 4.108 | 0.007 | 1.211 | 0.002 | - | - | 1.523 | 0.003 |
| Mana x ED | - | - | 1.903 | 0.004 | 13.861*** | 0.012 | - | - | - | - |
| | | | | | | | | | | |
| Post-hoc Management | Z | P | Z | P | Z | P | Z | P | Z | P |
| Org – SN == 0 | - | - | -2.711 | 0.017* | -2.714 | 0.011* | 3.736 | 0.002** | - | - |
| IPM – SN == 0 | - | - | -2.600 | 0.024* | -3.489 | 0.002** | 3.055 | 0.003** | - | - |
| IPM – Org == 0 | - | - | -0.094 | 0.861 | -2.488 | 0.002* | -1.522 | 0.319 | - | - |

[§] The model for pest regulation only contains data from the organic and IPM orchards

**Table S5.6.** Results of the initial linear mixed effects models for the **yield ecosystem service indicators and yield multifunctionality** and the linear models for **income and income stability**, showing marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$-values for all models. Test statistic and semi-partial $R^2_\beta$ are given for each retained variable after model reduction (OR = orchard cover, SNH = semi-natural habitat cover, SHDI = Shannon landscape diversity index, ED = landscape edge density).

| Response variables → Explanatory variables ↓ | Yield multifunctionality $R^2_m$= 0.238 $R^2_c$ = 0.521 | | Yield $R^2_m$= 0.193 $R^2_c$ = 0.264 | | Yield stability $R^2_m$= 0.086 $R^2_c$ = 0.134 | | Income $R^2_m$= 0.109 $R^2_c$ = 0.109 | | Income stability $R^2_m$= 0.279 $R^2_c$ = 0.279 | | Income multifunctionality $R^2_m$= 0.143 $R^2_c$ = 0.143 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ | *F* | $R^2_\beta$ |
| Management[§] | 6.529** | 0.055 | 9.355** | 0.134 | 3.894* | 0.024 | 0.234 | 0.008 | 0.117 | 0.009 | 0.098 | 0.006 |
| Location | 7.256** | 0.027 | 6.328** | 0.068 | 0.922 | 0.003 | - | - | - | - | - | - |
| SNH (%) | 4.492* | 0.016 | 2.555 | 0.012 | 5.548* | 0.032 | - | - | 0.804 | 0.005 | - | - |
| ED (m/ha) | - | - | 0.727 | 0.002 | - | - | 2.339 | 0.027 | 1.474 | 0.017 | 1.233 | 0.011 |
| SHDI | 2.926 | 0.008 | 1.498 | 0.006 | 5.113* | 0.029 | - | - | - | - | - | - |
| Diversity fungi | 1.671 | 0.007 | - | - | - | - | - | - | - | - | - | - |
| Diversity plants | 1.189 | 0.003 | 0.631 | 0.003 | 0.966 | 0.001 | 0.543 | 0.011 | 0.553 | 0.014 | 0.526 | 0.008 |
| Diversity arthropods | - | - | - | - | - | - | 1.521 | 0.013 | - | - | 0.211 | 0.002 |
| Natural enemy abundance | - | - | - | - | - | - | - | - | 0.089 | 0.022 | - | - |
| Soil respiration | 0.928 | 0.002 | - | - | - | - | - | - | - | - | - | - |
| Litter decomposition | 0.930 | 0.001 | - | - | - | - | - | - | - | - | - | - |
| Carbon stock | 0.065 | 0.001 | - | - | - | - | - | - | - | - | - | - |
| Apple seed set | - | - | 3.385 | 0.026 | - | - | - | - | - | - | - | - |
| Pollinator diversity | - | - | - | - | 1.582 | 0.004 | - | - | - | - | - | - |
| Arthropod diversity | - | - | - | - | 1.153 | 0.005 | - | - | - | - | - | - |
| | | | | | | | | | | | | |

[§] Models only contains data from the organic and IPM orchards

**Table S5.7.** Summary statistics of the piecewise structural equation models (PSEMs) for soil multifunctionality and soil ES indicators, considering both direct and indirect relationships between drivers and response variables. Each row represents a PSEM pathway for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fits was assessed using Fischer's C statistics.

| Response variable | Predictor variable | *Estimate* | *SE* | *P* |
|---|---|---|---|---|
| **Soil multifunctionality** | Orchard drive row (vs. crop row) | 1,234 | 0,168 | 0,000 |
| | Diversity plants | 0,418 | 0,138 | 0,008 |
| | Organic management (vs. IPM) | 0,207 | 0,091 | 0,027 |
| | Soil pH | 0,115 | 0,081 | 0,161 |
| | Richness fungi | -0,039 | 0,067 | 0,564 |
| Diversity plants | Orchard drive row (vs. crop row) | 0,712 | 0,149 | 0,000 |
| | Organic management (vs. IPM) | 0,343 | 0,129 | 0,017 |
| | Landscape Shannon diversity 100 m | 0,235 | 0,108 | 0,032 |
| | Edge density 1000 m | -0,244 | 0,125 | 0,054 |
| **Soil respiration** | Orchard drive row (vs. crop row) | 0,726 | 0,124 | 0,000 |
| | Diversity plants | 0,437 | 0,081 | 0,000 |
| | Richness fungi | 0,271 | 0,046 | 0,009 |
| | Soil C:N ratio | 0,141 | 0,054 | 0,029 |
| | Organic management (vs. IPM) | 0,114 | 0,042 | 0,046 |
| Diversity plants | Organic management (vs. IPM) | 0,474 | 0,151 | 0,007 |
| | Landscape Shannon diversity 100 m | 0,193 | 0,078 | 0,016 |
| | Orchard drive row (vs. crop row) | -0,126 | 0,132 | 0,342 |
| | Edge density 1000 m | -0,131 | 0,167 | 0,435 |
| Richness fungi | Orchard drive row (vs. crop row) | 0,678 | 0,160 | 0,000 |
| | Organic management (vs. IPM) | 0,258 | 0,101 | 0,012 |
| | Orchard cover 100 m | 0,207 | 0,113 | 0,016 |
| | Edge density 100 m | -0,120 | 0,109 | 0,047 |
| **Carbon stock** | Diversity plants | 0,265 | 0,056 | 0,000 |
| | Orchard drive row (vs. crop row) | 0,347 | 0,076 | 0,000 |
| | Landscape Shannon diversity 1000 m | 0,152 | 0,061 | 0,000 |
| | Semi-natural habitat 1000 m | 0,129 | 0,121 | 0,280 |
| | Richness bacteria | 0,076 | 0,067 | 0,264 |
| | Organic management (vs. IPM) | 0,179 | 0,272 | 0,520 |
| Diversity plants | Organic management (vs. IPM) | 0,474 | 0,151 | 0,007 |
| | Landscape Shannon diversity 100 m | 0,193 | 0,078 | 0,016 |
| | Orchard drive row (vs. crop row) | -0,126 | 0,132 | 0,342 |
| | Edge density 1000 m | -0,131 | 0,167 | 0,435 |
| **Nitrogen mineralization** | Orchard drive row (vs. crop row) | 0,649 | 0,138 | 0,000 |
| | Organic management (vs. IPM) | 0,286 | 0,110 | 0,015 |
| | Soil organic carbon content | -0,125 | 0,100 | 0,217 |
| | Richness bacteria | -0,022 | 0,073 | 0,760 |
| | Soil C:N ratio | -0,041 | 0,137 | 0,766 |
| | Diversity plants | 0,003 | 0,089 | 0,976 |
| **Litter stabilisation** | Soil pH | 0,285 | 0,120 | 0,021 |
| | Orchard drive row (vs. crop row) | 0,628 | 0,274 | 0,025 |
| | Diversity plants | 0,256 | 0,148 | 0,089 |

**(Table S5.7 continued)**

| | | | | |
|---|---|---|---|---|
| | Edge density 100 m | 0,262 | 0,181 | 0,153 |
| | Soil organic carbon content | 0,148 | 0,134 | 0,275 |
| | Organic management (vs. IPM) | 0,379 | 0,376 | 0,328 |
| | Richness fungi | -0,033 | 0,103 | 0,752 |
| Diversity plants | Organic management (vs. IPM) | 0,474 | 0,151 | 0,007 |
| | Landscape Shannon diversity 100 m | 0,193 | 0,078 | 0,016 |
| | Orchard drive row (vs. crop row) | -0,126 | 0,132 | 0,342 |
| | Edge density 1000 m | -0,131 | 0,167 | 0,435 |
| **Litter decomposition** | Orchard drive row (vs. crop row) | -0,386 | 0,192 | 0,005 |
| | Organic management (vs. IPM) | 0,183 | 0,098 | 0,015 |
| | Soil C:N ratio | 0,122 | 0,075 | 0,025 |
| | Diversity plants | -0,178 | 0,166 | 0,289 |
| | Richness plants | -0,157 | 0,220 | 0,479 |
| | Diversity fungi | -0,004 | 0,105 | 0,970 |
| Diversity plants | Organic management (vs. IPM) | 0,474 | 0,151 | 0,007 |
| | Landscape Shannon diversity 100 m | 0,193 | 0,078 | 0,016 |
| | Orchard drive row (vs. crop row) | -0,126 | 0,132 | 0,342 |
| | Edge density 1000 m | -0,131 | 0,167 | 0,435 |

**Table S5.8.** Summary statistics of the piecewise structural equation models (PSEMs) for biodiversity multifunctionality and biodiversity ES indicators, considering both direct and indirect relationships between drivers and response variables. Each row represents a PSEM pathway for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fits was assessed using Fischer's C statistics.

| **Response variable** | **Predictor variable** | ***Estimate*** | ***SE*** | ***P*** |
|---|---|---|---|---|
| Biodiversity multifunctionality | Orchard edge (vs. center) | 0,538 | 0,070 | 0,000 |
| | Organic management (vs. IPM) | 0,312 | 0,106 | 0,005 |
| | Semi-natural habitat 1000 m | 0,101 | 0,032 | 0,027 |
| | Orchard cover 1000 m | -0,081 | 0,030 | 0,042 |
| | Edge density 100 m | 0,005 | 0,072 | 0,948 |
| Diversity plants | Organic management (vs. IPM) | 0,252 | 0,056 | 0,000 |
| | Landscape Shannon diversity 100 m | 0,226 | 0,135 | 0,024 |
| | Edge density 1000 m | 0,002 | 0,064 | 0,971 |
| Diversity arthropods | Orchard edge (vs. center) | 0,576 | 0,136 | 0,000 |
| | Organic management (vs. IPM) | 0,420 | 0,123 | 0,003 |
| | Edge density 1000 m | 0,319 | 0,134 | 0,019 |
| | Orchard cover 100 m | -0,260 | 0,126 | 0,041 |
| | Diversity plants | 0,309 | 0,152 | 0,044 |
| Diversity plants | Organic management (vs. IPM) | 0,252 | 0,056 | 0,000 |
| | Landscape Shannon diversity 100 m | 0,226 | 0,135 | 0,024 |
| | Edge density 1000 m | 0,002 | 0,064 | 0,971 |
| Diversity fungi | Orchard drive row (vs. crop row) | 0,485 | 0,105 | 0,000 |
| | Semi-natural habitat 1000 m | 0,210 | 0,069 | 0,003 |
| | Orchard cover 1000 m | 0,172 | 0,080 | 0,032 |

**(Table S5.8 continued)**

| | | | | |
|---|---|---|---|---|
| | Organic management (vs. IPM) | -0,057 | 0,076 | 0,462 |
| Diversity bacteria | Orchard drive row (vs. crop row) | -0,512 | 0,060 | 0,000 |
| | Semi-natural habitat 1000 m | 0,251 | 0,169 | 0,138 |
| | Edge density 100 m | 0,071 | 0,084 | 0,401 |
| | Organic management (vs. IPM) | 0,024 | 0,114 | 0,837 |
| | Landscape Shannon diversity 1000 m | -0,022 | 0,173 | 0,900 |

**Table S5.9.** Summary statistics of the piecewise structural equation models (PSEMs) for pollination multifunctionality and pollination ES indicators, considering both direct and indirect relationships between drivers and response variables. Each row represents a PSEM pathway for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fits was assessed using Fischer's C statistics.

| **Response variable** | **Predictor variable** | ***Estimate*** | ***SE*** | ***P*** |
|---|---|---|---|---|
| Pollination multifunctionality | Organic management (vs. IPM) | 0,294 | 0,082 | 0,001 |
| | Orchard edge (vs. center) | 0,330 | 0,117 | 0,005 |
| | Semi-natural habitat 1000 m | 0,246 | 0,093 | 0,009 |
| | Landscape Shannon diversity 1000 m | 0,190 | 0,100 | 0,061 |
| | Edge density 1000 m | 0,119 | 0,087 | 0,174 |
| | Diversity plants | 0,094 | 0,070 | 0,176 |
| Apple seed set | Organic management (vs. IPM) | 0,522 | 0,178 | 0,005 |
| | Orchard edge (vs. center) | 0,147 | 0,059 | 0,035 |
| | Pollinator diversity apple | 0,086 | 0,131 | 0,510 |
| | Landscape Shannon diversity 100 m | 0,032 | 0,083 | 0,699 |
| | Diversity plants | 0,022 | 0,076 | 0,776 |
| Pollinator diversity strawberry | Diversity plants | 0,126 | 0,081 | 0,001 |
| | Organic management (vs. IPM) | 0,180 | 0,229 | 0,001 |
| | Semi-natural habitat 1000 m | 0,223 | 0,091 | 0,015 |
| | Orchard edge (vs. center) | 0,152 | 0,127 | 0,023 |
| | Edge density 1000 m | -0,130 | 0,112 | 0,248 |
| | Landscape Shannon diversity 100 m | 0,039 | 0,100 | 0,695 |
| | Distance to SN-habitat | -0,031 | 0,102 | 0,764 |
| Diversity plants | Landscape Shannon diversity 100 m | 0,293 | 0,087 | 0,001 |
| | Organic management (vs. IPM) | 0,257 | 0,124 | 0,001 |
| | Edge density 1000 m | 0,021 | 0,123 | 0,083 |
| Pollinator diversity apple | Semi-natural habitat 1000 m | 0,337 | 0,124 | 0,008 |
| | Organic management (vs. IPM) | 0,388 | 0,277 | 0,008 |
| | Orchard edge (vs. center) | 0,387 | 0,189 | 0,043 |
| | Landscape Shannon diversity 1000 m | -0,213 | 0,159 | 0,182 |
| | Orchard cover 1000 m | 0,076 | 0,106 | 0,476 |
| | Edge density 1000 m | 0,082 | 0,118 | 0,490 |
| | Diversity plants | -0,075 | 0,110 | 0,497 |
| | Distance to SN-habitat | -0,032 | 0,119 | 0,788 |
| Strawberry fruit set | Orchard cover 1000 m | -0,428 | 0,143 | 0,004 |
| | Orchard edge (vs. center) | 0,460 | 0,215 | 0,037 |

**(Table S2.9 continued)**

| | | | | |
|---|---|---|---|---|
| | Landscape Shannon diversity 1000 m | 0,247 | 0,134 | 0,071 |
| | Pollinator diversity strawberry | 0,175 | 0,174 | 0,318 |
| | Pollinator diversity strawberry | 0,152 | 0,168 | 0,370 |
| | Edge density 100 m | 0,070 | 0,128 | 0,587 |
| | Organic management (vs. IPM) | 0,051 | 0,148 | 0,737 |
| | Pollinator abundance strawberry | 0,018 | 0,137 | 0,894 |
| Strawberry seed sed | Orchard edge (vs. center) | 0,494 | 0,264 | 0,007 |
| | Pollinator diversity strawberry | 0,228 | 0,187 | 0,023 |
| | Semi-natural habitat 100 m | 0,170 | 0,141 | 0,237 |
| | Pollinator diversity strawberry | 0,211 | 0,201 | 0,301 |
| | Landscape Shannon diversity 1000 m | 0,145 | 0,139 | 0,304 |
| | Organic management (vs. IPM) | 0,111 | 0,332 | 0,743 |
| | Diversity plants | -0,007 | 0,158 | 0,818 |
| Pollinator diversity strawberry | Diversity plants | 0,127 | 0,157 | 0,004 |
| | Organic management (vs. IPM) | 0,186 | 0,203 | 0,008 |
| | Orchard edge (vs. center) | 0,125 | 0,250 | 0,042 |
| | Semi-natural habitat 1000 m | 0,206 | 0,190 | 0,029 |
| | Distance to SN-habitat | -0,127 | 0,190 | 0,510 |
| | Edge density 1000 m | -0,188 | 0,211 | 0,378 |
| | Landscape Shannon diversity 100 m | 0,065 | 0,178 | 0,717 |
| Diversity plants | Landscape Shannon diversity 100 m | 0,270 | 0,096 | 0,000 |
| | Organic management (vs. IPM) | 0,240 | 0,150 | 0,002 |
| | Edge density 1000 m | 0,023 | 0,131 | 0,175 |
| Apple fruit set | Pollinator diversity apple | 0,329 | 0,080 | 0,001 |
| | Diversity plants | 0,198 | 0,092 | 0,033 |
| | Edge density 1000 m | 0,194 | 0,098 | 0,048 |
| | Orchard edge (vs. center) | 0,109 | 0,133 | 0,414 |
| | Organic management (vs. IPM) | 0,098 | 0,119 | 0,418 |
| | Pollinator diversity apple | 0,039 | 0,070 | 0,582 |
| Pollinator diversity apple | Organic management (vs. IPM) | 0,377 | 0,287 | 0,012 |
| | Semi-natural habitat 1000 m | 0,226 | 0,097 | 0,021 |
| | Orchard edge (vs. center) | 0,390 | 0,191 | 0,043 |
| | Edge density 1000 m | 0,128 | 0,118 | 0,279 |
| | Diversity plants | -0,073 | 0,113 | 0,515 |
| | Orchard cover 1000 m | 0,058 | 0,110 | 0,601 |
| | Distance to SN-habitat | -0,045 | 0,114 | 0,690 |
| | Landscape Shannon diversity 1000 m | 0,009 | 0,105 | 0,930 |
| Diversity plants | Organic management (vs. IPM) | 0,246 | 0,062 | 0,000 |
| | Landscape Shannon diversity 100 m | 0,216 | 0,135 | 0,012 |
| | Edge density 1000 m | 0,004 | 0,066 | 0,851 |

**Table S5.10.** Summary statistics of the piecewise structural equation models (PSEMs) for pest control multifunctionality and pest control ES indicators, considering both direct and indirect relationships between drivers and response variables. Each row represents a PSEM pathway for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fits was assessed using Fischer's C statistics.

| Response variable | Predictor variable | *Estimate* | *SE* | *P* |
|---|---|---|---|---|
| Pest control multifunctionality | Semi-natural habitat 100 m | 0,166 | 0,066 | 0,013 |
| | Edge density 1000 m | -0,168 | 0,082 | 0,042 |
| | Diversity plants | 0,127 | 0,059 | 0,045 |
| | Orchard cover 1000 m | -0,120 | 0,069 | 0,082 |
| | Orchard edge (vs. center) | 0,151 | 0,115 | 0,190 |
| | Landscape Shannon diversity 100 m | -0,056 | 0,073 | 0,450 |
| | Organic management (vs. IPM) | -0,056 | 0,084 | 0,510 |
| Diversity plants | Organic management (vs. IPM) | 0,413 | 0,122 | 0,003 |
| | Landscape Shannon diversity 100 m | 0,254 | 0,093 | 0,007 |
| | Edge density 1000 m | 0,031 | 0,078 | 0,368 |
| Natural enemy egg predation | Orchard edge (vs. center) | 0,184 | 0,031 | <0,001 |
| | Semi-natural habitat 100 m | 0,259 | 0,055 | <0,001 |
| | Natural enemy abundance | 0,140 | 0,010 | <0,001 |
| | Edge density 100 m | 0,253 | 0,073 | <0,001 |
| | Organic management (vs. IPM) | 0,219 | 0,113 | 0,056 |
| | Natural enemy energy use | 0,085 | 0,051 | 0,103 |
| | Distance to SN-habitat | 0,015 | 0,087 | 0,862 |
| Natural enemy abundance | Orchard cover 1000 m | -0,261 | 0,077 | 0,001 |
| | Semi-natural habitat 100 m | 0,092 | 0,080 | 0,001 |
| | Organic management (vs. IPM) | 0,215 | 0,083 | 0,013 |
| | Distance to SN-habitat | -0,072 | 0,009 | 0,017 |
| | Orchard edge (vs. center) | 0,056 | 0,022 | 0,076 |
| | Edge density 100 m | -0,061 | 0,032 | 0,212 |
| Natural enemy abundance | Orchard cover 1000 m | -0,261 | 0,077 | 0,001 |
| | Semi-natural habitat 100 m | 0,092 | 0,080 | 0,001 |
| | Organic management (vs. IPM) | 0,215 | 0,083 | 0,013 |
| | Distance to SN-habitat | -0,072 | 0,009 | 0,017 |
| | Orchard edge (vs. center) | -0,056 | 0,022 | 0,076 |
| | Edge density 100 m | -0,061 | 0,032 | 0,212 |
| Natural enemy energy use | Semi-natural habitat 100 m | 0,133 | 0,037 | <0,001 |
| | Edge density 100 m | 0,188 | 0,070 | 0,011 |
| | Distance to SN-habitat | 0,090 | 0,051 | 0,102 |
| | Organic management (vs. IPM) | 0,061 | 0,058 | 0,417 |
| | Orchard edge (vs. center) | -0,008 | 0,020 | 0,641 |
| Pest regulation | Predator energy use | -0,277 | 0,046 | <0,001 |
| | Semi-natural habitat 100 m | -0,928 | 0,161 | <0,001 |
| | Orchard edge (vs. center) | 0,147 | 0,024 | <0,001 |
| | Edge density 1000 m | -0,713 | 0,121 | <0,001 |
| | Organic management (vs. IPM) | -0,612 | 0,234 | 0,005 |
| | Predator richness | -0,049 | 0,019 | 0,029 |

| | | | | |
|---|---|---|---|---|
| **(Table S5.10 continued)** | Orchard cover 1000 m | 0,162 | 0,810 | 0,036 |
| | Distance to SN-habitat | -0,164 | 0,135 | 0,218 |
| | Predator abundance | 0,007 | 0,010 | 0,513 |
| Natural enemy richness | Organic management (vs. IPM) | 0,222 | 0,061 | 0,001 |
| | Orchard cover 1000 m | -0,135 | 0,066 | 0,024 |
| | Semi-natural habitat 100 m | 0,076 | 0,021 | 0,033 |
| | Orchard edge (vs. center) | -0,007 | 0,009 | 0,579 |
| | Distance to SN-habitat | 0,008 | 0,034 | 0,923 |
| Natural enemy energy use | Semi-natural habitat 100 m | 0,137 | 0,034 | <0,001 |
| | Edge density 100 m | 0,175 | 0,062 | 0,009 |
| | Distance to SN-habitat | 0,086 | 0,047 | 0,092 |
| | Organic management (vs. IPM) | 0,074 | 0,061 | 0,618 |
| | Orchard edge (vs. center) | -0,064 | 0,052 | 0,802 |

**Table S5.11.** Summary statistics of the piecewise structural equation models (PSEMs) for yield multifunctionality and yield ES indicators, considering both direct and indirect relationships between drivers and response variables. Each row represents a PSEM pathway for which the path coefficient (= Estimate), standard error (SE) and p-value are given. The final model fits was assessed using Fischer's C statistics.

| **Response variable** | **Predictor variable** | ***Estimate*** | ***SE*** | ***P*** |
|---|---|---|---|---|
| Yield multifunctionality | Semi-natural habitat 1000 m | -0,216 | 0,086 | 0,003 |
| | Landscape Shannon diversity 100 m | -0,140 | 0,052 | 0,010 |
| | Orchard edge (vs. center) | 0,130 | 0,052 | 0,013 |
| | Organic management (vs. IPM) | -0,198 | 0,088 | 0,017 |
| | Nitrogen mineralisation | 0,198 | 0,106 | 0,120 |
| | Diversity bacteria | -0,179 | 0,115 | 0,146 |
| | Carbon stock | -0,091 | 0,105 | 0,423 |
| | Diversity plants | -0,039 | 0,049 | 0,429 |
| Yield | Organic management (vs. IPM) | -0,437 | 0,166 | 0,004 |
| | Orchard edge (vs. center) | 0,124 | 0,072 | 0,049 |
| | Semi-natural habitat 1000 m | -0,257 | 0,183 | 0,064 |
| | Landscape Shannon diversity 100 m | 0,283 | 0,196 | 0,153 |
| | Edge density 1000 m | 0,185 | 0,170 | 0,280 |
| | Diversity plants | -0,062 | 0,068 | 0,365 |
| Yield stability | Semi-natural habitat 1000 m | -0,252 | 0,139 | 0,009 |
| | Landscape Shannon diversity 100 m | -0,172 | 0,124 | 0,023 |
| | Organic management (vs. IPM) | 0,132 | 0,031 | 0,032 |
| | Pollinator diversity apple | 0,410 | 0,277 | 0,159 |
| | Diversity arthropods | 0,088 | 0,249 | 0,728 |
| | Diversity plants | 0,043 | 0,317 | 0,894 |

# PUBLICATION LIST

**A1 publications**

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*Shared first authors