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Managing biological control for fruit production in different European climates

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Für alle meine Obstbäuerinnen und Obstbauern am See

Willst du dich am Ganzen erquicken,
So musst du das Ganze im Kleinsten erblicken.

Johann Wolfgang von Goethe

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SUMMARY

Biological pest control in apple orchards is essential and depends on effective and sustainable agricultural management strategies at local and landscape scales. Local measures such as hedgerows, flowering strips, organic management as well as landscapes with a high diversity of cover types and low land-use intensity are assumed to support biological control specifically and ecosystem services in general. However, the influence of local measures, landscape characteristics and their interactions has rarely been studied in perennial crop systems across large latitudinal gradients. Studying ecosystem services across climatic regions is especially important in the face of climate change and induced shifts in species distribution. The present study assesses the effects of local and landscape factors on predatory arthropods and their prey, and on trade-offs between ecosystem services and fruit production in the intensive fruit production systems of three European countries. Local factors included quality of the adjacent habitat (e.g. cover of woody habitat and plant species richness) and two types of orchard management: integrated production (IP; based on the reduced and targeted application of synthetic agrochemicals) and organic management practices. Landscape factors included the amount of orchard cover in the surrounding landscape as a proxy for land-use intensity and landscape diversity. For three years I studied arthropod communities in 30 apple orchards in Germany, with a special focus on natural enemies and herbivores and their impact on tree health and fruit production. I analyzed data from these orchards and from 28 orchards in Spain and 28 orchards in Sweden, provided by collaborators working on the same European BiodivERsA project. As a member of a 17-scientist team, I investigated how agri-environmental schemes, management practices, and landscape composition can be enhanced to support (I) ecosystem services and biodiversity in general, (II) communities of predatory arthropods, and (III) specific predatory arthropod taxa.

The **first publication (Chapter 2)** offers an insight into the complex interactions of functional groups of arthropods (pollinators, predators, and pests) and their influence on fruit production in different environments. It presents natural enemies and their prey in the context of ecosystem service trade-offs. In cooperation with the project partners, I studied the effects of local and landscape factors on functional groups and their services and disservices in 86 European apple orchards in Germany, Sweden, and Spain, during one growing season (from March to October 2015) under a common study design and sampling protocol. Key functions of ecosystem service providers are biological pest control and pollination. Disservices are defined as fruit damage at harvest, and aphid infestation of target trees. Final yield (fruit production and seed set) is assessed as the ultimate measure for ecosystem service provisioning. Using structural equation models, we tested for trade-offs between ecosystem services and for effects of local and landscape variables. Across Europe organic management benefited natural enemies. Higher abundance of natural enemies in organic orchards partly compensated for higher fruit damage and lower yield in these systems. There was no general positive influence of agri-environmental schemes such as hedgerows or flower strips on natural enemies. However, a high flower cover in the understory indirectly increased final fruit yield by improving living conditions for wild bees. Diversity of beneficial arthropods was lower in landscapes with high land-use intensity.

The **second publication (Chapter 3)** focuses on natural enemy communities in apple orchards

across all three countries and differences in their responses to local and landscape factors. Together with partners in Spain, Sweden, and Germany, I give a closer look on each of seven groups of predatory arthropods: spiders (Araneae), beetles (Coleoptera), earwigs (Dermaptera), flies (Diptera), bugs (Heteroptera), lacewings (Neuroptera) and harvestmen (Opiliones). In 2015, we took beating samples in all 86 apple orchards to assess the abundance of predatory arthropods. Additionally, we calculated community energy use as a proxy for the communities' predation potential based on biomass and metabolic rates of predatory arthropods. In both IP and organic orchards, we detected contradicting influences of local and landscape factors on the studied predator groups. Organic management enhanced abundances of five out of seven predatory arthropod groups. It benefited spiders, beetles, earwigs, flies, and bugs, but the response was not consistent across countries. High local woody habitat cover enhanced earwig abundance in Sweden but not in Germany. Plant species richness negatively influenced bug abundance depending on country and management. Predation potential (energy use by the predator community) was higher in organic orchards in Spain but remained largely unaffected by local and landscape factors across Europe.

The **third publication (Chapter 4)** is a case study on a single predatory arthropod group, earwigs, and one of their main prey organisms, woolly apple aphids. Earwigs are expected to be important generalist predators in apple orchards, with woolly apple aphids being a common apple pest. I studied whether local factors such as the presence of woody habitats and organic management and landscapes with low land-use intensity enhance living conditions for earwigs in intensive fruit production systems. Earwigs were sampled using shelters in 30 apple orchards in Germany (2015-2016), and 28 orchards in Spain (2015), subjected to IP or organic management. At the same time, we assessed tree infestation by woolly apple aphids. Correlation analyses served to detect possible interactions between the abundance of earwigs and the availability of potential prey organisms. The results indicate that there is only a weak correlation between abundance of earwigs and tree infestation by woolly apple aphids. Earwigs of the species *Forficula auricularia* seem to respond indifferently to orchard management. Presence of adjacent woody elements reduced earwig abundance in IP orchards in Germany. In Spain we found two earwig species, *Forficula auricularia* and *F. pubescens*, but only *F. pubescens*, which did not occur in German orchards, profited from organic management.

The three different perspectives on predatory arthropods (Chapter 2-4) highlight the importance of local and landscape factors for ecosystem services in general and predatory arthropods in particular. Responses were not consistent between predator groups and countries, stressing the need to develop tailored and country-specific management schemes at the local and landscape scale beyond the promotion of organic management.

ZUSAMMENFASSUNG

Biologische Schädlingsregulierung ist für eine umwelt- und ressourcenschonende Apfelproduktion unabdingbar. Ihr Erfolg ist davon abhängig, dass auf lokaler Ebene und auf Landschaftsebene Bewirtschaftungsstrategien gefunden werden, die natürliche Gegenspieler fördern, ohne dabei den Schädlingsdruck zu erhöhen. Sowohl lokale Agrarumweltmaßnahmen, wie Hecken, Blühstreifen und biologische Bewirtschaftung, als auch Landschaften mit einer hohen Diversität an Landnutzungstypen und geringer Nutzungsintensität können Ökosystemdienstleistungen wie biologische Schädlingsregulierung fördern. Der Einfluss von lokalen Maßnahmen, von einer nützlingsfreundlichen Landschaft und von Interaktionen zwischen lokalen und Landschaftsfaktoren auf Ökosystemdienstleistungen wurde bisher nicht länderübergreifend in intensiv bewirtschafteten, mehrjährigen Anbausystemen überprüft. Vor dem Hintergrund des Klimawandels und damit einhergehenden Veränderungen in der Verbreitung von Arten muss die Wirkung von Agrarumweltmaßnahmen (hier einschließlich biologischer Bewirtschaftung) auf Ökosystemdienstleistungen über klimatische Regionen hinweg untersucht werden. Die vorliegende Arbeit erforscht den Einfluss lokaler Maßnahmen und Landschaftsfaktoren auf räuberische Arthropoden (hier Insekten und Spinnen) und ihre Beute sowie auf Zielkonflikte zwischen der Förderung von Biodiversität, Ökosystemdienstleistungen und Fruchtproduktion im Obstbau in drei Ländern Europas. Maßnahmen, die auf lokaler Ebene erfasst wurden, waren zum einen die Qualität angrenzender Habitate (z. B. das Vorhandensein von Gehölzstrukturen und eine hohe Pflanzendiversität) und zum anderen die Bewirtschaftung: integrierte Produktion (IP; basierend unter anderem auf der verringerten und gezielten Anwendung von chemisch-synthetischen Pflanzenschutzmitteln) und biologische Bewirtschaftung. Als Landschaftsfaktoren wurden die Landnutzungsintensität und die Diversität der Landschaft im Umkreis eines Kilometers berücksichtigt. Der Anteil an Obstanlagen diente dabei als Annäherungsmaß für eine erhöhte Nutzungsintensität. Über einen Zeitraum von drei Jahren habe ich im Rahmen der vorliegenden Dissertation Arthropoden-Gemeinschaften in 30 Apfelanlagen in Deutschland untersucht. Ein besonderer Fokus lag auf natürlichen Gegenspielern von Schädlingen sowie auf Herbivoren und ihrer Wirkung auf die Gesundheit der Obstbäume und die Fruchtproduktion. Meine Analysen bezogen sich sowohl auf die in Deutschland erhobenen Daten als auch auf Daten, die von meinen Biodiversa EcoFruit Projektpartnern in je 28 Apfelanlagen in Spanien und Schweden erhoben wurden. In einem Team von 17 Wissenschaftlern habe ich untersucht, wie Agrarumweltmaßnahmen, Anlagenbewirtschaftung und die umgebende Landschaft gestaltet werden können, um Ökosystemdienstleistungen und Biodiversität in Apfelanlagen zu fördern. Von dieser allgemeinen Betrachtung (Publikation I) ausgehend, habe ich mich damit beschäftigt, wie die Lebensräume für Gemeinschaften von räuberischen Arthropoden (Publikation II) sowie für einzelne Gruppen räuberischer Arthropoden in Apfelanlagen (Publikation III) verbessert werden können.

Die **erste Publikation (Kapitel 2)** ermöglicht einen Einblick in die komplexen Interaktionen funktionaler Arthropodengruppen (Bestäuber, Prädatoren und Schädlinge) und ihre Wirkung auf die Fruchtproduktion unter variierenden Umweltbedingungen. Die Studie analysiert Zielkonflikte bei der Förderung von Ökosystemdienstleistungen – unter anderem im Hinblick auf Ertrag, natürliche Gegenspieler und ihre Beute. In Kooperation mit unseren Projektpartnern habe ich dabei die Auswirkungen von lokalen und Landschaftsfaktoren auf die funktionalen Gruppen und auf von ihnen

erbrachte Ökosystemdienstleistungen sowie verursachte Schäden in 86 europäischen Apfelanlagen in Deutschland, Schweden und Spanien untersucht. Die Datenerfassung fand während einer Saison, zwischen März und Oktober 2015, unter Verwendung eines einheitlichen Versuchsdesigns statt. Schlüsselfunktionen von „Ökosystemdienstleistern“ sind hier biologische Schädlingsregulierung und Bestäubung, während Fruchtschäden zum Zeitpunkt der Ernte und Blattlausbefall als Schäden definiert wurden. Der Ertrag (erfasst als Fruchtproduktion und Samenansatz) diente in dieser Studie als Zielvariable für die Wirkung der Bereitstellung von Ökosystemdienstleistungen. Unter Verwendung von Strukturgleichungsmodellen wurden Zielkonflikte zwischen Ökosystemdienstleistungen, Biodiversitätsförderung und Fruchtproduktion untersucht. Die biologische Bewirtschaftung hatte über die drei Länder hinweg einen positiven Einfluss auf natürliche Gegenspieler. Die höhere Abundanz natürlicher Gegenspieler in Anlagen mit biologischer Bewirtschaftung kompensierte – zumindest teilweise – den erhöhten Fruchtschaden und den geringeren Ertrag in diesen Anlagen. Es konnte kein generell positiver Einfluss von Umweltmaßnahmen wie Hecken und blütenreichen Randstrukturen auf natürliche Gegenspieler festgestellt werden. Allerdings förderte eine hohe Blütendeckung im Unterwuchs und am Rand der Anlage indirekt den Fruchtertrag, indem sie sich positiv auf die Anzahl der Apfelblütenbesuche von Wildbienen auswirkte, von der wiederum die Bestäubungsleistung profitierte. Die Diversität von Nützlingen (räuberischen Arthropoden und Bestäubern) war in Landschaften mit hoher Nutzungsintensität geringer als in weniger intensiv genutzten Landschaften.

Die **zweite Publikation (Kapitel 3)** beschäftigt sich mit Gemeinschaften von räuberischen Arthropoden in Apfelanlagen in allen drei Ländern und untersucht den Einfluss von lokalen und Landschaftsfaktoren auf diese Gemeinschaften. Zusammen mit den Projektpartnern in Deutschland, Spanien und Schweden habe ich folgende sieben räuberische Arthropodengruppen näher betrachtet: Spinnen (Araneae), Käfer (Coleoptera), Ohrwürmer (Dermaptera), Fliegen (Diptera), Wanzen (Heteroptera), Netzflügler (Neuroptera) und Weberknechte (Opiliones). 2015 nahmen wir in allen 86 Apfelanlagen Klopfproben, um die Abundanz der Arthropoden zu erfassen. Zusätzlich wurde anhand der Biomasse und Metabolismusrate (Energieumsatz eines Organismus pro Zeiteinheit) der Arthropoden der Energieumsatz der Arthropodengemeinschaft berechnet. Er diente als Annäherungsmaß für das Prädationspotential der Gemeinschaften. Biologische Bewirtschaftung erhöhte die Abundanz in fünf der sieben Gruppen: Es profitierten Spinnen, Käfer, Ohrwürmer, Fliegen und Wanzen von biologischer Bewirtschaftung. Dabei war die Reaktion der Prädatorengruppen nicht kongruent in allen drei Ländern: Gruppen, die in einem Land von biologischer Bewirtschaftung profitierten, blieben in den anderen zwei Ländern davon teils unberührt. Wir fanden in IP- und Bio-Anlagen gegensätzliche Wirkungen von lokalen und Landschaftsfaktoren auf die untersuchten Prädatorengruppen: Ein größerer Anteil von angrenzenden Gehölzstrukturen in der direkten Umgebung der Apfelanlage erhöhte die Abundanz von Ohrwürmern in Schweden, verringerte sie jedoch in Deutschland. Eine hohe Pflanzendiversität hatte, abhängig von Land und Bewirtschaftung, einen negativen Einfluss auf die Abundanz von Wanzen. Das Prädationspotential (Energieumsatz der Prädatorengemeinschaft) war in Spanien in Bioanlagen höher als in IP-Anlagen, blieb aber in den übrigen Ländern unbeeinflusst von lokalen und Landschaftsfaktoren.

Die **dritte Publikation (Kapitel 4)** thematisiert den Einfluss von lokalen und Landschaftseinflüssen auf eine einzelne Arthropodengruppe (die Ohrwürmer) und einen für diese Gruppe wichtigen Beuteorganismus (die Apfelblutlaus). Ohrwürmer gelten als bedeutende generalistische Prädatoren in Apfelanlagen, Blutläuse als weit verbreitete Apfelschädlinge. Ich habe im Rahmen dieser Fallstudie untersucht, ob lokale Einflüsse wie das Vorhandensein von angrenzenden Gehölzstrukturen, eine biologische Bewirtschaftung der Anlage sowie Landschaften mit einer geringen Landnutzungsintensität die Lebensbedingung für Ohrwürmer in intensiven Anbausystemen verbessern. Dazu wurde in 30 Apfelanlagen in Deutschland (2015-2016) und 28 Apfelanlagen in

Spanien (2015) die Ohrwurmabundanz mittels Nisthilfen erfasst. In beiden Ländern wurden sowohl IP-Anlagen als auch biologisch bewirtschaftete Anlagen beprobt. Gleichzeitig wurde der Befall der Bäume durch Blutläuse erfasst. Um mögliche Zusammenhänge zwischen Ohrwurmabundanz und der Verfügbarkeit potentieller Beuteorganismen aufzuzeigen, wurden Korrelationsanalysen verwendet. Die Ergebnisse zeigten nur eine schwache Korrelation der Ohrwurmabundanz mit dem Blutlausbefall. Die Ohrwurmart *Forficula auricularia* blieb von der Bewirtschaftung der Anlage unbeeinflusst. Die Ohrwurmabundanz war in deutschen IP-Anlagen mit angrenzenden Gehölzstrukturen geringer als in IP-Anlagen ohne solche Strukturen. In Spanien waren die zwei Ohrwurmarten *Forficula auricularia* und *F. pubescens* in den Anlagen anzutreffen. Hier profitierte nur die in Deutschland nicht vorkommende Art *F. pubescens* von einer biologischen Bewirtschaftung der Apfelanlagen.

Die drei unterschiedlichen Perspektiven auf räuberische Arthropoden (Kapitel 2-4) zeigen, wie wichtig die Einflüsse von lokalen und Landschaftsfaktoren für Ökosystemdienstleistungen im Allgemeinen und räuberische Arthropoden im Besonderen sind. Dabei wird jedoch deutlich, dass Prädatoren je nach Land und Arthropodengruppe unterschiedlich auf solche Einflüsse reagieren. Agrarumweltmaßnahmen im Apfelanbau, dem wichtigsten mehrjährigen landwirtschaftlichen Produktionssystem in Europa, müssen über die Förderung von biologischer Bewirtschaftung hinaus an die Bedürfnisse einzelner Prädatorengruppen angepasst werden. Bei ihrer Auswahl müssen Zielkonflikte - beispielsweise zu der Förderung anderer Ökosystemdienstleistungen und der Ertragssicherung - abgewogen und vermieden werden. Vor dem Hintergrund möglicher, durch den Klimawandel induzierter Änderungen in der Artenverteilung innerhalb von Europa, sollten länderspezifische Gegebenheiten (wie Hauptschädlinge, ihr Voltinismus und ihre wichtigsten Gegenspieler) bei der Anpassung von Agrarumweltmaßnahmen und der Gestaltung der Agrarlandschaft berücksichtigt werden.

1. GENERAL INTRODUCTION

If you ask an apple grower what he needs for a good yield, his first answer will probably be, ‘Good soil, good weather, and healthy trees’. To improve productivity and health of apple trees, growers can choose from a broad range of management options and technologies. For chemical pest control, for instance, growers in Europe currently select from a set of 30 different insecticides and acaricides (Happe et al., 2019). Average costs of plant protection were estimated to make up about 40% of apple production costs (Yilmaz et al., 2015). At least part of these expenses can be effectively substituted by ecosystem services (Bale et al., 2008; Cross et al., 2015). In the toolbox of ecosystem services, two ecological processes are of vital importance for apple growers to enhance yield: biological control to reduce pest pressure, and pollination to enhance fruit production (Garibaldi et al., 2014; Mallinger and Gratton, 2015; Peisley et al., 2015). Supporting the two processes comes with one major asset: given their high impact both pollination and biological control are common goods and have low immediate and hidden costs (Bale et al., 2008). On the contrary, the high socio-economic and ecological value of nature’s contributions to people has so far largely been underestimated (Costanza et al., 2014; de Groot et al., 2012; TEEB, 2010). If apple growers and future generations want to count on them, it is necessary to enhance public awareness of their importance and to understand the habitat and resource requirements of biological control agents and pollinators in agricultural production systems.

Ecosystem services in fruit crops

In Europe, 75% of the land cover is utilized for agriculture (Robinson and Sutherland, 2002). Fruit production is one of its key sectors, covering 6.8% of EU agricultural output (Eurostat, 2017a). Apple (*Malus domestica* Borkh.) is the most important fruit crop in Europe in terms of harvest volume (12.6 million tonnes) (Eurostat, 2017a), and in 2015, 538,500 ha of European cropland was cultivated with apple orchards with 31,740 ha total planted area in Germany, 30,720 ha in Spain and 1,330 ha in Sweden (Eurostat, 2017b). *Malus domestica*, also known as *Malus pumila* Mill., is a cultivated representative of pome fruits (family Rosaceae) with Asian origin. In contrast to its native European relative, the wild crab apple *Malus sylvestris* (L.) Mill., it is commercially grown throughout the world for production of desert, culinary and cider apples (Alford, 2014).

Arthropods in apple orchards

Embedded in an agricultural matrix with high land-use intensity, orchards are important habitats for agrobiodiversity (Altieri, 1999). Habitat stability for arthropods in these perennial crop systems is considered higher than in annual crop systems since the host plant is available for years or even decades, and the system is unaffected by crop rotation or annual crop succession (Simon et al., 2010). Additionally, complex branching structure and availability of different strata such as crown and understory adds to the high habitat value of these systems for diverse communities of arthropods (Simon et al., 2010). Values for species richness of insects in apple orchards from the US and Europe reported by Szentkirályi & Kozár (1991) vary widely, ranging from 30 to 940 species; the authors suggest that a total of 400-800 insect species can be collected in orchards with low management intensity. Apart from length of collection period and the age of apple trees, quality of the adjacent habitat and disturbances, such as management intensity, and local plant diversity are major drivers of the observed high variability (Szentkirályi and Kozár, 1991).

Important apple pests

Apple trees in temperate regions can harbor up to 242 species of herbivorous insects (Brändle and Brandl, 2001) and a study from Hungary reported approximately 60 phytophagous arthropod species which are considered as apple pests (Jenser et al., 1999). The main pests with high economic impact in temperate apple orchards are phloem-feeders such as the rosy apple aphid *Dysaphis plantaginea* Passerini, the woolly apple aphid *Eriosoma lanigerum* Hausmann, and the green apple aphid *Aphis pomi* De Geer (Hemiptera: Aphididae) (Carroll and Hoyt, 1984), frugivores such as the codling moth *Cydia pomonella* L. (Fig. 1.1) and other herbivores including lepidopterans (Solomon et al., 2000; Unruh et al., 2016), the red spider mite, *Panonychus ulmi* Koch and other phytophagous mites (Simon et al., 2010), scale insects (Logan et al., 2017), and psyllids (Sauphanor et al., 1993). In accordance with the resource concentration hypothesis, the herbivores' fitness and survival may be enhanced in crops grown in monocultures and in landscapes with a high proportion of the host crop (O'Rourke and Petersen, 2017; Root, 1973). Given the high density of apple orchards in major production regions and the economic value of apple, one of the major production challenges is pest control, referring to the level of pest density, at which no economic injury or loss is caused by the pest (Kogan, 1998). Future challenges of pest suppression are expected to increase in two ways. First, as a consequence of ever-stricter regulations of chemical pesticides (Damalas and Eleftherohorinos, 2011; Karabelas et al., 2009); second, as a consequence of shifts in the geographic distribution of arthropods that are triggered by climate change (Peterson et al., 2010). Driven by global temperature rise, it is likely that pests that have so far been restricted to a specific area will move northwards, or risks of additional pest generations will increase due to shifts in phenology and voltinism (Logan et al., 2007; Olesen et al., 2011; Stoeckli et al., 2012).

Figure 1.1. Larva of codling moth *Cydia pomonella* feeding on apple in one of the German study orchards. © A.-K. Happe, 2017.

Biological pest control in apple orchards

Pests in apple orchards are naturally regulated by a combination of top-down processes, including predation, parasitization, and infection by entomopathogenic fungi and nematodes, and bottom-up processes such as host-plant quality and resistance (Hunter and Price, 1992; Rousselin et al., 2017; Stoeckli et al., 2008a).

Here, I focus on a specific process of top-down regulation: biological control by predatory arthropods. Predatory arthropods and birds are the main contributors to biological control in apple orchards (Cross et al., 1999; García et al., 2018). Solomon et al. (2000) reviewed important predators of apple pests in northern and central Europe, including spiders, insects and mites: Araneae, Coleoptera (e.g. Coccinellidae (Fig. 1.2), Cantharidae and Staphylinidae), Diptera (e.g. Syrphidae and Cecidomyiidae), Dermaptera, Heteroptera (e.g. Anthocoridae, Miridae and Nabidae), Neuroptera (e.g. Chrysopidae), and Phytoseiidae. A high predation potential depends on more than abundance and species richness of these predators; it depends on evenness of predator communities, i.e., the relative abundance of different taxa (Crowder et al., 2010; Gurr et al., 2017). The analysis of community composition is therefore an important aspect of this study.

Figure 1.2. Larva of coccinellid beetle *Harmonia axyridis* feeding on woolly apple aphid *Eriosoma lanigerum* in one of the German study orchards. © A.-K. Happe, 2017.

There are distinct economic and ecological benefits of biological control (Cross et al., 2015), for example, in the case of phytoseiid mites and earwigs. Pesticide-resistant phytoseiid mites feeding on red spider mites help to prevent acaricide resistance and significantly reduce the need for acaricide sprays, and pest control by earwigs reduces insecticide application (Cross et al., 2015). In addition to providing economic benefits by pest control, biological control may indirectly decrease hidden and neglected costs to environment and health systems caused by pesticide applications (Bourguet and Guillemaud, 2016).

According to a definition by Eilenberg et al. (2001), biological control is often based on the intentional introduction of natural enemies (‘release strategies’): for example, a biological control agent can be released with the expectation that it multiplies and reduces the target pest population during the growing season (‘inoculation biological control’). Another common release strategy, inundation biological control, usually depends on the mass release of biological control agents to sufficiently reduce the pest pressure before the control agents’ dispersal or inactivation (Eilenberg et al., 2001). Conservation biological control, the strategy on which this thesis focuses, does not depend on the release of natural enemies. Rather, it includes practices to protect and support existing control agents (here: predators) by habitat enhancement and by reducing the risk of mortality from pesticides (Begg et al., 2017; Gurr et al., 2017). It forgoes the introduction of natural enemies and is therefore considered a preventive and permanent form of biological control. Habitat enhancement secures the provision of shelter, nectar, alternative prey or hosts, and pollen for natural enemies (Holland et al., 2016; Landis et al., 2000; Rusch et al., 2016). However, in some cases, natural habitat fails to enhance biological pest control (Tscharntke et al., 2016): (1) factors other than top-down regulation may be more relevant for a pest population in the region, (2) natural habitat may be a source habitat of pests rather than natural enemies, (3) resource provision in the crop may outcompete resource availability for natural enemies in the natural habitat, (4) the quality and/or amount of the habitat is insufficient, or (5) superimposed by adverse management practices. The reduction of pesticide side-effects can be accomplished by adopting integrated pest management (Boller et al., 2004) or by omitting broad spectrum insecticides (Geiger et al., 2010; Gurr et al., 2017; Pretty and Bharucha, 2014). In addition to supporting pest control, conservation biological control contributes to the ecological intensification of agriculture by influencing several ecosystem services and sometimes disservices, for example, pollinators, detritivores, and weeds (Gurr et al., 2017). A consistent positive effect of conservation biological control on pest suppression has, however, been questioned: intraguild predation, niche complementarity, and functional redundancy between biological control agents may weaken its success in reducing pest problems (Finke and Denno, 2004; Straub et al., 2008).

Bale et al. (2008) consider it a limitation of biological control that it is more time consuming than pesticide application: predator populations need to build up for a successful regulation of pests and parasitized organisms will only die slowly. Conservation biological control tackles this problem; if successful, it will ensure that natural enemy populations have already built up in the orchard or in the neighboring habitat, facilitating spillover effects of predators to the crop, when herbivore populations peak (Macfadyen et al., 2015; Rousselin et al., 2017; Tscharntke et al., 2007).

Local- and landscape effects on biodiversity and biological control

Agricultural intensification and attempts to counteract it affect biodiversity and biological control at various scales (Geiger et al., 2010; Jonsson et al., 2012; Rundlöf et al., 2007). At the local scale, semi-natural habitats and organic management have been proposed as potential solutions to mitigate the loss of biodiversity and associated ecosystem services; at the landscape scale, landscape complexity and a reduced land-use intensity is of special relevance to counteract the loss of biodiversity and the deterioration of ecosystem services (Batáry et al., 2015; Chaplin-Kramer et al., 2011; Rusch et al., 2016).

The local scale - enhancing local habitats

Since the 1980's, agri-environmental schemes (AES) are part of European Union's Common Agricultural Policy to reduce the environmental impact of intensive agricultural practices (Primdahl et al., 2003). The EU co-funds about 50% to 75% of the costs of approved AES, including organic management and semi-natural habitat structures (Kleijn and Sutherland, 2003). In 2012 the EU spent €3.23 billion on AES; but despite this high financial effort, their effectiveness as a conservation tool for biodiversity and biological control has been questioned (Batáry et al., 2015; Birkhofer et al., 2018). Birkhofer et al (2018) evaluated the effectiveness of two EU-funded greening measures (fallows and permanent grasslands) on ground-dwelling natural enemies and associated aphid control in cereal fields. The authors observed spillover of some spiders from natural habitat into the crop but the effects of the measures were mixed and depended on the specific predator group. Neither fallows nor permanent grassland did generally relate to enhanced biological control in the adjacent crop. Despite concerns about their effectiveness as conservation tools, there is evidence that AES-habitats provide essential resources for biological control agents and pollinators (Albrecht et al., 2012; Holland et al., 2016; Mestre et al., 2018; Sutter et al., 2018; Tschumi et al., 2016). Resources provided for natural enemies by AES habitats (Table 1.1) comprise alternative prey, floral resources and shelter (Holland et al., 2016). For biological control agents in apple orchards, effective AES include, for instance, adjacent woody habitats and flower strips and local flower richness (Albert et al., 2017; Lefebvre et al., 2016; Saunders and Luck, 2018). In addition to immediate effects on resource provision for beneficial arthropods, AES can counteract the sublethal effect of pesticides on beneficial insects including natural enemies by reducing pesticide applications (Desneux et al., 2007).

Table 1.1. Resources provided for natural enemies by crop habitats and agri-environmental habitats (Holland et al., 2016) and chapters of this thesis in which they are covered.

Habitat	Resources for natural enemies[1]			Publication
	Alternative prey	Floral resources	Shelter	
Linear woody	+++	++*	++	I, II, III
Woody areal[2]	++	++*	+++	I, II, III
Grassy linear	+++	+	+++	I
Herbaceous ungrazed[2, 3]	+++	+++	++	I, II, III
Low input headlands[2]	+++	+	N	I, II, III
Undersowing and cover crops[3]	+	+	+	I, II, III
Other AES habitats	++	+*	+*	

[1] Scoring based upon a review by Holland et al. and expert opinion (Holland et al., 2016): High benefit (+++), moderate benefit (++) some benefit (+), no benefit (N) and reported scores based on expert opinion but no published evidence (*); [2] in the present study indirectly included as proportion of land cover of forests, grassland and total area of non-crop vs. orchard crop cover in 1 km; [3] in the present study estimated as plant species richness or flower cover in the adjacent habitat.

The local scale - orchard management

The two most common management strategies in European apple orchards are integrated production (IP) and organic management. IP is a production system that uses natural resources and regulation mechanisms to replace polluting inputs and minimizes external costs by balancing biological, technical and chemical methods (Boller et al., 2004). It considers all relevant factors of farming including for example nutrient cycles, pest and disease management, soil fertility, and cultivar selection. Integrated pest management (IPM) includes methods to replace, reduce or complement the application of synthetic pesticides in pest control (Pretty and Bharucha, 2015), and can be considered as part of the concept of IP in apple orchard (Malavolta and Cross, 2009). Compared to former conventional management, which is uncommon in the apple growing regions covered by this study, IP includes a broad range of management options such as applications of pheromones and the targeted applications of synthetic chemicals as selective pesticides. The second common management type is organic management, which is defined as a sustainable cultivation method with a greater emphasis on environmental protection; if external inputs such as fertilizers or insecticides are used, they have to be based on mineral or organic substances and a special permission has to be granted for the application of synthetic products if there are no suitable alternatives (EU, 2012, 2008; Seufert et al., 2017). In consequence, organic management practices are usually more expensive and labor-intensive and result in lower yield, which can, however, be compensated by better marketing prices (Batáry et al., 2017; Seufert et al., 2012; Seufert and Ramankutty, 2017). Organic management practices differ from IP mostly in terms of soil management and the omission of herbicides, for example, soil tillage is applied in organic orchards, opposed to herbicide use in IP orchards (Zehnder et al., 2007). Further distinctions can be found in the application of organic or mineral (vs. synthetic) agro-chemicals, including insecticides, fungicides, fertilizers and growth-regulators (Batáry et al., 2017; Malone et al., 2017; Seufert et al., 2017).

Organic management supports biodiversity and ecosystem services across large latitudinal scales (Muneret et al., 2018; Seufert and Ramankutty, 2017; Winqvist et al., 2012). Based on a study conducted in twelve European and African regions dominated by arable land, grassland and / or permanent land-use types, species richness is on average 10.5% higher in organic compared to conventional fields. Higher abundances of plants and bees partly explain these gains in species richness whereas the response of other organism groups to organic management was less clear (Schneider et al., 2014). Other authors estimated the positive effect of organic management on biodiversity to be even higher with a reported increase of 30%, and a higher effectiveness in intensively farmed regions depending on taxonomic identity, functional group and crop type (Tuck et al., 2014). There is evidence that organic management enhances biological control across different production systems and across climatic regions (Lichtenberg et al., 2017; Muneret et al., 2018). It can outcompete conventional management in control of pathogens and animal pests (but not weeds) without augmenting pest infestation (Muneret et al., 2018).

The landscape scale

Across different latitudes and crop types, landscapes with a high proportion of natural habitat enhance the abundance and diversity of natural enemies, for example by enhancing habitat-connectivity and facilitating colonisation of the crop habitat (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Chaplin-Kramer and Kremen, 2012). Focusing on different natural enemy groups, Dainese et al. (2016) showed that landscape context rather than local factors affect the delivery of natural pest control in crop fields. Natural enemies respond positively to amount of perennial habitat in the landscape (Pfiffner and Luka, 2000; Schmidt et al., 2008), and a high proportion of semi-natural habitats in the landscape enhances pest suppression (Veres et al., 2013).

Landscape effects often interact with local factors. For instance, landscape composition alters the effects of management and local habitat on predators and on the effectiveness of conservation biological control (Jonsson et al., 2015; Rusch et al., 2013). Additionally, at an intermediate level of landscape complexity (1-20% non-crop habitat), organic management is more effective in enhancing biodiversity than in very simple or complex landscapes with more than 20% non-crop habitat (Batáry et al., 2011; Concepción et al., 2012; Tscharntke et al., 2012, 2005).

Research objective and outline

Large-scale studies on biological control have so far focused on annual cropping systems (e.g. Bianchi et al., 2006; Dainese et al., 2016; Tschumi et al., 2016) and little is known about the interacting effects of landscape composition, local habitat features and local management on generalist predators in perennial crop systems such as apple orchards (Lefebvre et al., 2016; Malagnoux et al., 2015b; Marliac et al., 2016). In face of accelerating agricultural intensification there is urgent need to understand how local and landscape characteristics as well as their interactions shape communities of arthropods (predators, herbivores and pollinators) and ecosystem services in apple orchards (Fig. 1.3).

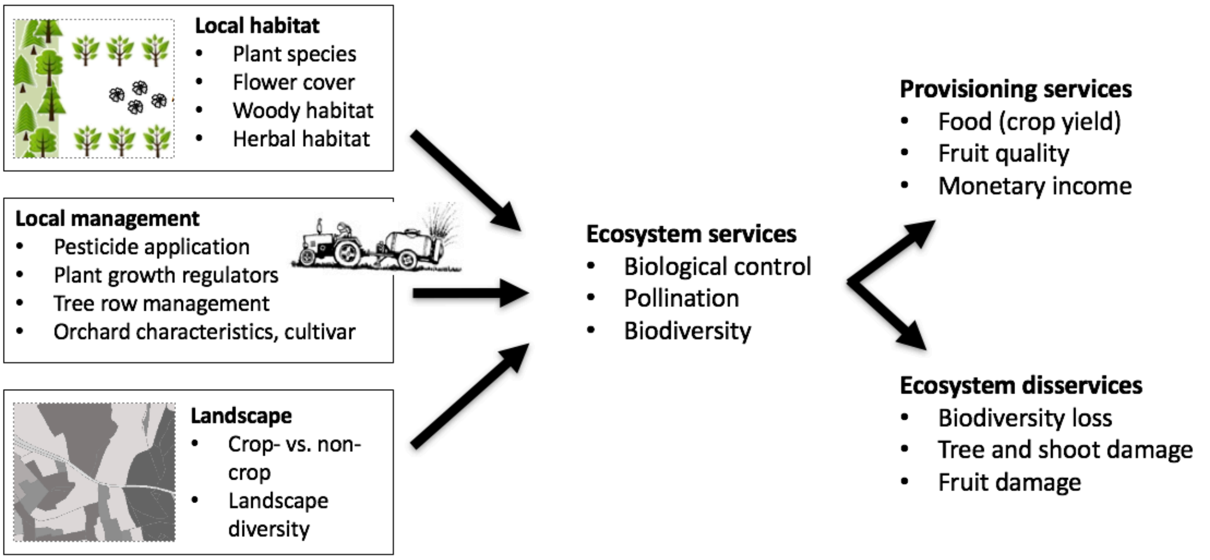

Figure 1.3. Impacts of local and landscape factors on ecosystem services and disservices in apple orchards. Specified for apple orchards (Samnegård et al., 2018) on the basis of a more general diagram on ecosystem services in agroecosystems by Power (2010).

I studied the effectiveness of local and landscape factors and their interactions to enhance ecosystem services and natural enemies at three different scales of interest: The first publication targets management trade-offs on ecosystem services in apple orchards across Europe, the second predatory arthropod communities, and the third a specific predator taxon, the earwig, and its prey. The overall aim was to improve our understanding for important and relevant habitat conditions for natural enemies but not herbivores and enhance ecosystem services in intensive fruit production systems across Europe. I adressed the following **research questions**:

(Q1) What landscape elements, local habitat features and management practices support beneficial arthropods (natural enemies and pollinators) across Europe?

a) What factors enhance ecosystem services (pollination and pest control)?

b) How does diversity of beneficial arthropods translate to seed set, fruit damage and final fruit yield?

c) Are there trade-offs between ecosystem services and final fruit yield?

(Q2) What local and landscape factors influence abundance patterns in communities of predatory arthropods in apple orchards?

a) Do predator communities differ between management types and countries?

b) How do individual predator taxa differ in their response to local and landscape factors?

(Q3) How do earwigs and their prey react to local and landscape factors?

Study orchards

We selected a total of 86 orchards in three countries representing major apple production regions in Europe. In South Germany, I studied 30 apple orchards, 15 IP and 15 organic, in the north of Lake Constance, a region with more than 2,800 ha of orchards. In North Spain and in South Sweden, my project partners selected 28 apple orchards, 14 IP and 14 organic in each country. These apple orchards were situated in the provinces of Lleida and Girona, accounting for 41% of the Spanish apple production, and in the province of Skåne, covering for 86% of the Swedish apple production (Jordbruksverket, 2014). The minimum distance between orchards of different management types was 1 km in Spain, 2 km in Germany, and 0.3 km in Sweden. The proportion of non-crop habitats within 1 km ranged from under 10% to over 30% to cover different landscape compositions and land use-intensities within each country (Chapter 3, Table S3.1, p. 53).

Methods

We used a combination of different well established sampling methods to assess predators and pests, and pest damage: (1) beating sampling of branches was used to survey free-ranging, canopy-dwelling predators (Mody and Linsenmair, 2004) including spiders, beetles, predatory flies, predatory bugs, earwigs, lacewings and harvestmen, (2) shelters to collect earwigs from hide-outs during the day (Sauphanor et al., 1993), (3) visual pest control recording shoots damaged by aphids (Miñarro et al., 2005) and recording percentage of damaged fruits at harvest (Mols and Visser, 2007). Surveys were conducted along 40-m-long row transects, starting at the edge of the orchard (beating sampling, pest and damage surveys) and on five randomly selected focal trees 20 m away from the edge, in the center of the transect (sampling of earwigs and pollinators). Transect rows were at least two rows away from rows of pollinizer cultivars and orchard edges to avoid dilution effects.

Local and landscape factors were assessed in 2015 in all countries based on (1) semi-structured interviews with growers (Motzke et al., 2013) on general management (IP *vs.* organic) and individual management practices such as agro-chemical applications (herbicides, pesticides, fertilizers, pheromone traps and AES availability adjacent to the orchard), (2) field surveys of adjacent AES such as hedgerows, (3) vegetation surveys during apple bloom 2015 within and adjacent to the orchard (20-m-radius from the edge) to record the number of plant species and flower cover using 1-m^2-quadrates prioritizing AES if available, (4) analysis of aerial photographs to measure the surface and distance of herbal and woody AES within 20 m distance and (5) land cover data (1-km-radius from the orchard center). Details on orchard and landscape characteristics are listed in Table S3.1, p. 53.

The bigger picture: Management trade-offs between ecosystem services across Europe

Local orchard conditions and landscape factors influence diversity and abundance of beneficial arthropods and pests, and their impact on final fruit yield. In this study, we developed a structural equation model based on predators, herbivores, pollinators, fruit damage and yield, with fruit production and seed set as endpoint variables, to disentangle direct and indirect effects of management, local and landscape variables.

Focusing on natural enemies: Communities of predatory arthropods across Europe

Organic management and agri-environmental schemes such as hedgerows and flowering strips are assumed to enhance beneficial arthropods and their contribution to biological pest control in fruit crops. Arthropods were surveyed in apple orchards in Germany, Sweden and Spain with beating samples taken shortly after flowering. We identified seven relevant groups of predatory arthropods: spiders, beetles, bugs, flies, earwigs, lacewings and harvestmen, and studied how local management, woody elements and landscape characteristics influenced their abundance patterns. By estimating energy use of the communities, I assessed the effects of landscape characteristics and orchard management on the predation potential. I show how effects of management intensity on predator community composition in the two studied management types differ between regions, and I investigate how effects at the local and landscape-scale differ for each predator group.

Focusing on a specific taxon and its prey: The case of earwigs and woolly apple aphids

During two study years, we sampled earwigs and woolly apple aphids in Germany and Spain using shelters. Earwigs are expected to be important generalist predators in apple orchards. Local and landscape effects were evaluated by considering extra-orchard habitats (e.g. hedgerows and forest edges) and percentage cover of fruit orchard in the landscape. The presence of woolly apple aphids, an important target prey of earwigs, was assessed in tree surveys, when earwig traps were emptied. I show the effects of organic management and the presence of semi-natural woody habitats on earwig abundance and the influence of landscape composition on woolly apple aphids.

2. PUBLICATION I: MANAGEMENT TRADE-OFFS ON ECOSYSTEM SERVICES IN APPLE ORCHARDS ACROSS EUROPE: DIRECT AND INDIRECT EFFECTS OF ORGANIC PRODUCTION

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Apple bloom at lake Constance. © A.-K. Happe, 2016.

ABSTRACT

1. Apple is the most important fruit crop in temperate areas, and profitable production depends on multiple ecosystem services including the reduction of pest damage and the provision of sufficient pollination levels. There is an inherent trade-off in the choice of management, as it affects species differently.

2. In this study, we quantified the direct and indirect effects of management (organic *versus* integrated pest management (IPM)) on species richness, ecosystem services and fruit production in 85 apple orchards in three European countries. We quantified how these effects were influenced by habitat composition at three spatial scales: within orchards, adjacent to orchards and in the surrounding landscape.

3. The results show that organic management resulted in 48% lower yield than IPM, but also that the variation between orchards was large with some organic orchards having a higher yield than the average yield of IPM orchards. The lower yield in organic orchards resulted directly from management practices, and from higher pest damage in organic orchards. These negative yield effects were partly offset by indirect positive effects from more natural enemies and higher flower visitation rates in organic orchards.

4. Two factors other than management affected species richness and ecosystem services. Higher cover of flowering plants within and adjacent to the apple trees increased flower visitation rates by pollinating insects and a higher cover of apple orchards in the landscape decreased species richness of beneficial arthropods.

5. The species richness of beneficial arthropods in the orchards was uncorrelated with fruit production, suggesting that diversity can be increased without large yield loss. At the same time, organic orchards had 38% higher species richness than IPM orchards, an effect that is likely due to differences in pest management.

6. Synthesis and applications. Our results indicated that organic management is more efficient than IPM in developing environmentally friendly apple orchards with higher species richness, but also that there is no inherent trade-off between species richness and yield. A main task for the development of sustainable production of apples is the development of more environmentally friendly means for pest control that do not negatively affect pollination services.

Keywords: IPM, natural enemies, pollination services, organic management, biological control, Structural Equation Model

INTRODUCTION

Fruit consumption is an important part of human nutrition, and the second most important fruit crop globally is apple (FAO statistics 2014, www.fao.org/statistics). Therefore, the sustainable production of apples is an important goal for human food provisioning. In temperate regions, the by far largest area of fruit production is apple orchards and, similar to other crops, agricultural intensification of these orchards during the last century has increased production through high input of inorganic fertilizers, pesticides and herbicides (Reganold et al., 2001). For instance, chemical pest control is essential for profitable apple production, as more than 50% of the crop may be lost in orchards with no control (Cross et al., 2015). Intensification in apple orchards, however, leads to increased production costs as well as to environmental detriments both within the orchard and in surrounding areas (Reganold et al., 2001). These detrimental effects have increased the interest in developing more environmentally friendly production, through either integrated production or organic management, in which the enhancement of ecosystem services from natural enemies can partly replace the use of chemical pesticides in suppressing pest populations (Dib et al., 2016; Simon et al., 2010).

The intensification of agriculture also threatens the delivery of pollination services from the wild pollinator community (Klein et al., 2018; Potts et al., 2010). For pollinator dependent crops such as apple, decreased pollination services result in lower seed and fruit set and in a lower profitability for the farmer (Garratt et al., 2016; Klein et al., 2018; Mallinger and Gratton, 2015). To obtain better pollination, orchard owners often use managed pollinators such as honeybees, and in some cases bumblebees. However, the efficiency of these managed pollinators is debated, and is often found to be lower than that of wild pollinators (Garratt et al., 2016; Mallinger and Gratton, 2015). The availability of managed pollinators may also vary between years leading to a vulnerable system if managed bees are relied upon to provide the majority of the pollination services (Breeze et al., 2011).

Agricultural intensification affects beneficial arthropods, and their delivery of ecosystem services, not only due to local management but also through simplification of the surrounding landscape (Lichtenberg et al., 2017). The abundance of both natural enemies and pollinators is often lower in simplified landscapes, due to lower amounts of alternative resources or fewer overwintering sites (Shackelford et al., 2013), but there is also often an interaction between the local management and structure of surrounding habitats. For instance, it seems that the negative effects of intensive field management on pollinating insects are mainly observed in relatively homogeneous landscapes (Rundlöf et al., 2008; Williams and Kremen, 2007).

In the European Union, subsidies have been available since the late 1980s to promote environmentally friendly farming systems, at both local and landscape scales (Primdahl et al., 2003). These agri-environmental schemes, which are mainly implemented on a voluntary basis, include “environmentally favorable extensification of farming”, “integrated farm management and organic agriculture” and “preservation of landscape and historical features such as hedgerows, ditches and woods". Even though subsidies have been in place for some time, their efficiency to promote biodiversity, and how they affect ecosystem services and yield in apple production systems is less clear (but see Albert et al., 2017). A problem with implementing efficient management strategies is that ecosystem services are often differently affected by the same management action (Shackelford et al., 2013). Different responses for diversity-related ecosystem services to the same management action may be expected because species vary in their life history, but maximizing the total output of ecosystem services on apple production necessitates that potential trade-offs arising from management are identified and accounted for (Power, 2010).

One basic trade-off between ecosystem services and agriculture emerges when management that aims to increase crop yield by stimulating plant growth (e.g. by adding nutrients and water, or by removing competing weeds) also indirectly reduce production by affecting the ecosystem services of pest control and pollination (Power, 2010). Trade-offs also occur in management aimed to affect diversity-related services or disservices (positive and negative effects from biodiversity, respectively), when actions to promote beneficial arthropods also benefit pest species, or when actions to reduce pest species also negatively affect beneficial species (Saunders et al., 2016; Tscharntke et al., 2016). For instance, several studies suggest that flower strips, which are commonly planted to benefit pollinators and natural enemies (Lichtenberg et al., 2017; Wratten et al., 2012), may not only affect the potential for pest control but also pest densities and crop damage (Tscharntke et al., 2016). Other studies suggest that flower strips to enhance natural enemies are most efficient when placed inside orchards (Saunders and Luck, 2018), but these strips may then compete with apple trees for nutrients and water (Granatstein and Sanchez, 2009). Similarly, pesticides may negatively affect natural enemies and pollinators, leading to reduced biocontrol (Dib et al., 2016; Fountain and Harris, 2015) and pollination services (Pisa et al., 2015; Stanley et al., 2015). Because apple production is often limited by pest damage and pollination, alternative pest control measures without negative effects on natural enemies and pollinators are preferable. Natural enemies and pollinators are generally promoted by retaining sheltering habitats within or next to the production areas or by providing nectar and pollen resources in the form of planted or conserved flowering plants present in alleyways, margins and hedgerows (Campbell et al., 2017; Miñarro and Prida, 2013).

In this study, we examined trade-offs between production and ecosystem services, and between ecosystem services and disservices, by comparing integrated pest management (IPM)[1] and organic apple production, as a broad classification of management systems. We evaluated the role of management (organic vs. IPM) in a study design accounting for agri-environmental structures and landscape composition affecting diversity at three spatial scales: within orchards, adjacent to orchards and in the surrounding landscape. The variables include both floral resources for pollinators and overwintering sites for all arthropods, estimated through the cover of flowering plants and the area of

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[1] In this publication, 'IPM' is used interchangebly with 'IP'. The studied 'IPM'-orchards followed the broader IP guidelines by Malavolta & Cross (2009), which go beyond pest management (see 'General introduction').

agri-environmental structures within and close to the orchard, and the amounts of bee-friendly habitats in a larger area around the orchard, which may increase the species pool for the local orchard. We also included the cover of orchard area around each focal orchard, as a measure of the homogenization of the landscape. The study was performed in 85 apple orchards in three European countries (Spain, Germany and Sweden), to cover regional variation in apple production. We collected data on flower visitation rates, pollination deficits, natural enemies, pests and fruit production, and used a structural equation model to disentangle the direct and indirect effects of management and environmental variables on seed set and fruit production.

MATERIALS & METHODS

Study regions

The study included three important apple-growing regions; northeastern Spain (SP), southern Germany (GE), and southernmost Sweden (SW) (Fig. 2.1). In Spain, we selected apple orchards located in the provinces of Lleida and Girona, Catalonia. In Germany, we selected apple orchards in the lake Constance region, Baden-Württemberg. In Sweden, we selected apple orchards on the east and west coasts of the county Skåne. The target apple varieties in the study orchards were common for each region: Gala and Golden Delicious in Spain, Braeburn in Germany, and Aroma and the sub-variety Amorosa (but included some Ingrid Marie and Rubinola) in Sweden.

Within each region, we selected 28 (SP and SW) or 30 (GE) orchards, half of which were managed organically and the other half were managed according to IPM guidelines (Malavolta and Cross, 2009). One Swedish orchard was excluded before analysis because it had been abandoned. The orchards were selected along a land-use gradient, using forest cover as a proxy, with approximately half the orchards harbouring agri-environmental structures (e.g. hedgerows, flower strips, margins with ruderal vegetation) in their close surroundings (up to 20m from the edge of the trees). IPM orchards were managed with a similar crop protection strategy and with foliar and mineral fertilizers at multiple times along the season. Crop protection in

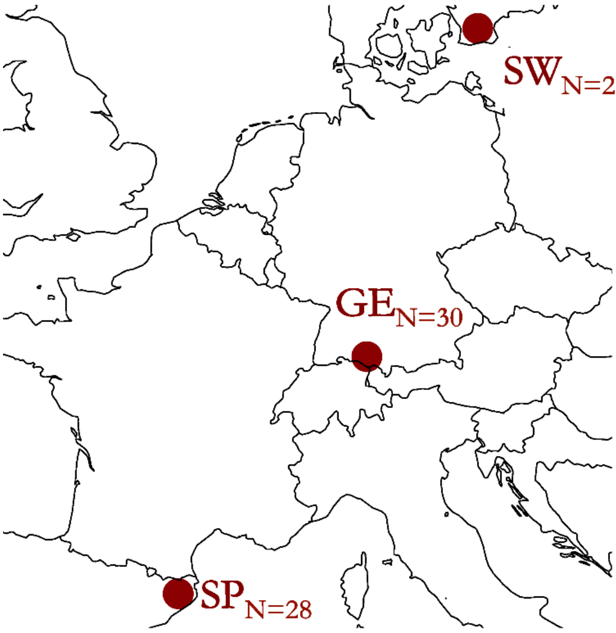


Figure 2.1. Map showing the study areas in Sweden (SW), Germany (GE) and Spain (SP).

these orchards involved a range of chemicals for pest, weed and disease control, but the specific active ingredients differed somewhat between countries and orchards. Among the organic orchards, the majority was certified in accordance with European or National legislation (Council Regulation (EC) No 834/2007), which involves more restrictive crop protection strategies and organic fertilizers. In these orchards, pest control mainly occurred through use of natural extracts (neem, pyrethrum), microorganisms (*Bacillus thuringiensis*), viruses (e.g. granulosis virus vs. codling moth), and through mating disruption of specific insect pests, while fungal control strategies involve compounds such as sulphur and lime sulphur. Thus, the contrast of IPM vs. organic management involves differences not only in the intensity and type of chemicals for pest control, but also in the input and availability of nutrients for crop plants (expectedly higher in IPM than in organic), due to the use of chemical fertilizers and chemical weed control (de Ponti et al., 2012). A few uncertified orchards in Sweden and Spain were managed as under organic guidelines with no chemical inputs, and these orchards were considered organic in this study.

Field sampling

Within orchards, we quantified natural enemies, pollinators, pollination success, pests/pest damage and fruit production. Field work was performed during 2015, and data collection was adjusted to the annual cycle of apple production in each region. Pollination was studied during flowering and pest incidence and damage were surveyed at relevant pest phenological stages. Due to climate differences, the timing of data collection varied between the three countries. We estimated natural enemy abundance by beating one apple branch of a representative size on 24 trees per orchard once within two weeks after apple flowering, and all collected natural enemies were identified to species or morphospecies. Trees used for beating samples were randomly selected in one 40 m transect per orchard, along a single row perpendicular to the orchard border (SP and SW) or two rows (GE). Natural enemy abundance was calculated as the total number of natural enemy individuals collected per transect, and the richness as the total number of natural enemy species per transect. In natural enemies, we included spiders, predatory coleopterans (mainly Cantharidae and Coccinellidae), earwigs, predatory heteropterans (mainly Anthocoridae), predatory dipterans (mainly Hybotidae, Empididae and Dolichopodidae), lacewings and harvestmen.

The visitation rate and richness of apple flower-visiting wild pollinators was estimated once per orchard from transect walks during apple flowering, in one transect close to the orchard border (0-20 m) and one transect in the orchard interior (20-40 m from border). Each walk lasted five minutes and was repeated three times throughout the day (total 30 min sampling per orchard). Visitation rates were calculated as the number of observed pollinator visits per 1000 flowers per 5 min. We recorded all pollinators visiting apple flowers, and collected species for identification in the lab. We only included wild bee and syrphid fly species in the estimate of flower visitation rates as other groups (e.g., beetles) are unlikely pollinators of apple (Kendall, 1973; Ramírez and Davenport, 2013). We pooled the species number of flower visitors and natural enemies to obtain an estimate of the total number of beneficial arthropod species per orchard (hereafter, beneficial species richness). To estimate pollination services, we performed a hand-pollination experiment on three trees per orchard, where each tree had one branch dedicated to open and and one to supplementary pollination treatments. For hand pollination, we used pollen from pollinizer trees growing within or adjacent to the orchard. Using this data, we estimated the pollination deficit as (seed set of supplementary pollinated flowers) – (seed set of open-pollinated flowers) for fruitlets in May-June. A positive value implies a pollination deficit, indicating insufficient pollination services. As an estimate of apple production, we calculated an index based on the fruit set, proportion damaged fruits and mean apple weight calculated for apples collected on three marked branches on five trees per orchard. The production index equals the weight of undamaged fruit per 100 flowers, and was calculated as (the proportion of undamaged apples at harvest) x (mean weight of harvested apples) x (fruit set). Fruit set is the percent flowers that produced fruits at harvest from 18 branches per orchard, the proportion of undamaged fruits equals one minus damage (see next paragraph), and mean weight was calculated from up to 18 apples per orchard.

We estimated pest densities and damage in two ways representing the main pest problems for orchard owners. First, we estimated aphid abundance by counting the proportion of branches infested by aphid colonies, for each aphid species separately on 13-60 trees per orchard. The main aphid pests in all study orchards and in apple orchard across Europe are rosy apple aphid (*Dysaphis plantaginea* (Passerini), hereafter RAA) and woolly apple aphid (*Eriosoma lanigerum* (Hausmann)) (Blommers, 1994). RAA was by far the most abundant species, particularly in Sweden and Spain, and is often considered as the most damaging aphid, so we only considered this species. Second, we estimated fruit damage from other pest species for 24 apples on 37 trees per orchard (888 fruits per orchard), in the same transects as the pollination study, at the time of harvest, and used these data to calculate the proportion of damaged apples. This measure reflects the damage of codling moth (*Cydia pomonella* L.), sawflies, geometrids and leaf rollers. The specific pests inflicting the damage differed between countries, with leaf rollers and winter moth (*Operophtera brumata* L.) doing most damage in the Swedish orchards, leaf rollers (Tortricidae) and sawflies (*Hoplocampa testudinea* Klug) in German orchards and codling moth in Spanish orchards. These estimates do not cover damage that cause fruit drop before harvest, but such loss would be reflected in the fruit set and thus in the apple production variable.

Estimating environmental variables

To understand the effect of local conditions, we estimated flowering plant cover and the area covered by agri-environmental structures (AES) within and in the close surroundings of each orchard. First, we estimated the cover of flowering plants once per orchard as the percent cover of plants attractive to pollinators (hereafter flower cover) near the time of apple flowering. Flowering plants include those species flowering at any time during the year and not only at the time of the survey, to assess the total amount of resources available for pollinators. To identify plant species attractive to pollinators, we used the BiolFlor Database (Kühn et al., 2004). Flower cover was estimated for each species from six

1x1 m^2 plots between apple rows and from six plots outside the apple rows and summed across species. Second, we estimated the total surface cover of AES in m^2 within 20 m of the transects. AES include hedgerows (including edges with old trees and tree rows), forest edges, forests (river forests, tree plantations), fallow lands (including abandoned fields), semi-natural grasslands (terraced field margins, embankments) and orchard meadows.

To understand landscape effects, we estimated the proportion of bee-friendly habitat for each orchard within 1 km from the transect center. We defined bee-friendly habitats for each country based on expert knowledge, including shrubland, dry land orchards and abandoned orchards in Spain, orchard meadows in Germany, and semi-natural grasslands in Sweden. We estimated the cover of apple orchards as the proportion of surface area covered by this crop within 1 km from the transect, as a proxy for homogeneous landscape composition and land-use intensity in our apple production regions. To quantify landscape characteristics, we used official digital maps for Spain and Germany (Carreras and Diego, 2009; LGL, 2016; SIOSE, 2015), spatially explicit data on land use from the Swedish Board of Agriculture (Integrated Administrative Control System, IACS) and Geographic Information Systems and Remote Sensing software ArcView 10.3.1 and MiraMon.

Statistical analyses

To assess the direct and indirect effects of management, local orchard conditions, adjacent site conditions and landscape composition across orchards, we developed a structural equation model (SEM) with fruit production as the endpoint variable. As intermediary variables, we used the total species richness of beneficial arthropods (flower visitors and natural enemies), natural enemy abundance, flower-visitation rate by wild pollinators, RAA abundance, pest damage at harvest and pollination deficit. To build the SEM, we combined seven mixed effects models (lme in the R package nlme) in a piecewise SEM (Lefcheck, 2016), with country as random effect. To reduce the number of variables, we first evaluated each individual lme and removed non-significant variables describing agri-environmental or landscape composition. Following this, we evaluated each lme by plotting standardized residual against fitted values and predictor variables. For pest damage, residual plots indicated heteroscedasticity between management and between countries. We therefore modelled variance in this submodel using the VarIdent-option. For apple production and flower visitation rate, residual plots indicated a log-linear relationship to predictive variables and these variables were log10-transformed before inclusion in the final model.

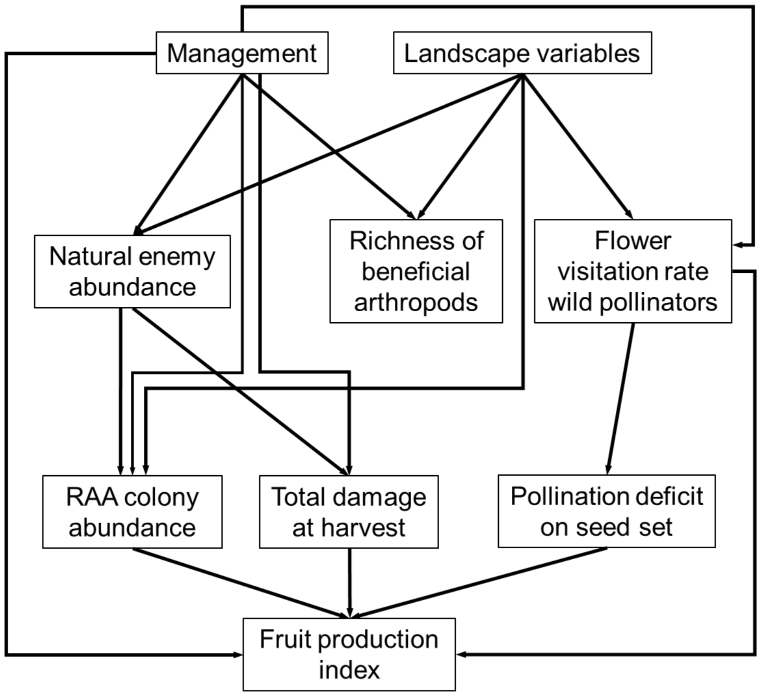
We assessed the initial SEM (Fig. 2.2a) by the D separation test to detect missing paths and tested the overall model with Fisher's C statistics. We added significant missing paths and removed non-significant paths until the AIC was no longer reduced. We accounted for two correlated errors; between species richness and natural enemy abundance, and between RAA abundance and total damage at harvest. When presenting the final SEM, we compared the relative importance of pathways using standardized path coefficients. To assess the generality of the model across countries, we ran the final SEM for each country separately as a post-hoc comparison. This step should be viewed cautiously as the model is applied on smaller data sets, but it serves the purpose of indicating if patterns in the SEM are mainly caused by patterns in one country. In this comparison, we present unstandardized parameter values because these provide a better comparison between countries. To assess the relationship between apple production and species richness, we related these variables following the removal of partial effects from other variables in the lme-models using the remef command (Hohenstein and Kliegl, 2015).

RESULTS

When analyzing the combined direct and indirect effects of management on fruit production, we found that organic orchards on average had a 48% lower fruit production compared to IPM orchards ($F_{1,76}$=20.9, $P < 0.0001$) and this effect size did not vary between countries ($F_{2,76}$=2.1, $P > 0.13$). However, the variation for each category was large and the production of the most productive organic orchards exceeded the mean of IPM orchards (Fig. 2.3). The initial SEM showed a good fit (Fisher's C = 69.4, df = 60, $P = 0.18$), but the D-separation test indicated a missing direct path from the natural enemy abundance to apple production (see SI table for data used in SEM). Adding this path increased the fit of the SEM (Fisher's C = 47.9, df = 56, $P = 0.54$), and did not change the model otherwise (Fig. 2.2b). In the final SEM, management had a strong direct effect, and several indirect effects, on apple production with lower production for organic orchards. Both natural enemy abundance and flower-visitation rates were higher in organic orchards, creating indirect positive effects from organic management on apple production (Fig. 2.2b). Fruit damage at harvest was higher in organic orchards, creating an indirect negative effect from organic management on apple production (Fig. 2.2b). It is also notable that effects from the area of AES and bee-friendly habitats were non-significant and were excluded already in the initial model. The only effects from the agri-environmental or landscape structures that were retained in the final SEM were positive effects of flower cover on wild pollinator visitation rates and negative effects of orchard cover on species richness of beneficial arthropods (Fig. 2.2b).

When comparing parameter values between countries and with the final SEM (Table 2.1), differences were relatively small. In three cases, parameter values for the three countries deviated based on the difference of parameter values and the magnitude of the standard error. First, estimated parameter values for the relationship between natural enemy abundance and fruit production was lower for Sweden and did not overlap with the estimates for other countries. Second, estimated values for the relationship between management and fruit damage were higher for Sweden and Spain compared to Germany. Finally, estimated parameter values for the relationship between management and aphid abundance (mainly RAA) were lower for Germany than for other countries.

a. Initial SEM model



b. Final SEM model

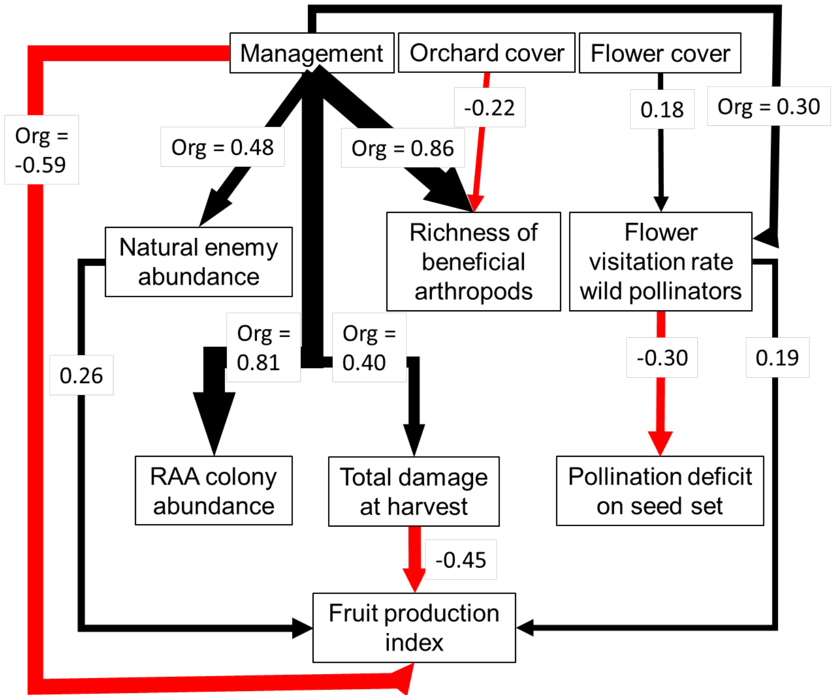


Figure 2.2. a) Initial and b) final structural equation model (SEM) showing significant direct and indirect paths from management, orchard landscape cover and flower cover. The landscape variables tested in the initial SEM were flower cover, AES cover, orchard cover and cover of bee-friendly habitats. Arrow thickness in the final SEM is proportional to the standardized path coefficients (figures next to the paths). The color of the path indicates the sign of the effect (red = negative, black = positive). The sign connected to management type refer to organic management relative to IPM. The model includes correlated errors between natural enemy abundance and richness of beneficial insects ($P < 0.0001$), and between RAA (rosy apple aphid) abundance and total damage at harvest ($P < 0.0001$) but these arrows are omitted in the figure

Table 2.1. Unstandardized path coefficients (mean ±SE) of the final model using the whole data set, with country as random effect, and the three data sets separately. For management, coefficients indicate differences of organic management to IPM

Response	Predictor	Total	SP	GE	SW
Fruit production	Management	-0.19±0.07 ($P < 0.005$)	-0.064±0.11	-0.23±0.14	-0.12±0.15
--	Fruit damage	-1.72±0.40 ($P < 0.004$)	-1.83±0.51	-1.84±3.12	-2.87±0.95
--	NE abundance	0.0062±0.0022 ($P < 0.007$)	0.0082±0.0050	0.0064±0.0059	0.0009±0.0036
--	Flower visitation	0.057±0.028 ($P < 0.05$)	0.046±0.063	0.004±0.078	0.096±0.075
Pollination deficit	Flower visitation	-0.77±0.31 ($P < 0.03$)	-1.49±0.45	-0.33±0.65	-0.07±0.51
Flower visitation	Flower cover	0.0075±0.0034 ($P < 0.03$)	0.013±0.005	0.0057±0.0058	-0.0028±0.009
--	Management	0.33±0.17 ($P < 0.05$)	0.32±0.25	0.048±0.33	0.69±0.26
Fruit damage	Management	0.034±0.009 ($P < 0.0003$)	0.11±0.04	0.025±0.008	0.12±0.02
RAA abundance	Management	0.26±0.05 ($P < 0.0001$)	0.36±0.11	-0.011±0.009	0.46±0.10
Richness of beneficials	Management	4.10±0.78 ($P < 0.0001$)	5.36±1.32	3.51±0.97	3.18±1.73
--	Orchard cover	-0.046±0.019 ($P < 0.02$)	-0.023±0.021	-0.12±0.03	-0.037±0.070
NE abundance	Management	6.49±2.46 ($P < 0.02$)	8.86±3.64	7.00±4.67	3.48±4.35

When assessing the relationship between fruit production and beneficial arthropod species richness, while partialling out the effect of orchard cover in the surrounding landscape, we found no relationship between fruit production and species richness (Fig. 2.4). This pattern was true for both organic and IPM orchards, but there was an effect of management where organic orchards had on average 38% more species for the same production of apples (13.0 vs. 9.4 species).

DISCUSSION

Management differences between organic and integrated pest management (IPM) in apple orchards evidently had strong effects on fruit production, pest damage, beneficial arthropod species richness and diversity-related ecosystem services. On average, fruit production was 48% lower in organic orchards, which is a larger difference than between organic and conventional management in other crops (Seufert et al., 2012).

Importantly, the overall effect on fruit production was due to a combination of direct management effects and indirect effects due to higher pest damage in organic orchards.

Pest control strategies in organic orchards are typically less effective than in orchards that use synthetic pesticides, and the commercial output of apple production is sensitive to damage, as damaged fruits cannot be sold as high quality apples for direct consumption on the market. The unidentified direct effects may be related to differences in fertilizer and water/irrigation use (Berry et al., 2006; Klein et al., 2015), as well as fungal disease control and weed management, which were not accounted for in our study. While pest damages were lower in IPM orchards, organic orchards were more strongly benefitting from diversity-related ecosystem services, as these orchards had both a higher abundance of natural enemies and a higher flower visitation rate from wild pollinators, increasing fruit production. While these indirect positive effects were not strong enough to overcome the negative effects of organic management on fruit production, the pattern suggests that methods to increase natural enemy abundance and wild pollinator visitation have the potential to reduce the yield gap between organic and IPM orchards. This conclusion is supported by the fact that some organic orchards had a fruit production that was well above the mean production of IPM orchards (Fig. 2.3).

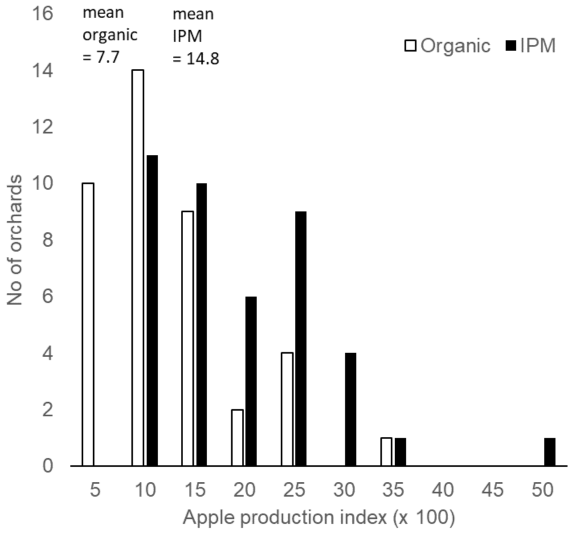


Figure 2.3. Distribution of the fruit production index for organic orchards and IPM orchards. For illustrative purposes, the index is corrected for differences between countries by multiplying the value of each orchard by the ratio of the overall and country means.

A concern for agricultural systems in general has been that increased production often causes a reduction in biodiversity, and that efforts to reduce these negative effects entail a cost in terms of reduced production (Clough et al., 2011; Gabriel et al., 2013). Our study does not support this concern for apple orchards. Species richness of beneficial arthropods and apple production in our study were largely uncorrelated (Fig. 2.4), and this pattern was similar in both organic and IPM orchards. If anything, there was a close to significant positive

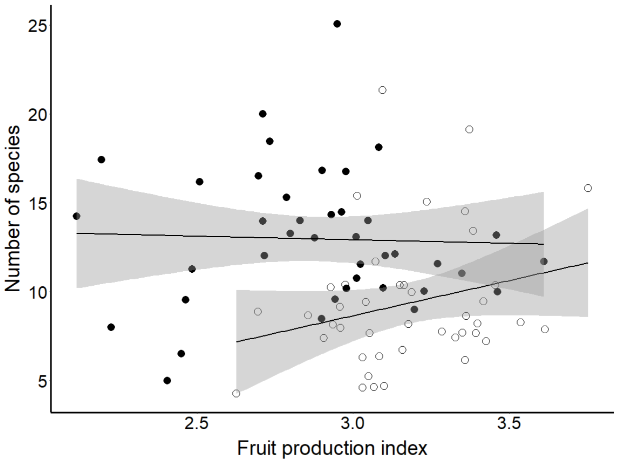


Figure 2.4. Partial residuals, prediction lines and confidence bands between species richness of beneficial arthropods and the fruit production index (log10-transformed), for organic (●) and IPM (○) orchards.

relationship between apple production and species richness for IPM orchards. Clough et al. (2011) similarly found no trade-off between crop yield and biodiversity in smallholder cacao production systems, suggesting that productivity costs related to the maintenance of a high biodiversity may be small for some systems. On the other hand, organic orchards in our study had on average 38% more beneficial species for similar levels of apple production, confirming the previous conclusion that organic management supports a higher local species richness of arthropods (Rusch et al., 2014). We can only speculate on the main causes of this difference, but it seems plausible that it is mainly due to differences in pest control methods that affect survival of non-target organisms (Lefebvre et al., 2017; cf., Park et al., 2015) or to differences in weed management effects on species diversity within the orchards (Gurr et al., 2003).

The effect of orchard management on arthropod richness often interacts with habitat composition at the local and landscape levels, where intensification and homogenization at the landscape level result in decreased arthropod richness in otherwise species-rich habitats (Landis, 2017). The use of various AES for conservation has long been promoted in the European Union (Primdahl et al., 2003), but the effectiveness of these measures has been questioned (Batáry et al., 2015; Tscharntke et al., 2016). In our study, we found that a higher cover of apple orchards in the surrounding landscape reduced species richness of beneficial arthropods within the orchard. A relatively uniform landscape with apple orchards may be less favourable for biodiversity than a more heterogeneous landscape, because most apple orchards in any landscape are managed according to IPM (Joshi et al., 2016; see also Marini et al., 2012). On the other hand, we did not find a direct effect of AES surface on either species richness of beneficial arthropods, natural enemy abundance and fruit production. However, it is premature to argue that AES are not useful in apple orchards since only a few orchards in our study had actively established these structures. Our measures mainly reflect the natural occurrence of these habitat types in the surroundings of the orchards, and a more targeted establishment of AES may result in greater benefits to biodiversity and related ecosystem services. Nevertheless, we found a clear positive direct effect of flower cover on pollinator visitation rates of apple flowers (supporting Campbell et al., 2017), which resulted in reduced pollination deficit (measured through seed set) and increased fruit production, suggesting that targeted establishment of flower strips may have positive effects on apple pollination.

When examining the role of natural enemies, we found that higher natural enemy abundance was related to higher fruit production, but this effect was not due to a negative relationship between natural enemy abundance and either aphid abundance or apple pest damage at harvest. This finding suggests that the natural enemies provide some biocontrol that was not captured by our pest sampling. The community of apple pests shows large differences between the different countries, and we therefore had to use relatively coarse measures of damage. It is possible that the natural enemies found in this study mainly regulated earlier pest insects and that this effect is not reflected in our measure of fruit damage. It is also evident that the group of natural enemies is heterogeneous, including spiders, coleopterans, dipterans, neuropterans, heteropterans, earwigs and harvestmen. Different natural enemies have different diets. Some groups are known to feed on and reduce apple pests (Cross et al., 2015) while the feeding habitats and effects on pest species are less understood for other groups. In addition to pest species, also natural enemies varied in abundance between countries, with a higher abundance of dipterans in Sweden and a higher abundance of heteropterans and earwigs in Germany (Happe et al. unpubl.)[2]. It is also evident that our focus on arthropod natural enemies ignore birds, which are known to reduce both caterpillar and aphid damage in apple (García et al., 2018; Mols and Visser, 2007).

Regional differences in management, landscape context and in the biota on apple trees may affect the effect of organic management vs. IPM. For instance, Kehinde et al. (2018) found that the bee abundance in vineyards was positively affected by organic management in Italy but not in South Africa, with potential effects on pollination. In our study, we found surprisingly strong regional similarities when comparing organic management and IPM. The SEM coefficients were mostly on the same order with a few exceptions. First, there was a weaker connection between the natural enemy density and fruit damage in Sweden, which may be due to differences in the pest community where winter moth was a dominant pest only in Sweden. It is possible that the present natural enemies are less able to affect the winter moth outbreak. Second, there was a weaker connection between management and pest damage and aphid abundance in Germany, where aphid control was equally strong in both organic and IPM. Aphid densities during the sampling year may have been low in Germany for other reasons, reducing the effect of management.

Conclusion

In conclusion, our study shows differences in the delivery of ecosystem services between organic and IPM apple orchards, where both natural enemy abundance (measuring biocontrol services) and flower visitation rate (measuring pollination services) were higher in organic orchards. Moreover, pollination services were positively affected by the flower cover surrounding the orchard. Nevertheless, the average IPM orchard reached a higher final apple production even though the variation between orchards was high and the organic orchard with the highest production was producing well above the average IPM orchard. The main reason for the differences in production does not seem to be related to the observed differences in ecosystem services as there was a strong direct (and unexplained) effect of management on apple production. Yet our study also suggests that there is scope for increasing the diversity of beneficial arthropods without reducing production. If differences in species richness between organic and IPM are due mainly to pest control strategies then this pattern would support a continued focus on developing targeted pest control methods that are also environmentally friendly.

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[2] See next chapter, published as Happe et al., 2019.

Data availability

All data for the SEM analysis and the statistical code is included as supplemental information.

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3. PUBLICATION II: PREDATORY ARTHROPODS IN APPLE ORCHARDS ACROSS EUROPE: RESPONSES TO AGRICULTURAL MANAGEMENT, ADJACENT HABITAT, LANDSCAPE COMPOSITION AND COUNTRY

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Coccinellid beetle and aphids. © A.-K. Happe, 2017.

ABSTRACT

Local agri-environmental schemes, including hedgerows, flowering strips, organic management, and a landscape rich in semi-natural habitat patches, are assumed to enhance the presence of beneficial arthropods and their contribution to biological control in fruit crops. We studied the influence of local factors (orchard management and adjacent habitats) and of landscape composition on the abundance and community composition of predatory arthropods in apple orchards in three European countries. To elucidate how local and landscape factors influence natural enemy effectiveness in apple production systems, we calculated community energy use as a proxy for the communities' predation potential based on biomass and metabolic rates of predatory arthropods. Predator communities were assessed by standardised beating samples taken from apple trees in 86 orchards in Germany, Spain and Sweden. Orchard management included integrated production (IP; i.e. the reduced and targeted application of synthetic agrochemicals), and organic management practices in all three countries. Predator communities differed between management types and countries. Several groups, including beetles (Coleoptera), predatory bugs (Heteroptera), flies (Diptera) and spiders (Araneae) benefited from organic management depending on country. Woody habitat and IP supported harvestmen (Opiliones). In both IP and organic orchards we detected aversive influences of a high-quality surrounding landscape on some predator groups: for example, high covers of woody habitat reduced earwig abundances in German orchards but enhanced their abundance in Sweden, and high natural plant species richness tended to reduce predatory bug abundance in Sweden and IP orchards in Spain. We conclude that predatory arthropod communities and influences of local and landscape factors are strongly shaped by orchard management, and that the influence of management differs between countries. Our results indicate that organic management improves the living conditions for effective predator communities.

Keywords: Agri-environmental scheme; Biological control; Integrated pest management; Natural enemy; Organic management; Woody habitat.

INTRODUCTION

Sustainable agricultural practices and enhanced habitat conservation at local and landscape scales are considered key solutions to stop the accelerating degradation of ecosystem services (IPBES, 2018). Biological control of agricultural pests is a prominent example of nature's contribution to human welfare. Favourable local and landscape factors can enhance predator communities and biological control (Bengtsson et al., 2005; Bianchi et al., 2006; Tschumi et al., 2016). In taking responsibility for sustainable land use and ecosystem services, we need to identify the effects of factors that explain the variability in arthropod communities and their potential services at different spatial scales, from climatic region, to landscape, to the orchard itself and its immediate local surroundings.

The country scale comprises several factors beyond macroclimate and biogeographic species pools. These include national policies on pesticides, differences in landscape habitat loss, identity of common crops, and availability of public advisory services. At the landscape scale, natural enemies benefit from a high proportion of semi-natural habitats (Chaplin-Kramer and Kremen, 2012; but see Hawro et al., 2015; Tscharntke et al., 2005). However, landscape effects on natural enemies also depend on taxon-specific mobility and dispersal capacity (Gallé et al., 2019; Schweiger et al., 2005). For spiders, habitat diversity and landscape composition are major determinants of occurrence at the landscape scale (Schweiger et al., 2005). In contrast, less mobile predatory arthropods such as earwigs remain mostly unaffected by the proportion of crop *vs*. non-crop cover in the landscape (Happe et al., 2018a). Landscape simplification as reflected by a high proportion of intensive agricultural cover reduces biological pest control (Rusch et al., 2016; Tscharntke et al., 2016). Consequently, a reduced proportion of intensive agricultural land and a high landscape complexity are often regarded as of special relevance to enhance biological control (Jonsson et al., 2015). For example, in landscapes dominated by cultivated land, biological control of aphids in different annual crop systems can be reduced by 46% when compared with more heterogeneous landscapes (Rusch et al., 2016).

Besides country and landscape effects, local factors such as adjacent habitat and orchard management influence natural enemies. At both landscape and local scales, the European Union subsidises agri-environmental schemes to enhance the ecological value of agro-ecosystems (Batáry et al., 2015). These schemes differ between countries and can, for example, protect diverse types of agro-ecosystems and cultural landscapes, support organic farmers, and enhance local habitat quality for natural enemies (e.g. in case of beetle banks and flower strips) (Batáry et al., 2015; Ekroos et al., 2014). Semi-natural woody habitats such as hedgerows or traditional orchards may shelter overwintering predatory arthropods such as coccinellid beetles and spiders (Elliott et al., 2002; Mestre et al., 2018). Improvement of local habitat quality in the orchard surroundings, for example by hedgerow restoration, can promote beneficial insects and natural pest control (Miñarro and Prida, 2013; Morandin et al., 2016). These habitats are more beneficial for predators than for pests and support predatory arthropods in fruit crops by enhancing habitat connectivity (Bailey et al., 2010). In addition to woody habitats, herbaceous plants may improve living conditions for natural enemies and the delivery of ecosystem services (Lichtenberg et al., 2017; Norris and Kogan, 2005). Flower-rich boundaries of crop orchards are particularly important for natural enemies that depend on pollen or nectar, which provide sugars and amino acids, for at least one part of their life cycle. These floral resources are essential for hoverflies, lacewings, hymenopteran parasitoids and omnivorous bugs such as anthocorids (Gurr et al., 2017; Wäckers and van Rijn, 2012). Herbal boundaries can also enhance the trait diversity of spiders, which may increase the biological control potential of spider communities (Gallé et al., 2019).

Another factor acting at the local scale is organic management. It increases the abundance, diversity, and service of natural enemies in various perennial and annual crop systems (Lichtenberg et al., 2017; Muneret et al., 2018; Todd et al., 2011). However, its positive effect on the abundance of predatory arthropods, e.g. of spiders, differs between landscapes (Bengtsson et al., 2005). The interaction of landscape and local management is well predicted by the intermediate landscape complexity hypothesis, which states that organic management is more beneficial at low and intermediate levels of landscape complexity, but less effective in highly-intensified and in natural landscapes (Tscharntke et al., 2012). Similarly, the impact of local habitat on the occurrence of natural enemies in orchards strongly depends on management (Lefebvre et al., 2016), but studies on interactions between management, adjacent habitat, and landscape factors on natural enemy communities are still rare (García et al., 2018; Martin et al., 2016). Comprehensive studies including these factors and their interactions are needed to develop agricultural practices and policies to promote effective and sustainable biological control across Europe.

In the production of apple, the most important European fruit crop (Eurostat, 2017a), maintaining biological control is particularly important. Biological control by predatory arthropods in apple orchards has a high economic value as it may substantially reduce insecticide applications (Cross et al., 2015). Predators such as birds, earwigs, lacewings, bugs, coccinellids, syrphids and spiders have been identified as important biocontrol agents in apple orchards (Porcel et al., 2018; Simon et al., 2010; Solomon et al., 2000). They contribute crucially to the regulation of severe apple pests such as the rosy apple aphid *Dysaphis plantaginea* Passerini, the woolly apple aphid *Eriosoma lanigerum* Hausmann, and tortricid moths including the codling moth *Cydia pomonella* L. (Solomon et al., 2000). Hence, enhancement of these natural enemies can lower the level of pest pressure and decrease fruit damage (Cahenzli et al., 2017; Letourneau and Bothwell, 2008). Indirect positive effects from increased natural enemy abundance can even partly compensate for lower yield in organic apple orchards compared to integrated production (IP) orchards (Samnegård et al., 2018).

Here, we assess the effects of orchard management and features of adjacent habitats (local factors) as well as the effects of landscape composition (proportion of fruit orchard cover) and diversity (landscape factors) on predatory arthropods in the major apple production regions of three

European countries (Spain, Germany, Sweden). Our aim is to identify favourable local and landscape factors to support predatory arthropods and to enhance their predation potential. We assess abundance of predatory arthropods in the study orchards and calculate their energy use by integrating predator body mass as a trait-based measure for predation potential (Perović et al., 2018). Energy use has been suggested as a proxy for prey consumption by predators and may serve as a currency for assessing ecosystem functioning (Brose et al., 2008; Hines et al., 2015). We test the following hypotheses:

(1) The composition of predatory arthropod communities differs between countries and management types (organic *vs.* IP). (2) Responses to agricultural management and to local and landscape factors are taxon-specific: (a) most predatory arthropods (except earwigs) benefit from reduced orchard cover at the landscape scale and from enhanced landscape diversity; (b) a high cover of local, orchard-adjacent woody habitats as well as organic management support predatory arthropods but organic management may be more effective at intermediate levels of orchard cover; (c) abundance of flower-visiting predatory arthropods (e.g. bugs, lacewings and hoverflies) is higher in orchards with high local plant species richness. (3) Effects of local agri-environmental schemes and landscape factors differ between management types; they are more effective in supporting predatory arthropods in IP than in organic orchards. (4) Organic management, high quality local habitats, a reduced orchard cover at the landscape scale and increased landscape diversity enhance the overall biological control potential of predator communities, measured as community energy use.

MATERIALS & METHODS

Predator communities

Predator communities were surveyed in 2015 in 86 apple orchards in Spain, Germany and Sweden. Orchard management included integrated production (IP) and organic management (ORG). Survey orchards were located in northeast Spain (Catalonia, hereafter 'SP'; 14 IP and 14 ORG), southwest Germany (lake Constance region, Baden-Württemberg, hereafter 'GE'; 15 IP and 15 ORG), and south Sweden (Skåne, hereafter 'SW'; 14 IP and 14 ORG) (Fig. 3.1; see Table S3.1 for orchard characteristics). The minimum distance between orchards of different management types was 1 km in SP, 2 km in GE, and 0.3 km in SW. We conducted beating sampling on one branch of each of 24 randomly selected trees per orchard along one (SP and SW) or two (GE) transects. Branches were selected to occur at a standardized height of 1.2 – 1.5 m, and sampling targeted a branch section conforming to the diagonal width of the beating tray (0.60 m). Transects measured 40 m and started at the edge of the orchard. To cover different exposures, we sampled branches on both sides of each transect. We took samples when fruitlets were starting to grow (10 - 40% of final fruit size; SP: May 19 - June 2; GE: June 15 - 22; SW: June 3 - 9) between 9 am and 5 pm. Arthropods were sorted from vegetation material and stored in 70% ethanol for quantification and identification under the stereo microscope. Predator abundance was calculated as the total number of predatory arthropods collected per orchard.

Landscape composition and diversity

We assessed landscape categories (Fig. 3.1) based on official digital maps for SP and GE (Carreras and Diego, 2009; LGL, 2016; SIOSE, 2015), and spatial land-use data from the Swedish Board of Agriculture (Integrated Administrative Control System, IACS) for SW. The Geographic Information Systems and Remote Sensing software used were ArcView 10.3.1 and MiraMon. Landscape analysis targeted cover (%) of orchards (excluding orchard meadows), grassland, arable land and forest (Table S3.1) within a 1 km radius around the centre of each transect. To avoid collinearity, we used % orchard cover as a measure of landscape composition. A high proportion of fruit orchard cover can be seen as a measure for homogeneous landscape composition and as a proxy for high land-use intensity in the studied apple production regions (Samnegård et al., 2018). Additionally, to quantify landscape diversity, we calculated the Shannon diversity index, $SHDI = -\sum_{i=1}^{R} p_i \ln p_i$ where p_i is the proportion of landscape patches belonging to the ith type of land cover (Shannon, 1948). The SHDI is recommended for landscape analyses in an ecological context (Nagendra, 2002). Landscape categories used to calculate SHDI were % cover of orchards, grassland, arable land, forest, semi-natural habitat (e.g. orchard meadows, woody habitats), sealed land, water bodies and 'other cover types' within a 1 km radius.

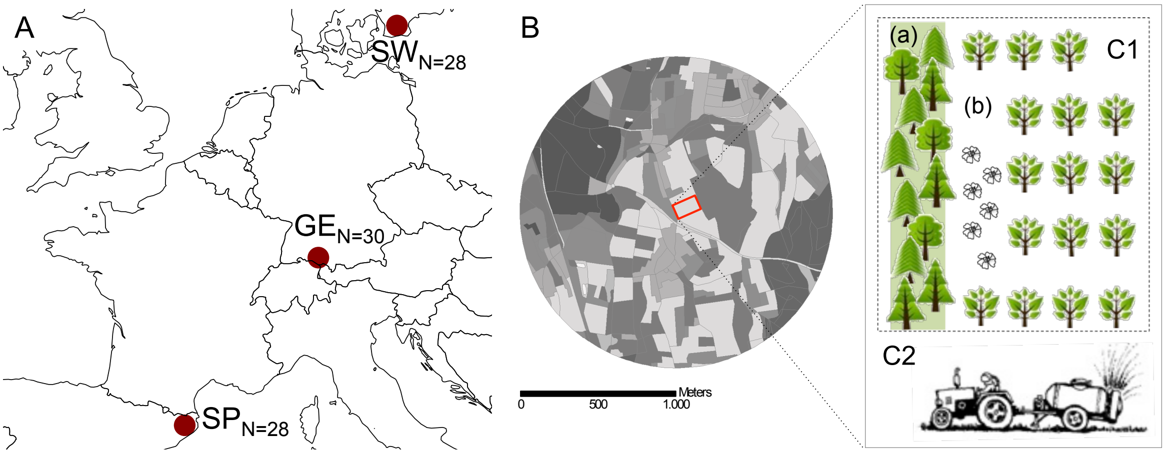

Figure 3.1. Scales considered in this study: (A) country: Spain (SP), Germany (GE) and Sweden (SW); (B) landscape: composition and diversity within a 1km radius around the orchard; (C) local scale: includes (C1) local habitat quality, i.e. (a) semi-natural woody habitat cover and (b) plant species richness, and (C2) orchard management (integrated production vs. organic management).

Local habitat quality

Hedgerows, forest edges and other woody elements, including orchard meadows, were considered relevant semi-natural woody habitats at the local scale (Fig. 3.1). We calculated the cover (m^2) of these woody structures within a radius of 20 m from the first tree (orchard edge) of the survey transects (Table S3.1). Local habitat quality and availability of floral resources was estimated by plant species richness in habitats adjacent to orchards (Fig. 3.1). We conducted vegetation surveys within a radius of 20 m from the first tree of the survey transects (orchard edge), during apple bloom. We assessed overall species richness of plants in the herb- and shrub-layer using six quadrats of 1 m^2 per orchard in GE and SW. In SP, plant species richness was assessed in three quadrats of 1 m^2 per habitat type (e.g. abandoned field, embankment, forest edge, grassy pathway, and hedgerow) and orchard. To account for differences in the number of quadrats per orchard in SP, we used sample-based rarefaction (Gotelli and Colwell, 2001).

Orchard management

All apple growers conducted standard pesticide treatments using air-assisted sprayers, following label recommendations and advice from local plant protection consultants. IP growers applied synthetic insecticides, fungicides and fertilizers following IOBC guidelines (Malavolta and Cross, 2009). ORG orchards were certified under European and national legislation (Council Regulation (EC) No 834/2007). ORG growers used natural plant extracts, microorganisms, viruses, mating disruption, and fungicides based on sulphur, copper and lime sulphur for pest and disease control (Table S3.2). ORG growers tilled tree rows instead of applying herbicides and used only organic fertilizers. Management intensity within categories IP and ORG differed between countries because national regulations restrict the use of some active compounds, e.g. Azadirachtin, Pyrethrine, Pirimor or Phosmet (Table S3.2). Growers can adjust management intensity within the range of national regulations but we did not get access to data on treatments for all orchards. Some extensive orchards in SW and two orchards in SP were uncertified but were considered organic because they were managed as under organic guidelines, with no chemical inputs.

Energy use of the predator community

Metabolic rate, *i.e.* the amount of energy expended by an organism at rest, has been identified as a key trait of arthropods in responding to the environment, affecting biological control services at local and landscape scales (Moretti et al., 2017; Perović et al., 2018). The energy use of the local predator community integrates each species abundance and body mass and can, to some extent, be used as a proxy of predation potential because individual metabolic rates determine consumption rates according to the metabolic theory of ecology (Brown et al., 2004). The community energy use of the local predator community is frequently used in the context of food webs (Brose et al., 2008; Thompson et al., 2012). Here, we apply it as an indicator for predation potential. It was calculated for each orchard based on dry body mass and abundance of collected specimens of each predator species (Table S3.3) using a metabolic model (Ehnes et al., 2011):

$$\ln C = \sum_{s=1}^{S} \left[\left(\ln i_s + a_s \ln M_s - E_s \left(\frac{1}{kT} \right) \right) \times A_s \right] \quad (3.1.)$$

where C = predator community energy use (J h^{-1}), M_s = dry mass (g) of species s, k = Boltzmann's constant (8.62×10^{-5} eV K^{-1}), T = average local summer temperature in Kelvin and A_s = total abundance of species s. Intercepts i_s, allometric exponents a_s and activation energies E_s (eV) are taxon-specific and differ for arachnids and insects (see Table 2 in Ehnes et al., 2011). The community energy use is thus summed across all S species and multiplied by their respective abundance.

To parameterize the model, we measured dry mass (mg) of one adult female (if available and sex could be identified; otherwise dry mass of an adult male, or an unidentified adult was used) of each species. The individual was dried until mass constancy was reached (at least 48 hours at 45 °C). Juvenile stages and morphospecies (species that could not be identified to species level but were morphologically distinct) were assigned a taxon-specific average dry mass (and metabolic rate) value (for example, unidentified coccinellid larvae would be assigned the average coccinellid dry mass; Table S3.3). To calculate the average of summer temperature in each region, we used the minimum and maximum average of the June mean daily temperature, based on data from the last 30 years (WMO, 2018) for WMO-listed cities closest to the study area: Lleida (SP; 22.3 °C), Girona (SP; 20.5 °C), Freiburg (GE; 18.0 °C) and Malmö (SW; 15.5 °C).

Statistical analysis

All statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016). We first checked for effects of country (SP, GE and SW) and management (IP *vs.* ORG) on the predator community composition using the 'vegan' package (Oksanen et al., 2016). We applied the 'adonis' function to conduct a permutational multivariate analysis of variance (Anderson, 2001; Oksanen et al., 2016) based on Bray-Curtis dissimilarities, which were calculated from the relative abundance (proportion at orchard level) of each taxon. To test for homogeneity of multivariate dispersion (variance), we applied the 'betadisper' function (Anderson, 2006). Subsequently, we calculated indicator values of taxa (IndVal; the product of the relative frequency and relative average abundance in clusters) for each management type in each country separately (Dufrêne and Legendre, 1997) using the 'indval' function of the 'labdsv' package (Roberts, 2016).

Nonmetric multidimensional scaling (NMDS) ordination plots visualised differences in community composition across management types and countries. For SP, we excluded one IP orchard from multivariate analysis because no predatory arthropods were found. We added arrows to indicate the grouping of predator taxa (predictors) using the 'vegan' function 'envfit' at $P \leq 0.001$ with 10,000 permutations. Some orchards had the same proportion value and overlapped in the ordination and therefore not all included orchards are displayed.

To assess management effects on the abundance of each predator group (spiders, beetles, earwigs, predatory flies, predatory bugs, lacewings, and harvestmen) between countries, we used generalised linear models (GLM) with Poisson distribution; accounting for overdispersion by using a quasi-GLM or negative binomial distribution when necessary. We included 'country' and 'management' as categorical predictors, allowing for first order interactions. Variability accounted for (% deviance explained = null deviance - residual deviance / null deviance) is presented to show the goodness of fit of the model. Whenever a variable with multiple levels was significant in the GLM, we applied post-hoc tests (Table S3.4) using the 'glht' function for multiple comparisons of means (simultaneous tests for general linear hypotheses) with Tukey contrasts.

We used GLMs to analyse the effects of local and landscape factors on predator abundance for each predator group in each country separately. We included management (IP *vs.* ORG), and the continuous variables local woody habitat cover, local plant species richness, % cover of fruit orchards and landscape diversity (SHDI). We allowed first level interactions among management and other predictors. Given the expected quadratic response of management effect to landscape cover predicted by the intermediate landscape complexity hypothesis (Tscharntke et al., 2012), we additionally allowed for an interaction of management with the second order term of the two landscape variables, % cover of fruit orchards and SHDI. Subsequently, we excluded terms that were non-significant ($P > 0.05$) based on a stepwise backwards procedure to avoid model over-parameterisation.

We applied GLMs with Poisson distribution. In cases of overdispersion or heteroscedasticity of residuals between predictor levels, we either fitted GLMs with a negative binomial error distribution or generalised linear mixed-effects models (GLMM) (lme4 package; Bates et al., 2015) with Poisson distribution including orchard identity as an observation-level random effect (Harrison, 2014). In case of zero inflation, we used the AD model builder of the 'glmmADMB' package (Skaug et al., 2016).

To test the effect of local and landscape factors on community energy use (J h^{-1}), we applied linear models. Energy use was log-transformed, adding a value corresponding to half the value of the smallest amount of energy use in the case of zero energy use. We calculated rarefied plant species richness for SP using the function 'rarefy' in the 'vegan' package (Oksanen et al., 2016). We tested for collinearity between predictors by calculating variance inflation factors (VIF; Naimi et al., 2014). When we detected collinearity (VIF > 3) after scaling, strongly correlated variables or their interactions were dropped (Zuur et al., 2010). We checked distributions and Spearman rank correlations between all relevant response variables as well as local and landscape variables (Figs. S3.4-6). Normality and homoscedasticity of residuals were checked by visual inspection using the 'DHARMa' package (Hartig, 2017) for all but zero-inflated models (not implemented in the 'DHARMa' package). Finally, we used the car package (Fox and Weisberg, 2011) to conduct likelihood ratio tests to establish the significance of the main factors in all GLMs, GLMMs and linear models. Figure 2 and figures in the appendix were visualized using the 'ggplot2' package (Wickham, 2016).

RESULTS

We sampled 1,509 predatory arthropods in 86 orchards. The arthropods were identified as belonging to 91 species in 77 genera. Additional 17 morphospecies belonged to unidentified genera (resulting in

108 species in total; Fig. S3.1, Table S3.3). The predators belonged to seven arthropod groups: spiders (Araneae, 40 spp.), beetles (Coleoptera, 24 spp.), earwigs (Dermaptera, 2 spp.), predatory flies (Diptera, 28 spp.), predatory bugs (Heteroptera, 9 spp.), lacewings (Neuroptera, 3 spp.), and harvestmen (Opiliones, 2 spp.). Overall, predator abundance was higher in ORG than in IP orchards (Table S3.3). Orchards in GE showed higher predator abundances than in SP and SW (Table 3.1, Fig. 3.2). Specifically, in SP, we found less than half as many predatory arthropods than in GE or SW (Table 3.1, Fig. 3.2). Spiders were abundant in all countries, with *Araniella opisthographa* Kulczyński being the most abundant species and *Philodromus* Walckenaer being the most abundant genus. Other frequent taxa were bugs, mainly anthocorids and mirids, beetles, mainly cantharids, adult and larval coccinellids, and predatory dipterans, mainly dolichopodids, empidids, hybotids and larval syrphids.

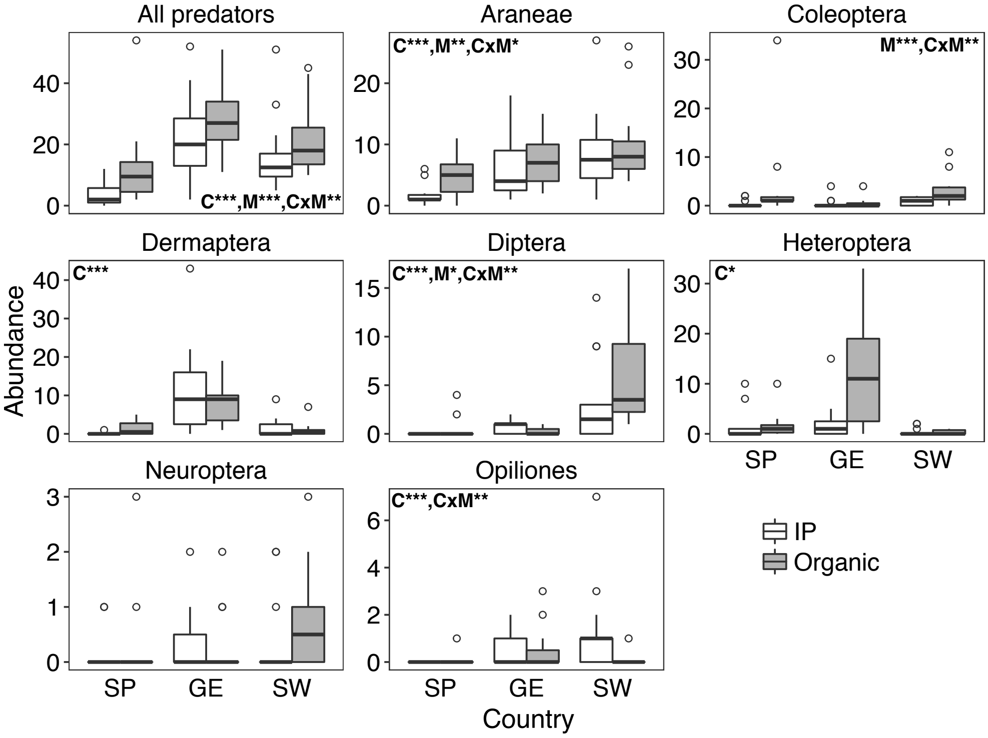

Figure 3.2. Abundance (number of individuals per 24 trees per orchard) of seven predator taxa in apple orchards in Spain (SP), Germany (GE) and Sweden (SW). Effects of country (C) and management (M; integrated production 'IP' *vs.* organic 'ORG') on the abundance of each taxon are indicated within each plot (see Table S3.4 for summary statistics and post-hoc tests). Empty circles indicate outliers.

Table 3.1. Effects of local and landscape factors[1] on (A) abundance of seven predatory arthropod groups and on (B) energy use of the predator community in apple orchards in Spain (SP), Germany (GE) and Sweden (SW); for each predator group, total abundance across sites for each country (number of individuals in all orchards) and the number of orchards in which the predator group was recorded (in parentheses) are indicated in bold. Effects on (B) total energy use by the predator community in bold as well. Orchard cover (%) was assessed at landscape scale (within 1 km), orchard management (IP *vs.* organic), plant species richness and woody habitat cover (m^2) at local scale (within 20 m). χ^2 - and *P*-values[2] are given for reduced models (stepwise-backward selection) with estimates ± S.E. in parentheses. 'NA' indicates that no analysis was possible, 'n.s.' that no significant effect was found.

	SP (N=28)	GE (N=30)	SW (N=28)
(A) Abundance			
All predatory arthropods	**224 (27)**^{a}	**755 (30)**^{b}	**530 (28)**^{a}
Management	χ^2 = 16.07 (1.25±0.31) P < 0.001 ***	χ^2 = 3.27 (0.37±0.20) P = 0.070	n.s.
Orchard cover (%)^1	χ^2 = 3.17 (0.43±0.23) P = 0.075	n.s.	n.s.
Management × orchard cover (%)^1	χ^2 = 7.08 (-0.84±0.31) P = 0.008 **	n.s.	n.s.
Araneae	**89 (23)**^{a}	**201 (30)**^{a}	**261 (28)**^{a}
Management	χ^2 = 10.69 (1.11±0.35) P = 0.001 **	n.s.	n.s.
Coleoptera	**58 (14)**$^{c, d}$	**13 (7)**^{c}	**55 (21)**^{a}
Management	n.s.	n.s.	χ^2 = 9.52 (1.17±0.39) P = 0.002 **
Dermaptera	**21 (8)**^{a}	**290 (26)**^{a}	**36 (14)**^{c}
Management	χ^2 = 11.72 (3.00±1.12) P < 0.001 ***	n.s.	χ^2 = 6.89 (-2.08±0.79) P = 0.009 **
Woody habitat cover^1	n.s.	χ^2 = 9.73 (-0.003±0.001) P = 0.002 **	χ^2 = 4.87 (1.00±0.45) P = 0.027 *
Diptera	**6 (2)**^{c}	**15 (13)**^{c}	**136 (23)**^{b}
Management	n.s.	χ^2 = 3.00 (-1.01±0.58) P = 0.083	χ^2 = 3.93 (0.92±0.46) P = 0.047 *
Heteroptera	**43 (15)**^{b}	**213 (22)**^{a}	**9 (7)**^{c}
Management	χ^2 = 7.54 (2.83±0.87) P = 0.006 **	χ^2 = 11.8 (1.63±0.46) P < 0.001 ***	n.s.
Plant species richness^1	χ^2 = 13.20 (-2.18±0.60) P < 0.001 ***	n.s.	χ^2 = 3.27 (-0.90±0.50) P = 0.070
Management × plant species richness^1	χ^2 = 6.66 (1.76±0.68) P = 0.010 **	n.s.	n.s.
Neuroptera	**6 (4)**^{c}	**9 (7)**^{c}	**15(10)**^{c}
Opiliones	**1 (1)**	**14 (9)**^{c}	**18 (9)**^{c}
Management	NA	n.s.	χ^2 = 6.05 (-2.76±1.12) P = 0.014 *
Woody habitat cover^1	NA	χ^2 = 3.94 (0.78±0.39) P = 0.047 *	n.s.
(B) Energy use	**9.83 J h^{-1}**	**55.1 J h^{-1}**	**17.9 J h^{-1}**
Management	$F_{1,26}$ = 23.95 (1.59±0.33) P = <0.001***	n.s.	n.s.
Woody habitat cover^1	n.s.	$F_{1,28}$ = 3.08 (-0.002±0) P = 0.09	n.s.

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[1] continuous variables were scaled to decrease VIF below 3; [2] ANOVA type III; [a] GLM: negative binomial with log-link; [b] GLMM: poisson with log-link and observation level random effect in case of overdispersion; [c] zero-inflation models glmmADMB with observation level random effect in case of overdispersion; [d] positive effect of plant species richness on Coleoptera in Spain (χ^2 = 24.99 (+), $P < 0.001$) if outlier is included (orchard E7: 33 years old)

In SP, we found more *Forficula pubescens* Gené earwigs than *F. auricularia* L., but earwigs were generally rare in the samples. In GE and SW all earwigs were *F. auricularia* (Table S3.3). In GE, earwigs and predatory bugs comprised a large proportion of the predator community (Fig. 3.2). Dipterans were more abundant in SW than in the other countries (Table 3.1). Lacewings and harvestmen had low abundances in most orchards (Fig. 3.2, Table 3.1). As expected, there were strong positive correlations between abundance and predator community energy use in each country (SP: $\rho = 0.86$, $P < 0.001$; GE: $\rho = 0.54$, $P = 0.002$; SW: $\rho = 0.71$, $P < 0.01$).

Predator responses to management in different countries

The interaction between country and management was significant for all predators (summed up over all groups) and for four out of seven predator groups (Fig. 3.2, Table S3.4). Depending on the country, the predator community composition differed between ORG and IP orchards (ADONIS: $pseudo\text{-}F_{5,79} = 2.51$, $P = 0.018$, $R^2 = 0.32$, Fig. 3.3). Dispersion among groups (multivariate spread) was homogeneous (betadispersion: $pseudo\text{-}F_{5,79} = 1.78$, $P = 0.126$). The analysis of indicator values for orchard management in each country revealed only one indicator taxon for IP orchards in SW: Opiliones: 0.5 (9), $P_{\mathrm{adj}} = 0.027$; IndVal with frequency in parentheses. For ORG orchards, several indicator taxa were observed: three in SP (Coleoptera: 0.7 (14), $P_{\mathrm{adj}} = 0.018$; Araneae: 0.6 (23), $P_{\mathrm{adj}} = 0.047$, Dermaptera: 0.5 (8), $P_{\mathrm{adj}} = 0.026$), one in GE (Heteroptera: 0.7 (22), $P_{\mathrm{adj}} = 0.015$), two in SW (Coleoptera: 0.7 (21), $P_{\mathrm{adj}} = 0.060$; Diptera: 0.7 (23), $P_{adj} = 0.060$)).

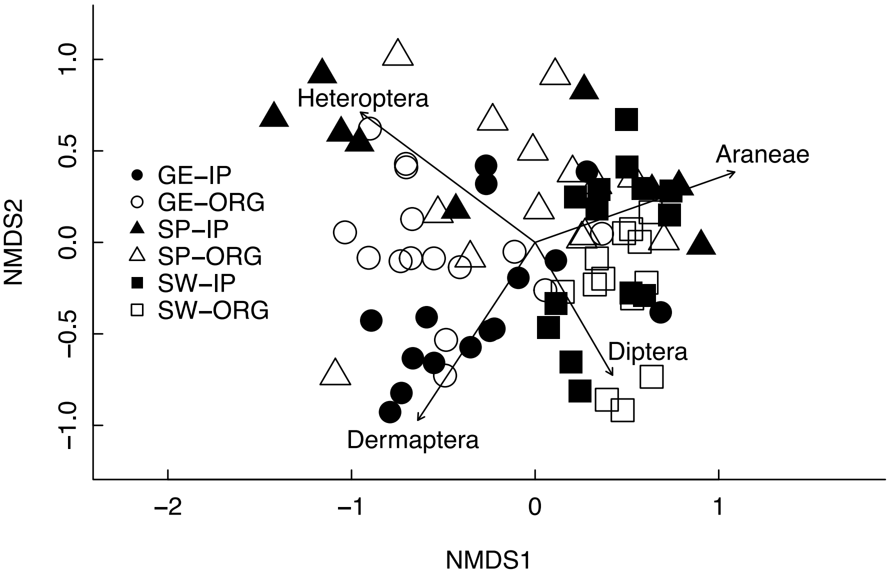

Figure 3.3. Ordination of predatory arthropod communities in apple orchards in Spain (SP), Germany (GE) and Sweden (SW) for two management types: integrated production (IP) and organic management (ORG). Grouping of taxa (arrows) along the two first axes of the NMDS (stress = 16.8%, 20 procrustes). Arrow length indicates the strength of predictors (taxa) fitted onto the ordination for $P \leq 0.001$.

Country-specific responses to local and landscape factors

Effects of local and landscape factors differed between countries and predatory arthropod groups (Table 3.1). We observed no consistent response of predatory arthropod groups to either of the tested local and landscape factors or to interactions between management and other factors across all three countries. In SP, high orchard cover at the landscape scale was associated with predator abundance in IP but not in ORG orchards, where predator abundance was constantly high (Fig. S3.2). Landscape diversity did not explain variability in predator abundance in any of the countries. We did not find a management-dependent peak in predator abundances at intermediate levels of orchard cover or intermediate landscape diversity. Local woody habitat cover influenced only two predator groups, earwigs and harvestmen. It enhanced harvestmen abundances in GE but showed contrasting effects on earwig abundances in different countries. It was associated with high earwig abundance in SW but with reduced abundance in GE (Table 3.1). In SP, woody habitat cover was very low (Table S3.1) and did not influence predator abundances. Local plant species richness (Table S3.5) in adjacent habitats reduced the abundance of predatory bugs in Spanish IP orchards (SP: $P = 0.010$, Table 3.1; Fig. S3.2). The effect of plant species richness was similar but not statistically significant for Heteroptera in Swedish IP and ORG orchards ($P = 0.070$; Table 3.1). The analysis of local and landscape factors confirmed the sensitivity of predatory arthropods to orchard management (as already suggested by indicator values) for all predator groups except for beetles in SP (Table 3.1). However, most predator groups were influenced in only one or two countries, and the effects of management were not consistent (Table 3.1). In SP, the positive influence of ORG management on predator groups was reflected in predator community energy use. However, effects of management on energy use were not always similar to effects on abundance. Energy use was generally less sensitive than abundance (Table 3.1).

DISCUSSION

Predator responses to management in different countries

We expected the responses of the predator communities to apple management to be consistent across Europe. Instead, predator communities showed country-specific differences in their sensitivity to management. Total predator abundance differed between management types only in Spain (SP) (significantly) and Germany (GE) (marginally significant), with higher abundances in ORG. This finding can be partly explained by country-specific differences in management intensity in both management types (IP and ORG), such as the restricted use of several insecticides in Sweden (SW) for both management types. However, lack of pesticide data at the orchard level in SW limits our understanding of management intensity in this region (Table S3.2). Alternatively, some of the different responses of the regional predator communities to management may be explained by latitudinal differences. These differences may for example influence predator and prey faunas, tree cultivar, and predominant land-cover types and local habitats (Mody et al., 2017; Nyffeler and Sunderland, 2003).

However, predator community responses to management at the country scale can be better understood when considering specific taxonomic groups (Fig. 3.2). It has been proven that predators such as lacewings, coleopterans, earwigs, and bugs are sensitive to insecticides applied in apple orchards (Fountain and Harris, 2015; Mills et al., 2016). Sub-lethal effects of both organic and synthetic pesticides on predatory bugs and other predatory arthropods are well known (Biondi et al., 2012; Desneux et al., 2007; Müller, 2018). Porcel et al. (2018) reported enhanced natural enemy abundance (and increased biological control of aphids) in organic apple orchards compared to conventional apple orchards; predatory bugs, which played a key role in regulating the growth of aphid colonies, were the group that benefited most from organic management. Our results support these findings and point to at least three differences in insecticide application between countries (Table S3.2). (1) ORG management reduced abundances of earwigs and harvestmen in SW and had marginally significant negative effects on predatory flies in GE. The only commonly applied ORG-insecticide in SW known for side effects on earwigs was Pyrethrine (Peusens and Gobin, 2008). Products based on this active ingredient were not permitted in SP and only rarely applied in GE. The application of neem (*Azadirachta indica*) products as ORG insecticides in GE and SP but not in SW may partly explain patterns of dipteran abundance. Azadirachtin, a component of neem oil that repels feeding and inhibits moulting, can harm dipterans, especially those in their larval stages (Schmutterer, 1997; Spollen and Isman, 1996). (2) Focusing on IP orchards, we found lower predator abundances for spiders and earwigs in SP that can be explained as side effects of synthetic insecticides. IP growers in SP (exclusively) applied several insecticides containing the active compounds Chlorpyrifos or Deltamethrin, both known for their harmful side effects on spiders (Markó et al., 2009; Pekár and Beneš, 2008), and Phosmet, which belongs to the group of organophosphates, known for their harmful side effects on earwigs (Malagnoux et al., 2015a; Peusens and Gobin, 2008). (3) Regular application of Pirimicarb and Thiacloprid in IP may explain a positive effect of ORG on bugs in GE (van de Veire et al., 2002; van de Veire and Tirry, 2003).

However, the absence of spray information at the orchard level limits our capacity to link agrochemical applications to predator abundance. In addition, soil management in the tree row (herbicide application in IP; mulching and mechanical weed control or tillage in ORG) can affect epigeic predators and earwigs (Miñarro et al., 2009; Moerkens et al., 2012). The non-consistent response of earwigs to management in SW and SP may have been triggered by differences in regional management and in species composition. In SP, we found two earwig species, whereas only one species was present in SW (and GE). The two species found in SP markedly differed in their sensitivity to management: *Forficula auricularia* was common in both IP and ORG orchards, whereas *F. pubescens* was much less abundant in IP orchards (Happe et al., 2018a). On the other hand, earwigs' sensitivity to tillage during hibernation and below-ground brood care may explain lower *F. auricularia* abundances in ORG orchards in SW (Moerkens et al., 2012). When interpreting abundance patterns of predatory arthropods, it should be considered that species richness and regional species composition differed not only for earwigs but also for other focal groups such as predatory flies and spiders (Fig. S3.1, Table S3.3). In addition to the toxic effects of pesticides, differences between ORG and IP may be partly explained by the higher pest densities in ORG orchards, which may support larger predator populations (Samnegård et al., 2018).

Country-specific responses to local and landscape factors

Intensive orchard management may alter or even counteract other local factors as well as landscape factors (Tscharntke et al., 2016), and landscape features may alter the effectiveness of local habitat and organic management in supporting biological control (Jonsson et al., 2015; Tscharntke et al., 2012). In this study, orchard management directly influenced the abundance of six out of seven predatory arthropod groups (sometimes in opposite directions, Table 3.1). Yet, interactions between management and local or landscape factors were only evident in two cases. Firstly, plant species richness was associated with low predatory bug abundance in IP but not in ORG, indicating that effects of local habitat are management-dependent. Secondly, ORG management enhanced predator abundance only at low levels of orchard cover in Spanish landscapes. The intermediate landscape complexity hypothesis highlights the effectiveness of ORG management to support biodiversity at intermediate cover levels of semi-natural habitats and non-crop areas, which provide arthropod biodiversity to crops through spillover effects (Batáry et al., 2010; Tscharntke et al., 2012). High levels of orchard cover at landscape scale reduced the availability and accessibility of semi-natural habitats. This may be of special relevance in IP orchards, where predatory arthropods are subjected to greater hazards. A peak in predator abundance in ORG orchards at intermediate levels of landscape diversity or orchard cover was not evident.

At the local scale, woody habitat had mixed effects on predator abundances. High local woody habitat coverage enhanced earwig abundance in SW (but reduced it in GE), and harvestmen abundance in GE. In the context of augmenting biological control, woody habitat quality has often been characterised in terms of woody plant species richness, cover and connectivity (Dainese et al., 2016; Malagnoux et al., 2015b). For example, linyphid spiders have been reported to use continuous unbroken hedgerows with a high diversity of woody species as source habitats, spilling over to neighbouring crops (Garratt et al., 2017). Differences in quality of woody structures may have driven the contrasting responses of earwigs and harvestmen to woody elements in the three countries. On the other hand, plant species richness did not alter earwig or harvestmen abundances in either country (Table 3.1). It may be that regional differences in the response of the two groups were triggered by spillover constrained by the density of prey in the woody habitat. Results for harvestmen (and lacewings) should be interpreted cautiously because the number of individuals was low (Table 3.1).

Other studies have provided evidence that enhancing local plant diversity by establishing flower strips improves living conditions for beneficial arthropods (Batáry et al., 2015; Letourneau et al., 2011; Lichtenberg et al., 2017). A high local flower richness is especially important for natural enemies in orchards that lack woody habitats in the vicinity (Saunders and Luck, 2018). Contrary to these findings, we observed negative influences of plant species richness on predatory bugs in SW (marginally significant), and no effects on the other groups. Some particularly prominent bugs in apple orchards (*e.g.* anthocorids, Table S3.3) use floral nectar and pollen as a food resource (Wäckers and van Rijn, 2012). However, plant species richness did reduce rather than enhance bug abundance and the response of bugs to plant species richness was inconsistent among countries. The presence and flower cover of a few favoured plant species may be more relevant than total plant species richness (Wäckers and van Rijn, 2012). On the other hand, bugs could be more attracted by flower-rich adjacent habitats than by intensively managed IP orchards. Results for orchards in SP could support this explanation: In SP high plant species richness was associated with low bug abundance in IP but not in ORG orchards (Fig. S3.2). Management intensity may reduce the attractiveness of the orchard as a habitat, especially if food resources for beneficial arthropods are affected. For instance, insecticide applications can diminish prey insects, and weed control may reduce plant species richness and flower cover (Cross et al., 2015; Miñarro, 2012; Simon et al., 2010). In this case, high-quality adjacent habitats, such as sown flower strips, can potentially provide a suitable if not a better environment for a wide range of herbivores. As a result, natural enemies may not disperse from the adjacent habitat into the crop (Holland et al., 2016; Tscharntke et al., 2016). This could also explain the lower earwig abundance in orchards with enhanced woody habitat cover in GE (Happe et al., 2018a).

Effects of local and landscape factors on overall predation potential (measured as energy use) mainly resembled the response of the largest and most abundant taxon in each country. Such large, abundant predatory arthropods (e.g. spiders in SP and earwigs in GE) are likely to contribute strongly to biological control of their specific prey taxa. In general, community energy use was less sensitive than abundance to local and landscape factors, reflecting body mass distribution (Fig. S3.3). The effectiveness of predators is well predicted by mean predator body size with larger predators showing higher per capita consumption rates (Emmerson and Raffaelli, 2004; Rusch et al., 2016). Positive influence of higher abundance and biomass on biological control is necessarily constrained in cold climates by energetic demand (Londoño et al., 2015; Schneider et al., 2012). Energy use may therefore be more relevant than abundance and biomass to describe the biological control potential of predator communities along a geographical gradient with large climatic differences.

Conclusion

Our results suggest that management plays an important role in shaping communities of predatory arthropods in orchards across Europe. ORG management enhanced abundance of some predator groups depending on country but only a few generalist predator groups benefited from high quality local habitat. Landscape composition and interactions of orchard management with local and landscape factors seemed to be less relevant for predators than local management and habitat quality.

Predation potential (energy use by the predator community) can be enhanced by ORG management but it remains largely unaffected by local and landscape factors. We conclude that conservation measures and agri-environmental schemes to foster effective predator communities in apple orchards need to be well adapted to the target region. They should take the taxonomic identity of predatory arthropods and region-specific management intensity into account. The local knowledge of growers and their advisers on specific site conditions and requirements from ecosystem services may be the key to more targeted and dynamic management strategies.

Data available at https://doi.org/10.1016/j.agee.2018.12.012 (see supplementary tables S3.3–5).

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SUPPLEMENTARY MATERIAL

Table S3.1. Orchard and landscape characteristics in integrated production (IP) and organic (ORG) orchards in Spain, Germany and Sweden. NA indicates that data were not available. Significant differences between management types within each country are shown in bold (t-tests/Mann-Whitney U; $P < 0.05$).

	Spain		Germany		Sweden	
	IP (N=14)	ORG (N=14)	IP (N=15)	ORG (N=15)	IP (N=14)	ORG (N=14)
Location	41°37'N, 0°38'E (Lleida); 41°59'N, 2°49'E (Girona)		Constance, 47°43'N, 9°23'E		Skåne, 55° 59'N, 13°26'E	
Temperature (°C, mean of 2015)	14.4 (Lleida); 14.9 (Girona)		11.1		9.5	
Annual precipitation (mm, 2015)	199.7; 541		736		724	
Cultivars	Golden, Golden Delicious		Braeburn		Aroma, Amorosa, Ingrid Marie, Rubinola	
Rootstock	M9		M9		M9	
Tree height (m)	2.0 - 3.5		2.2 - 3.7		2.5 - 4.0	
Spacing (m)	min 3 × 1, max 4 × 5		min 3 × 1, max 4 × 5		min 3.5 × 0.9, max 5 × 4	
Pruning	spindle		spindle		spindle (most), open vase (some)	
Size (ha)[a,b]	1.7±1.1	2.4±2.8	1.0±0.6	0.9±0.6	**15.8±11.1**	**3.7±3.7**
Tree age (years)[a]	11.4±7.3	13.3±8.3	9.7±3.7	9.9±3.0	15.5 ± 3.7	21.1±19.9
Land-use cover (%)[a]						
Orchard	41.6±30.5	32.5±31.1	34.1±16.4	27.0±11.1	15.4±12.2	11.2±12.8
Forest	1.0±2.0	2.6±3.3	19.3±17.3	19.5±15.6	14.3±14.1	19.7±14.2
Arable land	51.8±29.2	51.0±34.0	20.9±12.8	27.2±15.8	40.9±32.7	29.6±19.3
Grassland	0.62±0.93	1.26±2.71	11.9±5.6	14.0±6.2	4.97±5.89	8.65±9.79
Landscape diversity[a]	1.09±0.28	1.15±0.35	**1.33±0.07**	**1.46±0.11**	1.77±0.49	1.89±0.16
Woody habitat (m^2)[a]	33.2±124.3	50.0±100.7	129.0±176.8	152.7±189.4	182.1±188.5	308.0±276.9
Plant species richness[a]	**8.3±3.1**	**11.7±4.3**	13.3±5.1	16.5±10.5	11.9±4.5	13.1±6.6
Farming	fresh consumption		fresh consumption		fresh consumption, cider	
Hail nets	some		yes		no	

[a] mean ± SD for orchard size, tree age, major land use categories (% cover in 1 km radius), landscape diversity (Shannon diversity index), local woody habitat cover (in a 20-m zone adjacent to orchard) and local plant species richness; [b] size of target cultivar for SP and GE; size of orchard based on aerial photographs including other cultivars and parcels for SW.

Sources: DWD, 2017. Climate data for Germany. Deutscher Wetterdienst, http://www.dwd.de, accessed 2017-07-05; IDESCAT, 2017. Climatologia. Instituto de Estadística de Cataluña, https://www.idescat.cat, accessed 2017-07-15; SMHI 2018. Climate data for Lund. Swedish Meteorological and Hydrological Institute, https://www.smhi.se, accessed 2018-09-13.

Table S3.2. Differences in use of agrochemical products between integrated production (IP) and organic (ORG) apple orchards in Spain, Germany and Sweden. Active substances, product examples are given. Products were 'NP' not permitted in apple orchards during study time; '-' not applied; '+' applied rarely (1-2 orchards); '++' applied regularly (>2 orchards).

Active substance	Commercial product name (examples)	Spain		Germany		Sweden	
		IP	ORG	IP	ORG	IP	ORG
Insecticides							
Azadirachtin	NeemAzal-T/S® (Trifolio-M GmbH)	+	++	-	++	NP	NP
Bacillus thuringiensis	XenTari® (Biofa) / Dipel® ES (Cheminova) / Turex 50 WP	+	+	-	++	+	+
Chlorantraniliprole	Coragen® (Dupond)	++	NP	+	NP	NP	NP
Chlorpyrifos	Inaclor 25 PM (Sipcam Inagra) / DurasbanTM 75 WG (Dow AgroScience) / Reldan® E (Dow AgroScience)	++	NP	-	NP	NP	NP
Deltamethrin	Proteus® O-TEQ (Bayer)	++	NP	-	NP	NP	NP
Flonicamid	Teppeki® (ISK Biosciences Europe)	++	NP	++	NP	++	NP
Granulosis virus	Capex® 2 *Adoxophyes orana* gv (Andermatt Biocontrol AG) / Madex® MAX Cydia pomonella gv (Agrinova)	+	++	++	++	++	++
Heterorhabditis bacteriophora	Nemasys G (BASF Agro)	-	-	-	-	+	+
Imidacloprid	Confidor® 20 LS (Bayer), Shardox 20 (Sharda CropChem)	+	NP	-	NP	NP	NP
Indoxacarb	Steward® (Stähler)	+	NP	+	NP	++	NP
Kaolin	Surround® WP (Stähler)	+	+	+	++	NP	NP
Methoxyfenozide	Gladiator® (Dow AgroSciences) / Runner® (Bayer)	+	NP	++	NP	NP	NP
Phosmet	Imidian® WP (BASF Agro)	++	NP	NP	NP	NP	NP
Pirimicarb	Pirimor®, Aphox® (Syngenta)	+	NP	++	NP	NP	NP
Piriproxyphen	Expedient® 10 EC (Sapec Agro)	++	NP	NP	NP	NP	NP
Plant oil	Micula® (Biofa)	NP	NP	+	+	NP	NP
Pyrethrine + oil	Spruzit® Neu (Progema GmbH)	NP	NP	-	+	-	++
Quassin	*Quassia amara* extract	NP	NP	-	++	NP	NP
Spirotetramat	Movento SC® (Bayer)	++	NP	++	NP	+	NP
Steinernema sp.	Capsanem® (Koppert), Nemasys / Nemasys L (BASF Agro)	-	-	-	-	+	+
Tebufenozid	Mimic® (Spiess-Urania)	+	NP	-	NP	NP	NP
Thiacloprid	Calypso® (Bayer) / Proteus O-TEQ (Bayer)	+	NP	++	NP	+	NP
		17	**4**	**10**	**7**	**8**	**5**

Active substance	Commercial product name (examples)	Spain		Germany		Sweden	
		IP	ORG	IP	ORG	IP	ORG
Acaricides							
Abamectine	Vertimec® (Syngenta)	++	NP	NP	NP	+	NP
Acequinocyl	Kanemite® SC (Cheminova)	NP	NP	++	NP	NP	NP
Acetamiprid	Mospilan® SG (Cheminova)	+	NP	-	NP	+	NP
Fenpyroximat	Kiron® (Cheminova)	+	NP	+	NP	+	NP
Hexithiazox	Diabolo SC® (Afrasa)	+	NP	NP	NP	+	NP
Milbemectin	Milbeknock® (Spiess-Urania)	+	NP	++	NP	NP	NP
Paraffin oil	Oviphyt (CCL) / Para Sommer (Cheminova)	++	++	++	++	++	+
Spirodiclofen	Envidor® (Bayer)	+	NP	+	NP	NP	NP
		7	**1**	**5**	**1**	**5**	**1**
Fungicides							
Aureobasidium pullulans	Blossom ProtectTM *Aureobasidium pullulans* (Biofa)	+	+	+	+	NP	NP
Captan	Merpan® 80 WDG (Adama) / Malvin® WG (Stähler)	++	NP	++	NP	NP	NP
Copper(II) hydroxide	e.g. Cuprozin® / Funguran® progress (Spiess-Urania)	++	++	++	++	NP	NP
Dithianon	Delan® WG (BASF)	++	NP	++	NP	++	NP
Lime sulphur	Curatio® (Biofa)	+	++	++	++	-	+
Potassium bicarbonate	e.g. VitiSan® (Biofa)	+	+	-	++	NP	NP
Sulphur	e.g. Stulln® 80% WG (agrostulln GmbH) / Kumulus® WG (BASF)	++	++	++	++	++	++
Trifloxystrobin	Flint® (Bayer)	++	NP	++	NP	NP	NP
Prohexadione calcium	Regalis® Plus (BASF)	++	NP	++	NP	NP	NP
		9	5	8	5	2	2
Herbicides							
Flumioxazin	Vorox® F (Spiess-Urania)	NP	NP	+	NP	NP	NP
Glyphosate	Roundup® (Monsanto) / Touchdown® (Syngenta)	++	NP	++	NP	++	NP
Glufosinate-ammonium	Basta® (Bayer) / Finale® (Bayer)	++	NP	++	NP	NP	NP
		2	**0**	**3**	**0**	**1**	**0**
Total no. of pesticide products		**35**	**10**	**26**	**13**	**16**	**8**

Sources: Farmer and expert interviews, national regulations, spraying reports (SP: 3 IP and 4 ORG; GE: 5 IP and 5 ORG); WOG 2017. Rundschreiben Nr. 02/2017, 2017-01-24 der Württemberg. Obstgenossenschaft Raiffeisen eG, LTZ 2017. Integrierter Pflanzenschutz im Erwerbsobstbau (p. 42); FÖKO & BÖLN 2016. Gesunderhaltung der Kulturpflanzen im ökol. Apfelanbau (p. 40); Jordbruksverket 2017. Växtskyddsmedel 2017 – frukt. Jönköping, Sweden, www.jordbruksverket.se, accessed 2018-06-13.

Table S3.3. Species list for predator taxa in integrated production (IP) and organic (ORG) apple orchards including abundance by country (Spain (SP), Germany (GE), Sweden (SW)) and management type, dry mass (mg) and energy use (J h^{-1}) based on average summer temperature (mean for SP, GE and SW). Dry mass and energy use were averaged at the taxon level, if species had not been identified ('unid').

ORDER / Family	Genus / species	Author	SP		GE		SW		Total	Dry weight (mg)	Energy use (J h^{-1})
			IP (n=14)	ORG (n=14)	IP (n=15)	ORG (n=15)	IP (n=14)	ORG (n=14)			
ARANEAE											
Agelenidae	unid Agelenidae	C. L. Koch, 1837	0	0	0	2	0	0	2	2.61	0.048
Anyphaenidae	*Anyphaena accentuata*	Walckenaer, 1802	0	0	0	0	1	2	3	5.87	0.076
Anyphaenidae	unid Anyphaenidae	Bertkau, 1878	0	0	7	3	0	0	10	5.87	0.076
Araneidae	*Araniella opisthographa*	Kulczyński, 1905	0	0	8	15	19	20	62	8.86	0.096
Araneidae	*Mangora acalypha*	Walckenaer, 1802	0	2	0	0	0	0	2	0.74	0.024
Araneidae	unid Araneidae	Clerck, 1757	0	2	10	14	0	0	26	2.91	0.051
Clubionidae	*Clubiona*	Latreille, 1804	0	2	0	0	2	2	6	4.74	0.067
Clubionidae	unid Clubionidae	Wagner, 1887	0	0	2	6	0	0	8	4.74	0.067
Dictynidae	*Dictyna arundinacea*	Linnaeus, 1758	0	0	0	0	3	0	3	0.26	0.013
Dictynidae	*Dictyna uncinata*	Thorell, 1856	0	0	3	4	4	1	12	0.42	0.017
Dictynidae	*Lathys humilis*	Blackwall, 1855	0	0	0	0	0	2	2	0.22	0.012
Dictynidae	unid Dictynidae	O. Pickard-Cambridge, 1871	0	4	1	0	0	0	5	0.30	0.014
Linyphiidae	*Araeoncus humilis*	Blackwall, 1841	0	0	0	0	1	0	1	0.18	0.011
Linyphiidae	*Diplostyla concolor*	Wider, 1834	0	0	0	1	0	0	1	0.34	0.015
Linyphiidae	*Dismodicus bifrons*	Blackwall, 1841	0	0	0	0	0	1	1	0.46	0.018
Linyphiidae	*Entelecara acuminata*	Wider, 1834	0	0	0	0	7	8	15	0.21	0.012
Linyphiidae	*Gongylidium rufipes*	Linnaeus, 1758	0	0	0	0	1	0	1	0.34	0.015
Linyphiidae	*Hylyphantes graminicola*	Sundevall, 1830	0	0	0	0	0	1	1	0.29	0.014
Linyphiidae	*Hypomma cornutum*	Blackwall, 1833	0	0	0	0	1	0	1	0.48	0.018
Linyphiidae	*Lepthyphantes*	Menge, 1866	3	4	0	0	0	0	7	0.51	0.019
Linyphiidae	*Tenuiphantes tenuis*	Blackwall, 1852	0	0	1	1	0	1	3	0.24	0.012
Linyphiidae	unid Linyphiidae	Blackwall, 1859	8	2	2	4	2	4	22	0.34	0.015
Mimetidae	*Ero aphana*	Simon, 1881	0	0	1	0	0	0	1	1.55	0.036
Miturgidae	*Zora* sp.	C. L. Koch, 1847	1	0	0	0	0	0	1	1.55	0.036
Philodromidae	*Philodromus*	Walckenaer, 1826	3	23	0	0	27	28	81	3.69	0.058
Philodromidae	*Philodromus albidus*	Kulczyński, 1911	0	0	0	0	0	1	1	3.69	0.058
Philodromidae	*Philodromus aureolus*	Clerck, 1757	0	0	0	1	2	6	9	3.69	0.058
Philodromidae	*Philodromus cespitum*	Walckenaer, 1802	0	0	0	3	1	2	6	2.13	0.043
Philodromidae	*Philodromus praedatus*	O. Pickard-Cambridge, 1871	0	0	0	2	0	0	2	3.69	0.058
Philodromidae	unid Philodromidae	Thorell, 1870	0	0	12	8	0	0	20	3.69	0.058
Salticidae	*Euophrys* sp.	C. L. Koch, 1834	0	0	0	0	1	0	1	0.33	0.015
Salticidae	*Marpissa*	C. L. Koch, 1846	0	0	0	0	1	0	1	1.90	0.040
Salticidae	*Marpissa muscosa*	Clerck, 1757	0	0	0	4	0	0	4	5.09	0.070
Salticidae	*Salticus zebraneus*	C. L. Koch, 1837	0	0	0	0	0	2	2	0.35	0.015
Salticidae	unid Salticidae	Blackwall, 1841	0	2	3	3	0	0	8	1.92	0.040
Tetragnathidae	*Tetragnatha*	Latreille, 1804	0	1	0	0	0	5	6	5.52	0.073
Tetragnathidae	*Tetragnatha dearmata*	Thorell, 1873	0	0	1	0	0	0	1	4.29	0.063
Theridiidae	*Anelosimus*	Simon, 1891	0	5	0	0	0	0	5	0.20	0.011
Theridiidae	*Anelosimus vittatus*	C. L. Koch, 1836	0	0	0	0	2	5	7	1.27	0.032
Theridiidae	*Dipoena*	Thorell, 1869	1	1	0	0	0	0	2	0.11	0.008
Theridiidae	*Enoplognatha ovata*	Clerck, 1757	0	1	0	0	18	6	25	0.66	0.022
Theridiidae	*Neottiura bimaculata*	Linnaeus, 1767	0	0	0	0	0	1	1	0.64	0.022
Theridiidae	*Paidiscura pallens*	Blackwall, 1834	0	0	0	0	3	10	13	0.13	0.009
Theridiidae	*Phylloneta*	Archer, 1950	0	0	0	0	3	6	9	0.41	0.017
Theridiidae	*Phylloneta impressa*	L. Koch, 1881	0	0	2	4	0	0	6	1.65	0.037
Theridiidae	*Platnickina tincta*	Walckenaer, 1802	0	0	1	0	0	2	3	0.64	0.022
Theridiidae	*Robertus*	O. Pickard-Cambridge, 1879	2	6	0	0	0	0	8	0.64	0.022
Theridiidae	*Robertus* sp.	O. Pickard-Cambridge, 1879	0	0	0	0	1	0	1	0.64	0.022
Theridiidae	*Theridion varians*	Hahn, 1833	0	0	2	2	7	0	11	0.73	0.023
Theridiidae	unid Theridiidae	Sundevall, 1833	1	2	20	8	12	17	60	0.64	0.022
Thomisidae	*Diaea dorsata*	Fabricius, 1777	0	0	0	0	1	0	1	3.76	0.059
Thomisidae	*Ozyptila praticola*	C. L. Koch, 1837	0	0	0	0	1	0	1	4.86	0.068
Thomisidae	*Runcinia*	Simon, 1875	1	3	0	0	0	0	4	1.75	0.038
Thomisidae	unid Thomisidae	Sundevall, 1833	0	0	5	6	0	0	11	3.76	0.059
Thomisidae	*Xysticus*	C. L. Koch, 1835	2	4	0	0	2	3	11	4.65	0.066
Thomisidae	*Xysticus audax*	Schrank, 1803	0	0	0	0	0	1	1	4.65	0.066
	unid Araneae		0	3	12	17	0	1	33	0.33	0.015

ORDER / Family	Genus / species	Author	SP		GE		SW		Total	Dry weight (mg)	Energ y use (J h^{-1})
			IP (n=14)	ORG (n=14)	IP (n=15)	ORG (n=15)	IP (n=14)	ORG (n=14)			
COLEOPTERA											
Cantharidae	*Cantharis decipiens*	Baudi, 1871	0	0	0	0	0	2	2	15.21	0.127
Cantharidae	*Cantharis fusca*	Linnaeus, 1758	0	0	0	0	4	7	11	18.76	0.149
Cantharidae	*Cantharis livida*	Linnaeus, 1758	0	0	0	0	3	2	5	16.65	0.136
Cantharidae	*Cantharis nigricans*	Muller, 1766	0	0	0	0	0	2	2	15.21	0.127
Cantharidae	*Cantharis pellucida*	Fabricius, 1792	0	0	0	0	0	1	1	15.21	0.127
Cantharidae	*Cantharis rufa*	Linnaeus, 1758	0	0	0	0	1	0	1	15.21	0.127
Cantharidae	*Cantharis* sp.	Linnaeus, 1758	0	0	0	0	0	1	1	10.21	0.094
Cantharidae	*Malthodes marginatus*	Latreille, 1806	0	0	0	0	0	8	8	11.71	0.104
Cantharidae	*Rhagonycha fulva*	Scopoli, 1763	0	1	0	0	0	0	1	3.56	0.042
Cantharidae	*Rhagonycha lignosa*	Muller, 1764	0	0	0	0	1	1	2	3.56	0.042
Cantharidae	*Rhagonycha nigriventris*	Motschulsky, 1860	0	0	0	0	0	4	4	3.56	0.042
Cantharidae	unid Cantharidae		0	0	0	1	0	0	1	11.71	0.104
Coccinellidae	*Adalia bipunctata*	Linnaeus, 1758	0	0	0	0	0	2	2	6.57	0.067
Coccinellidae	*Coccinella septempunctata*	Linnaeus, 1758	0	4	0	0	0	7	11	9.97	0.092
Coccinellidae	Cryptolaemus	Mulsant, 1853	0	5	0	0	0	0	5	0.45	0.009
Coccinellidae	*Exochomus quadripustulatus*	Linnaeus, 1758	0	0	2	1	0	0	3	2.27	0.030
Coccinellidae	*Harmonia axyridis*	Pallas, 1773	0	0	1	3	0	0	4	9.40	0.088
Coccinellidae	*Propylea 14 punctata*	Linnaeus, 1758	0	9	0	0	3	3	15	2.69	0.034
Coccinellidae	*Stethorus*	Weise, 1885	2	0	0	0	0	0	2	0.13	0.003
Coccinellidae	unid Coccinellidae larvae		0	28	2	1	0	1	32	4.80	0.053
Malachiidae	*Colotes maculatus*	Laporte de Castelnau, 1838	0	1	0	0	0	0	1	0.01	0.001
Melyridae	*Dasytes aeratus*	Stephens, 1829	0	0	0	0	0	1	1	3.50	0.042
Salpingidae	*Salpingus planirostris*	Fabricius, 1787	0	0	0	0	1	0	1	3.50	0.042
Staphylinidae	unid Staphylinidae		3	5	1	1	0	0	10	0.42	0.008
DERMAPTERA											
Forficulidae	*Forficula auricularia*	Linnaeus, 1758	0	7	168	122	22	14	333	22.09	0.169
Forficulidae	*Forficula pubescens*	Gené, 1837	1	13	0	0	0	0	14	3.25	0.039
DIPTERA											
Athericidae	unid Athericidae		0	0	3	1	0	0	4	0.62	0.011
Dolichopodidae	*Microphor anomalus*	Meigen, 1824	0	0	0	0	2	17	19	0.17	0.004
Dolichopodidae	unid Dolichopodidae		0	1	2	1	3	1	8	0.35	0.007
Dolichopodidae	unid Microphorinae		0	0	4	2	0	0	6	0.53	0.010
Empididae	*Empis caudatula*	Loew, 1867	0	0	0	0	7	11	18	0.24	0.005
Empididae	*Empis nigripes*	Fabricius, 1794	0	0	0	0	0	1	1	0.29	0.006
Empididae	*Empis nuntia*	Meigen, 1838	0	0	0	0	5	2	7	0.48	0.009
Empididae	*Empis* sp.	Linnaeus, 1758	0	0	0	0	3	1	4	0.34	0.007
Empididae	*Hilara albipennis*	von Roser, 1840	0	0	0	0	0	2	2	0.20	0.005
Empididae	*Hilara fuscipes*	Fabricius, 1794	0	0	0	0	0	2	2	0.62	0.011
Empididae	*Hilara longivittata*	Zetterstedt, 1842	0	0	0	0	0	3	3	0.26	0.006
Empididae	*Hilara maura*	Fabricius, 1776	0	0	0	0	0	2	2	0.63	0.011
Empididae	*Hilara quadrula*	Chvala, 2002	0	0	0	0	1	0	1	0.43	0.008
Empididae	*Rhamphomyia umbripennis*	Meigen, 1822	0	0	0	0	0	3	3	0.39	0.008
Empididae	unid Empididae		0	4	0	0	0	0	4	0.71	0.012
Hybotidae	*Bicellaria spuria*	Fallen, 1816	0	0	0	0	0	2	2	0.10	0.003
Hybotidae	*Drapetis incompleta*	Collin, 1926	0	0	0	0	0	1	1	0.03	0.001
Hybotidae	*Euthyneura myrtilli*	Macquart, 1836	0	0	0	0	0	2	2	0.09	0.003
Hybotidae	*Platypalpus*	Macquart, 1827	0	0	0	0	1	16	17	0.27	0.006
Hybotidae	*Platypalpus agilis*	Meigen, 1822	0	0	0	0	2	10	12	0.32	0.007
Hybotidae	*Platypalpus annulipes*	Meigen, 1822	0	0	0	0	2	0	2	0.26	0.006
Hybotidae	*Platypalpus cursitans*	Fabricius, 1775	0	0	0	0	0	4	4	0.65	0.012
Hybotidae	*Platypalpus interstinctus*	Collin, 1926	0	0	0	0	1	0	1	0.13	0.003
Hybotidae	*Platypalpus leucocephalus*	von Roser, 1840	0	0	0	0	1	2	3	0.27	0.006
Hybotidae	*Platypalpus longicornis*	Meigen, 1822	0	0	0	0	1	1	2	0.21	0.005
Hybotidae	*Platypalpus longiseta*	Zetterstedt, 1842	0	0	0	0	4	2	6	0.17	0.004
Hybotidae	*Platypalpus minutus*	Meigen, 1804	0	0	0	0	3	1	4	0.22	0.005
Hybotidae	*Platypalpus pallidiventris*	Meigen, 1822	0	0	0	0	6	2	8	0.19	0.005
Hybotidae	*Platypalpus verralli*	Collin, 1926	0	0	0	0	2	1	3	0.29	0.006

ORDER / Family	Genus / species	Author	SP		GE		SW		Total	Dry weight (mg)	Energy use (J h^{-1})
			IP (n=14)	ORG (n=14)	IP (n=15)	ORG (n=15)	IP (n=14)	ORG (n=14)			
Hybotidae	unid Hybotidae		0	0	0	0	0	2	2	0.22	0.005
Micropezidae	unid Micropezidae		0	0	0	0	1	0	1	0.32	0.007
Rhagionidae	unid Rhagionidae		0	0	2	0	0	0	2	0.24	0.005
Syrphidae	unid Syrphidae larvae		0	1	0	0	0	0	1	6.91	0.070
HETEROPTERA											
Anthocoridae	*Anthocoris*	Fallen, 1814	0	1	0	0	1	0	2	0.53	0.010
Anthocoridae	*Anthocoris nemoralis*	Fabricius, 1794	0	0	1	0	0	0	1	0.53	0.010
Anthocoridae	*Anthocoris nemorum*	Linnaeus, 1761	0	0	0	0	2	3	5	0.53	0.010
Anthocoridae	*Orius*	Wolff, 1811	0	2	13	104	0	0	119	0.16	0.004
Anthocoridae	*Orius minutus*	Linnaeus, 1758	0	0	4	8	1	1	14	0.05	0.002
Anthocoridae	unid Anthocoridae		0	0	0	10	0	0	10	0.16	0.004
Miridae	*Campylomma*	Reuter, 1878	20	19	0	0	0	0	39	0.16	0.004
Miridae	*Campylomma verbasci*	Meyer-Dür, 1843	0	0	0	2	0	0	2	0.16	0.004
Miridae	*Deraeocoris*	Kirschbaum, 1856	0	0	0	4	0	0	4	0.63	0.011
Miridae	*Heterotoma planicornis*	Pallas, 1772	0	0	15	47	0	0	62	0.10	0.003
Miridae	*Plagiognathus arbustorum*	Fabricius, 1794	0	0	0	3	0	0	3	1.22	0.019
Nabidae	*Himacerus apterus*	Fabricius, 1798	0	0	2	0	0	0	2	1.41	0.021
Nabidae	*Nabis* sp.	Latreille, 1802	0	0	0	0	1	0	1	4.24	0.048
Nabidae	unid Nabidae		0	1	0	0	0	0	1	2.95	0.037
NEUROPTERA											
Chrysopidae	*Chrysoperla carnea*	Stephens, 1836	0	0	0	0	5	7	12	3.88	0.045
Chrysopidae	unid Chrysopidae		1	2	0	1	0	0	4	3.88	0.045
Coniopterygidae	*Coniopteryx tineiformis*	Curtis, 1834	0	0	0	0	0	1	1	3.88	0.045
Hemerobiidae	*Micromus variegatus*	Fabricius, 1793	0	0	0	0	0	1	1	3.88	0.045
	unid Neuroptera		1	2	5	3	0	1	12	3.88	0.045
OPILIONES											
	unid Opiliones		0	0	6	7	17	1	31	1.37	0.020
Phalangiidae	unid Phalangiidae		0	1	1	0	0	0	2	3.47	0.041
			50	174	325	430	230	300	1509	360.56	4.564

Table S3.4. Effects of country (Spain (SP), Germany (GE) and Sweden (SW)) and management type (integrated production (IP); organic management (ORG)) on abundance of predator taxa to supplement Figure 3.2. Statistical results derived from GLM (F-values for quasi-Poisson, χ^2 for Poisson and negative binomial; ANOVA type III) and post-hoc tests with Tukey contrasts indicating direction of differences between countries. Significant results ($P < 0.05$) in bold.

Taxon	Explanatory variable	Statistics (F/ χ^2, df, P value, post-hoc)	Deviance (anova.glm)	Deviance explained by model (%)
All	**Country**	**$\chi^2_{2,80} = 48.6$, $P < 0.001$ (SP < GE, SW)**	**45.9**	43.4
	Management	**$\chi^2_{1,80} = 18.4$, $P < 0.001$ (IP < ORG)**	**14.8**	
	Country × Management	**$\chi^2_{2,80} = 9.8$, $P = 0.008$**	**9.8**	
Araneae	**Country**	**$\chi^2_{2,80} = 33.0$, $P < 0.001$ (SP < GE, SW)**	**31.3**	32.4
	Management	**$\chi^2_{1,80} = 8.4$, $P = 0.004$ (IP < ORG)**	**5.6**	
	Country × Management	**$\chi^2_{2,80} = 7.3$, $P = 0.026$**	**7.3**	
Coleoptera	Country	$\chi^2_{2,80} = 4.7$, $P = 0.092$	40.8	29.52
	Management	**$\chi^2_{1,80} = 22.3$, $P < 0.001$ (IP < ORG)**	**52**	
	Country × Management	**$\chi^2_{2,80} = 10.5$, $P = 0.005$**	**10.5**	
Dermaptera	**Country**	**$F_{2,80} = 28.6$, $P < 0.001$ (GE > SP, SW)**	**353.73**	53.25
	Management	$F_{1,80} = 1.5$, $P = 0.225$	3.5	
	Country × Management	$F_{2,80} = 3.0$, $P = 0.057$	26.7	
Diptera	**Country**	**$\chi^2_{2,80} = 36.7$, $P < 0.001$ (GE < SW)**	**80.8**	58.5
	Management	**$\chi^2_{1,80} = 4.1$, $P = 0.041$**	**1.9**	
	Country × Management	**$\chi^2_{2,80} = 10.7$, $P = 0.005$**	**10.7**	
Heteroptera	**Country**	**$\chi^2_{2,80} = 8.6$, $P = 0.014$**	**54.1**	44.9
	Management	$\chi^2_{1,80} = 1.9$, $P = 0.165$	4.8	
	Country × Management	$\chi^2_{2,80} = 5.8$, $P = 0.056$	5.8	
Neuroptera	Country	$\chi^2_{2,80} = 1.6$, $P = 0.565$	4.3	7.5
	Management	$\chi^2_{1,80} = 0.9$, $P = 0.336$	1.2	
	Country × Management	$\chi^2_{2,80} = 1.3$, $P = 0.527$	1.3	
Opiliones	**Country**	**$\chi^2_{2,80} = 23.9$, $P < 0.001$ (SP < GE)**	**19.3**	33.1
	Management	$\chi^2_{1,80} = 0.1$, $P = 0.740$	7.1	
	Country × Management	**$\chi^2_{2,80} = 11.5$, $P = 0.003$**	**11.5**	

Table S5. Species list of plants including presence by country

No.	Species	Author	Family	Spain	Germany	Sweden
1	*Abies alba*	Mill..	Pinaceae	0	1	0
2	*Acer campestre*	L.	Aceraceae	0	1	0
3	*Acer platanoides*	L.	Aceraceae	0	0	1
4	*Acer pseudoplatanus*	L.	Aceraceae	0	1	0
5	*Achillea millefolium*	L.	Asteraceae	0	1	1
6	*Aegopodium podagraria*	L.	Apiaceae	0	1	1
7	*Alliaria petiolata*	(M. Bieb.) Cavara & Grande	Brassicaceae	0	0	1
8	*Alnus glutinosa*	(L.) J. Gaertn	Betulaceae	0	1	0
9	*Alnus incana*	(L.) Moench	Betulaceae	0	0	1
10	*Alnus* sp.	Mill.	Betulaceae	0	0	1
11	*Amelanchier lamarckii cf. canadensis*	F. G. Schroed.	Rosaceae	0	1	0
12	*Anagallis arvensis*	L.	Primulaceae	1	1	0
13	*Anchusa hybrida*	Ten.	Boraginaceae	1	0	0
14	*Anthemis* sp.	L.	Asteraceae	1	0	0
15	*Anthriscus sylvestris*	(L.) Hoffm.	Apiaceae	0	0	1
16	*Arabidopsis thaliana*	(L.) Heynh.	Brassicaceae	0	1	1
17	*Arabis glabra*	L.	Brassicaceae	0	0	1
18	*Arenaria serpyllifolia*	L.	Caryophyllaceae	0	1	0
19	*Artemisia vulgaris*	L.	Asteraceae	0	0	1
21	*Athyrium filix-femina*	(L.) Roth	Dryopteridaceae	0	1	0
22	*Atriplex hortensis*	L.	Chenopodiaceae	0	1	0
23	*Barbarea intermedia*	Boreau	Brassicaceae	0	1	0
24	*Bellis perennis*	L.	Asteraceae	0	1	1
25	*Beta vulgaris*	L.	Chenopodiaceae	1	0	0
26	*Betula pendula*	Roth	Betulaceae	0	1	1
27	*Borago officinalis*	L.	Boraginaceae	1	0	0
28	*Brassica napus*	L.	Brassicaceae	0	1	0
29	*Bryonia dioica*	Jacq.	Cucurbitaceae	1	0	0
30	*Calendula officinalis*	L.	Asteraceae	1	0	0
31	*Capsella bursa-pastoris*	(L.) Med.	Brassicaceae	1	1	1
32	*Cardamine pratensis*	L.	Brassicaceae	0	1	0
33	*Cardaria draba*	L.	Brassicaceae	1	0	0
34	*Carpinus betulus*	L.	Betulaceae	0	1	1
35	*Centaurea scabiosa*	L.	Asteraceae	0	0	1
36	*Cerastium fontanum*	Baumg.	Caryophyllaceae	0	1	1
37	*Cerastium glomeratum*	Thuill.	Caryophyllaceae	1	1	0
38	*Cerastium holosteoides*	Fr.	Caryophyllaceae	0	1	0
39	*Cerastium* sp.	L.	Caryophyllaceae	0	1	1
40	*Cerastium* sp.2			0	0	1
41	*Chelidonium majus*	L.	Papaveraceae	1	0	0
42	*Chenopodium* sp.	L.	Amaranthaceae	1	0	0
43	*Circaea intermedia*	Ehrh.	Onagraceae	0	1	0
44	*Cirsium arvense*	(L.) Scop.	Asteraceae	0	1	1

45	*Clematis vitalba*	L.	Ranunculaceae	0	1	0
46	*Convolvulus arvensis*	L.	Convolvulaceae	1	1	0
47	*Convolvulus* sp.	L.	Convolvulaceae	1	0	0
48	*Conyza* sp.	L.	Asteraceae	1	0	0
49	*Cornus sanguinea*	L.	Cornaceae	0	1	0
50	*Corylus avellana*	L.	Betulaceae	0	1	1
51	*Crepis capillaris*	(L.) Wallr.	Asteraceae	0	1	0
52	*Crepis* sp.	L.	Asteraceae	1	1	1
53	*Crepis* sp.2	L.	Asteraceae	1	0	0
54	*Daucus carota*	L.	Apiaceae	0	1	0
55	*Daucus* sp.	L.	Apiaceae	1	0	0
56	*Diplotaxis erucoides*	(L.) DC.	Brassicaceae	1	0	0
57	*Diplotaxis tenuifolia*	(L.) DC.	Brassicaceae	0	1	0
58	*Epilobium montanum*	L.	Onagraceae	0	0	1
60	*Equisetum arvense*	L.	Equisetaceae	0	1	1
61	*Equisetum pratense*	Ehrh.	Equisetaceae	0	0	1
62	*Erigeron canadensis*	L.	Asteraceae	0	1	0
63	*Erophila verna*	L.	Brassicaceae	0	0	1
64	*Eruca vesicaria*	(L.) Cav.	Brassicaceae	1	0	0
65	*Erucastrum nastrutiifolium*	(Poir.) O. E. Schulz	Brassicaceae	1	0	0
66	*Erucastrum* sp.	C. Presl	Brassicaceae	1	0	0
67	*Euonymus europaeus*	L.	Celastraceae	0	1	0
68	*Euphorbia cyparissias*	L.	Euphorbiaceae	0	1	0
69	*Euphorbia falcata*	L. n. cons.	Euphorbiaceae	1	0	0
70	*Euphorbia helioscopia*	L.	Euphorbiaceae	0	1	0
71	*Euphorbia* sp.	L.	Euphorbiaceae	1	0	0
72	*Fagopyrum esculentum*	Moench	Polygonaceae	0	1	0
73	*Fagus sylvatica*	L.	Fagaceae	0	1	1
74	*Fallopia japonica*	(Houtt.) Ronse Decr.	Polygonaceae	0	1	0
75	*Ficaria verna*	Huds.	Ranunculaceae	0	1	0
76	*Filipendula ulmaria*	(L.) Maxim.	Rosaceae	0	1	1
77	*Foeniculum vulgare*	Mill.	Apiaceae	1	0	0
78	*Forsythia × intermedia*	Zabel	Oleaceae	0	1	0
79	*Fragaria vesca*	L.	Rosaceae	0	0	1
80	*Fraxinus excelsior*	L.	Oleaceae	0	1	1
81	*Fumaria officinalis*	L.	Papaveraceae	1	0	0
82	*Galeopsis tetrahit*	L.	Lamiaceae	0	1	0
83	*Galinsoga quadriradiata*	Ruiz & Pav.	Asteraceae	0	1	0
84	*Galium album*	Mill.	Rubiaceae	0	1	0
85	*Galium aparine*	L.	Rubiaceae	1	1	1
86	*Galium mollugo*	L.	Rubiaceae	0	1	0
87	*Galium palustre*	L.	Rubiaceae	0	1	0
88	*Galium* sp.	L.	Rubiaceae	1	1	1
89	*Galium sylvaticum*	L.	Rubiaceae	0	1	0
90	*Galium verum*	L.	Rubiaceae	0	0	1
91	*Geranium columbinum*	L.	Geraniaceae	0	1	0

92	*Geranium dissectum*	L.	Geraniaceae	0	1	0
93	*Geranium molle*	L.	Geraniaceae	1	0	1
94	*Geranium pyrenaicum*	Burm. n. cons. prop.	Geraniaceae	0	1	1
95	*Geranium robertianum*	L.	Geraniaceae	0	1	1
96	*Geranium* sp.	L.	Geraniaceae	1	1	0
97	*Geranium* sp.2	L.	Geraniaceae	1	0	0
98	*Geum rivale*	L.	Rosaceae	0	0	1
99	*Geum* sp.	L.	Rosaceae	0	0	1
100	*Geum urbanum*	L.	Rosaceae	0	1	1
101	*Glechoma hederacea*	L.	Lamiaceae	0	1	1
102	*Glechoma hederacea* subsp. *hirsuta*	Waldst. & Kit.	Lamiaceae	0	1	0
103	*Hedera helix*	L.	Araliaceae	0	1	0
104	*Hedera* sp.	L.	Araliaceae	1	0	0
105	*Heracleum mantegazzianum*	Sommier & Levier	Apiaceae	0	0	1
106	*Heracleum sphondylium*	L.	Apiaceae	0	0	1
107	*Hieracium* sp.	L.	Asteraceae	0	1	0
108	*Hypericum maculatum*	Crantz	Clusiaceae	0	0	1
109	*Hypericum perforatum*	L.	Clusiaceae	0	0	1
110	*Impatiens glanulifera*	Royle	Balsaminaceae	0	1	0
111	*Impatiens noli-tangere*	L. n. cons.	Balsaminaceae	0	1	0
113	*Juglans regia*	L.	Juglandaceae	0	1	0
114	*Lactuca serriola*	L.	Asteraceae	1	0	0
116	*Lamium album*	L.	Lamiaceae	0	1	1
117	*Lamium amplexicaule*	L.	Lamiaceae	1	0	1
118	*Lamium galeobdolon*	Huds.	Lamiaceae	0	1	1
119	*Lamium hybridum*	Vill.	Lamiaceae	1	0	0
120	*Lamium purpureum*	L.	Lamiaceae	0	0	1
121	*Lamium* sp.	L.	Lamiaceae	1	0	1
122	*Lapsana communis*	L.	Asteraceae	0	0	1
123	*Larix decidua*	Mill.	Pinaceae	0	1	0
124	*Lathyrus pratensis*	L.	Fabaceae	0	1	0
125	*Leucanthemum* sp.	Mill.	Asteraceae	0	1	0
126	*Leucanthemum* vulgare	Lam.	Asteraceae	0	1	0
127	*Ligustrum vulgare*	L.	Oleaceae	0	1	0
128	*Lobullaria maritima*	(L.) Desv.	Brassicaceae	1	0	0
129	*Lonicera periclymenum*	L.	Caprifoliaceae	0	0	1
130	*Lonicera* sp.	L.	Caprifoliaceae	0	0	1
131	*Lonicera xylosteum*	L.	Caprifoliaceae	0	1	0
132	*Lotus corniculatus*	L.	Fabaceae	0	1	0
133	*Lupinus* sp.	L.	Fabaceae	0	1	0
134	*Maianthemum bifolium*	(L.) F.W.Schmidt	Asparagaceae	0	0	1
135	*Malus domestica*	Mill.	Rosaceae	0	1	1
136	*Malva sylvestris*	L.	Malvaceae	1	0	0
137	*Mantisalca salmantica*	(L.) Briq. & Cavill.	Asteraceae	1	0	0
138	*Marrubium vulgare*	L.	Lamiaceae	1	0	0

139	*Matricaria chamomilla*	L.	Asteraceae	1	1	0
140	*Medicago falcata*	L.	Fabaceae	1	1	0
141	*Medicago lupulina*	L.	Fabaceae	0	1	1
142	*Medicago sativa*	L.	Fabaceae	1	1	1
143	*Medicago* sp.	L.	Fabaceae	1	0	1
144	*Mentha arvensis*	L.	Lamiaceae	0	1	0
145	*Mercurialis perennis*	L.	Euphorbiaceae	0	1	0
146	*Moehringia trinervia*	(L.) Clairv.	Caryophyllaceae	0	0	1
147	*Myosotis arvensis*	(L.) Hill	Boraginaceae	0	1	1
148	*Myosotis* sp.	L.	Boraginaceae	0	1	0
149	*Olea europaea*	L.	Oleaceae	1	0	0
150	*Onobrychis viciifolia*	Scop.	Fabaceae	0	1	0
151	*Papaver argemone*	L.	Papaveraceae	0	0	1
152	*Papaver rhoeas*	L.	Papaveraceae	1	1	0
153	*Persicaria maculosa*	Gray n. cons.	Polygonaceae	0	1	0
154	*Petasites hybridus*	(L.) G. Gaertn. et al	Asteraceae	0	0	1
155	*Phacelia tanacetifolia*	Benth.	Boraginaceae	0	1	0
156	*Picea abies*	(L.) H.Karst.	Pinaceae	0	1	0
157	*Picris* sp.	L.	Asteraceae	1	0	0
158	*Pilosella officinarum*	L.	Asteraceae	0	0	1
159	*Plantago conoronopus*	L.	Plantaginaceae	1	0	0
160	*Plantago lanceolata*	L.	Plantaginaceae	1	1	1
161	*Plantago major*	L.	Plantaginaceae	0	1	1
162	*Plantago media*	L.	Plantaginaceae	1	1	0
163	*Plantago* sp.	L.	Plantaginaceae	1	0	0
164	*Polygonatum multiflorum*	(L.) All.	Asparagaceae	0	0	1
165	*Polygonum aviculare*	L.	Polygonaceae	1	1	1
166	*Polygonum* sp.	L. n. cons.	Polygonaceae	1	0	0
167	*Potentilla anserina*	L.	Rosaceae	0	1	0
168	*Potentilla reptans*	L.	Rosaceae	1	1	1
169	*Potentilla* sp.	L.	Rosaceae	0	0	1
170	*Primula veris*	L.	Primulaceae	0	0	1
171	*Prunus avium*	L.	Rosaceae	0	1	1
172	*Prunus domestica* subsp. *syriaca*	(Borkh.) Janch. ex Mansf.	Rosaceae	0	1	0
173	*Prunus* sp.	L.	Rosaceae	1	0	0
174	*Prunus spinosa*	L.	Rosaceae	0	1	0
175	*Pteridium* sp.		Dennstaedtiaceae	0	0	1
176	*Pyrus communis*	L.	Rosaceae	0	1	0
177	*Quercus petraea*	(Mattuschka) Liebl.	Fagaceae	0	1	0
178	*Quercus robur*	L.	Fagaceae	0	1	1
179	*Ranunculus arcris*	L.	Ranunculaceae	0	1	0
180	*Ranunculus bulbosus*	L.	Ranunculaceae	0	0	1
182	*Ranunculus repens*	L.	Ranunculaceae	0	1	1
183	*Ranunculus* sp.	L.	Ranunculaceae	1	0	1
184	*Fallopia japonica*	(Houtt.) Ronse Decr.	Polygonaceae	0	1	0

185	*Ribes alpinum*	L.	Grossulariaceae	0	0	1
186	*Rosa* sp.	L. n. cons.	Rosaceae	0	1	1
187	*Rubia peregrina*	L.	Rubiaceae	1	0	0
188	*Rubus caesius*	L.	Rosaceae	0	0	1
189	*Rubus fruticosus*	L. n. cons.	Rosaceae	0	1	0
190	*Rubus idaeus*	L.	Rosaceae	0	0	1
191	*Rubus* sp.	L.	Rosaceae	0	1	1
192	*Rubus ulmifolius*	Schott	Rosaceae	1	0	0
193	*Rumex acetosa*	L. n. cons.	Polygonaceae	0	0	1
194	*Rumex crispus*	L.	Polygonaceae	0	1	1
195	*Rumex obtusifolius*	L.	Polygonaceae	0	1	1
196	*Rumex sanguineus*	L.	Polygonaceae	0	1	0
197	*Rumex* sp.	L.	Polygonaceae	1	0	0
198	*Salix caprea*	L.	Salicaceae	0	1	0
199	*Salix matsudana* 'Tortuosa'	L.	Salicaceae	0	1	0
200	*Salix* sp.	L. n. cons.	Salicaceae	0	0	1
201	*Salix viminalis*	L.	Salicaceae	0	1	0
202	*Sambucus nigra*	L.	Adoxaceae	0	1	1
203	*Saponaria officinalis*	L.	Caryophyllaceae	0	0	1
204	*Scabiosa columbaria*	L.	Caprifoliaceae	0	1	0
205	*Senecio* sp.	L.	Asteraceae	0	0	1
206	*Senecio vulgaris*	L.	Asteraceae	1	1	1
207	*Sherardia arvensis*	L.	Rubiaceae	1	1	0
208	*Silene* sp.	L. n. cons.	Caryophyllaceae	0	1	0
209	*Silybum marianum*	(L.) Gaertn.	Asteraceae	1	0	0
210	*Solanum dulcamara*	L.	Solanaceae	0	1	0
211	*Solanum nigrum*	L.	Solanaceae	1	0	0
212	*Solidago canadensis*	L.	Asteraceae	0	1	0
213	*Sonchus oleraceus*	L.	Asteraceae	0	1	0
214	*Sonchus* sp.	L.	Asteraceae	1	0	0
215	*Sorbus aucuparia*	L.	Rosaceae	0	0	1
216	*Stachys sylvatica*	L.	Lamiaceae	0	1	0
217	*Stellaria holostea*	L.	Caryophyllaceae	0	0	1
218	*Stellaria longifolia*	Muhl. ex Willd.	Caryophyllaceae	0	0	1
219	*Stellaria media*	(L.) Vill.	Caryophyllaceae	0	1	1
220	*Stellaria* sp.	L.	Caryophyllaceae	0	1	0
221	*Symphoricarpus albus*	(L.) S.F.Blake	Caprifoliaceae	0	1	0
222	*Taraxacum officinale* agg.		Asteraceae	1	1	0
223	*Taraxacum* sp.	F.H.Wigg. n. cons.	Asteraceae	0	0	1
224	*Trientalis europaea*	L. n. cons.	Primulaceae	0	0	1
225	*Trifolium campestre*	Schreb.	Fabaceae	0	1	1
226	*Trifolium dubium*	Sibth.	Fabaceae	0	1	1
227	*Trifolium medium*	L.	Fabaceae	0	0	1
228	*Trifolium pratense*	L.	Fabaceae	0	1	0
229	*Trifolium repens*	L.	Fabaceae	0	1	1
230	*Trifolium* sp.	L.	Fabaceae	1	1	1

231	*Trifolium* sp.2	L.	Fabaceae	1	0	0
232	*Trifolium* sp.3	L.	Fabaceae	1	0	0
233	*Tripleurospermum maritimum* subsp. *inodorum*	(Merat) M.Lainz	Asteraceae	0	1	0
234	*Ulmus glabra*	Huds.	Ulmaceae	0	1	1
235	*Urtica dioica*	L.	Urticaceae	1	1	1
236	*Valerianella locusta*	(L.) Laterr.	Caprifoliaceae	0	1	0
237	*Veronica anagallis aquatica*	L.	Plantaginaceae	0	1	0
238	*Veronica arvensis*	L.	Plantaginaceae	1	1	0
239	*Veronica chamaedrys*	L.	Plantaginaceae	0	1	1
240	*Veronica filiformis*	Sm.	Plantaginaceae	0	1	0
241	*Veronica hederifolia*	L.	Plantaginaceae	0	1	1
242	*Veronica persica*	Poir.	Plantaginaceae	0	1	1
243	*Veronica polita*	Fr.	Plantaginaceae	0	1	0
244	*Veronica serpyllifolia*	L.	Plantaginaceae	0	0	1
245	*Veronica* sp.	L.	Plantaginaceae	1	1	1
246	*Veronica* sp.2	L.	Plantaginaceae	1	0	0
248	*Veronica verna*	L.	Plantaginaceae	0	0	1
249	*Viburnum opulus*	L.	Adoxaceae	0	1	0
250	*Vicia cracca*	L.	Fabaceae	0	1	1
251	*Vicia hirsuta*	(L.) Gray	Fabaceae	0	0	1
252	*Vicia sativa*	L.	Fabaceae	0	0	1
253	*Vicia sepium*	L.	Fabaceae	0	1	1
254	*Vicia* sp.	L.	Fabaceae	1	1	1
255	*Viola arvensis*	Murray	Violaceae	0	0	1
256	*Viola* sp.	L.	Violaceae	0	1	0
257	*Weigelia* sp.	Thunb.	Caprifoliaceae	0	1	0

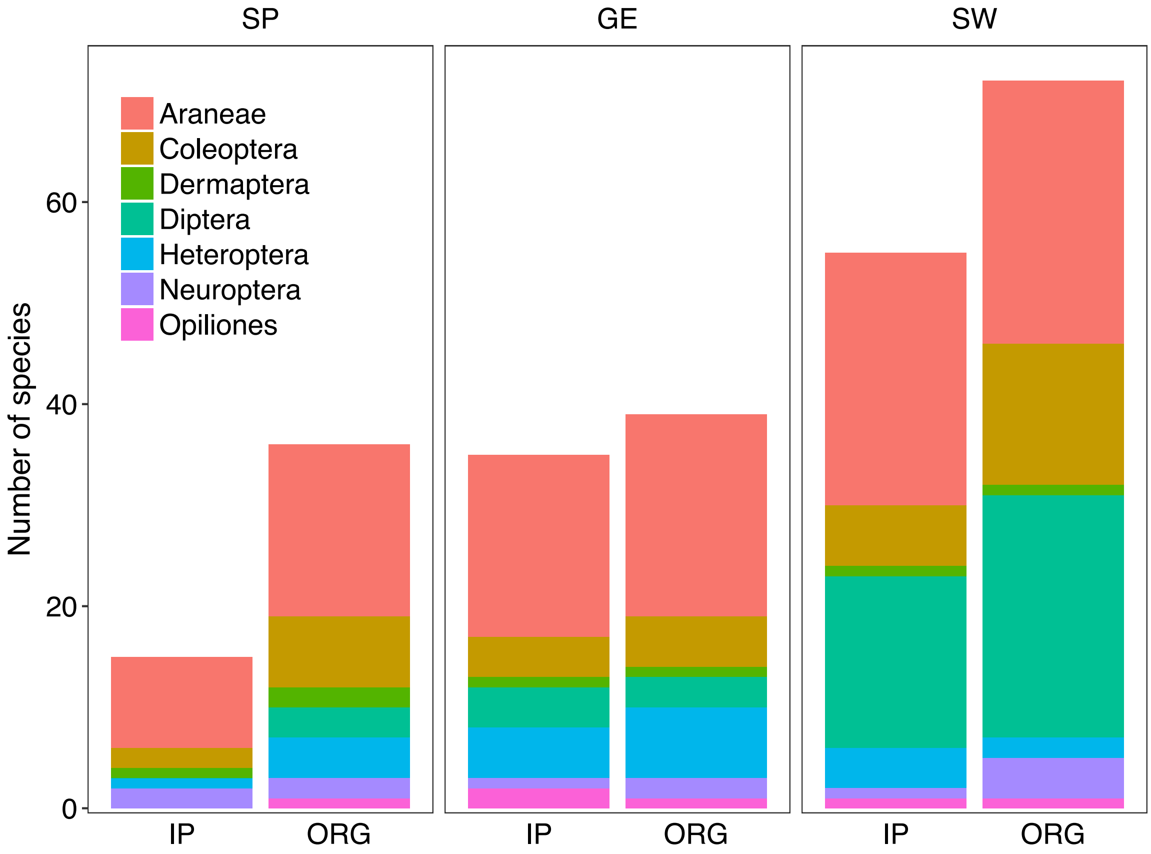

Figure S3.1. Species richness of predatory arthropods in integrated production (IP) and organic (ORG) apple orchards in Spain (SP), Germany (GE) and Sweden (SW)

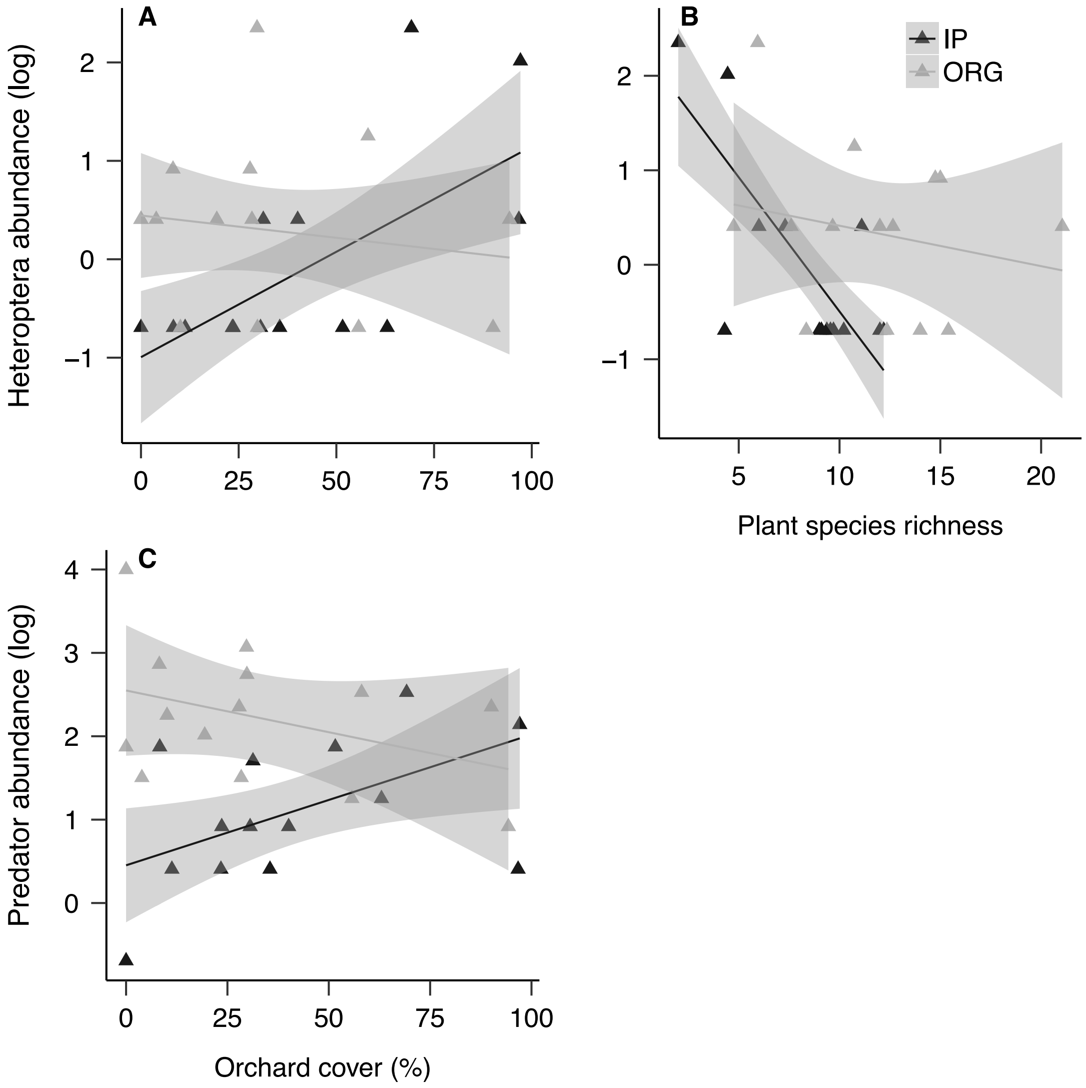

Figure S3.2. Response (A) of Heteroptera to % orchard cover in a 1-km-radius, (B) of Heteroptera to local plant species richness, and (C) of all predators to % orchard cover in integrated production (IP) and organic management (ORG) in Spain. Graphs are shown for significant local and landscape effects (glm, Table 3.1) but linear models are fit using the function ‘rlm’ from the ‘MASS’ package (robust regression using an M estimator with 95% confidence region). Note: plant species richness in SP differed significantly between ORG and IP (Table S3.1).

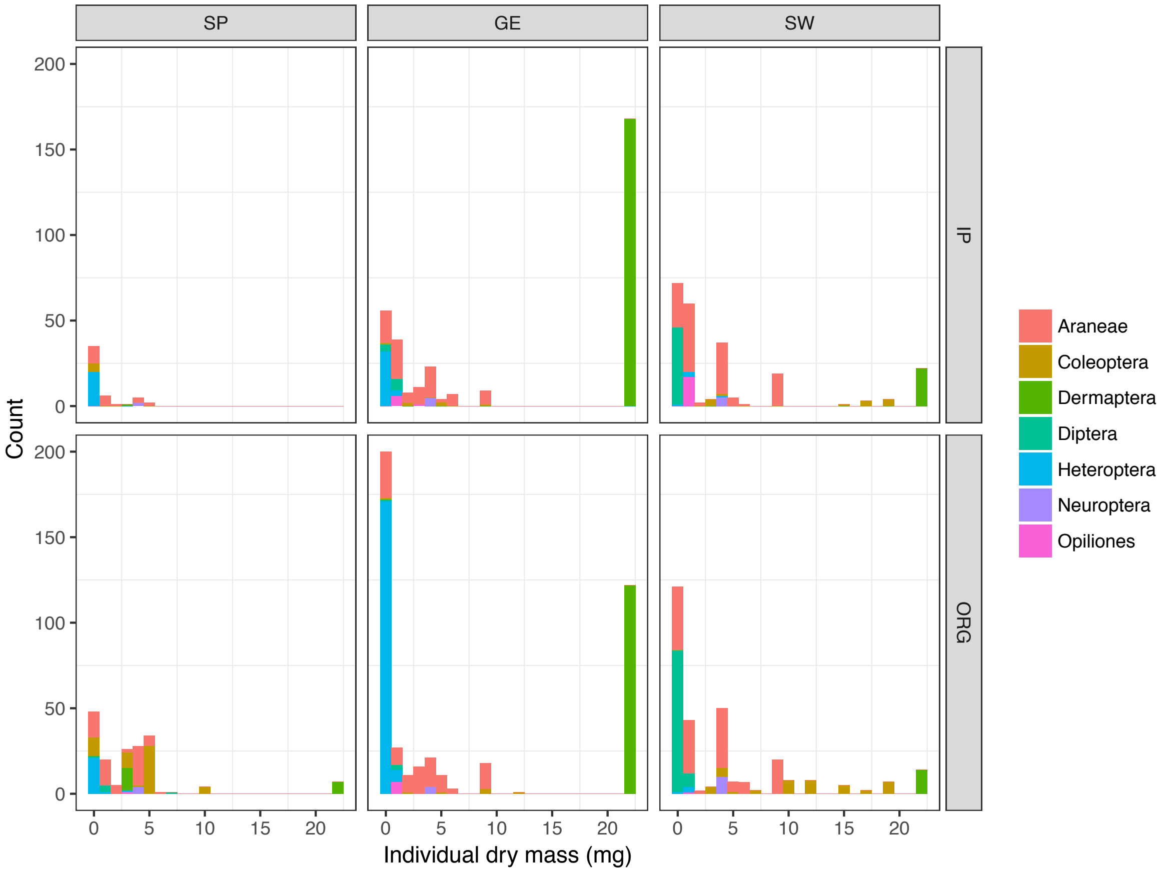

Figure S3.3. Predator biomass distribution in integrated production (IP) and organic (ORG) apple orchards in Spain (SP), Germany (GE) and Sweden (SW).

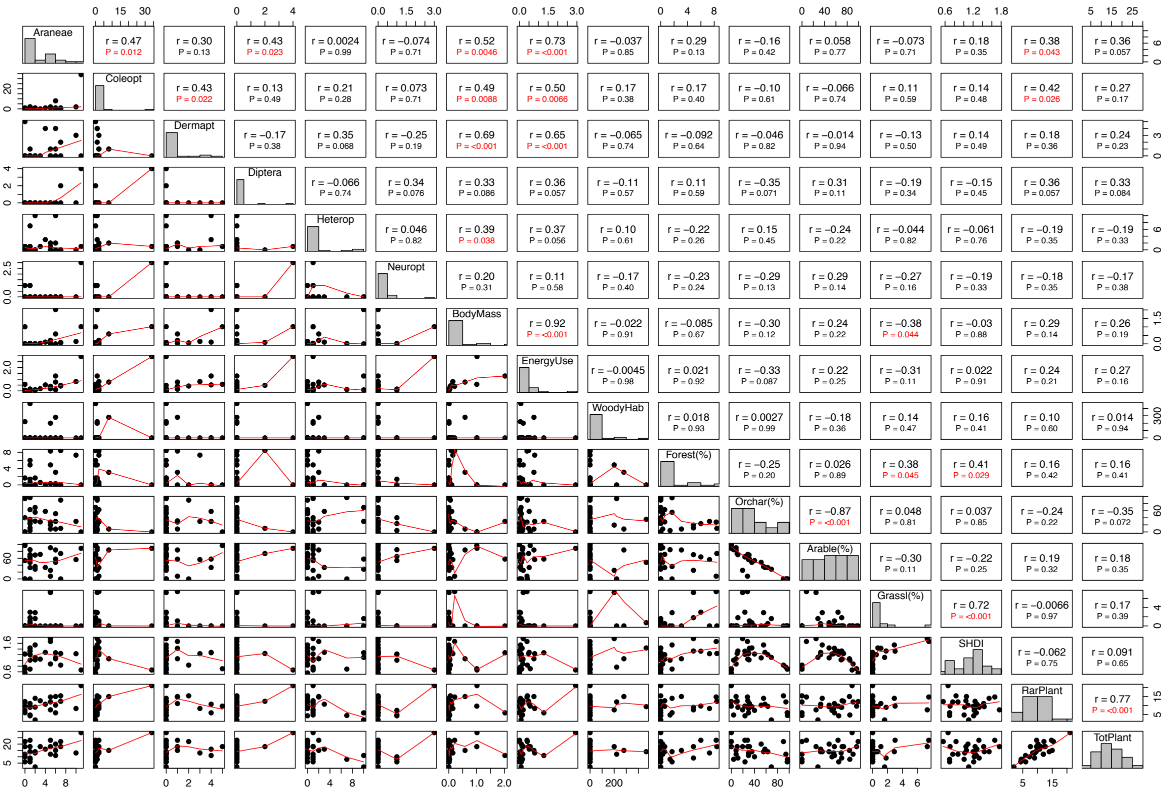

Figure S3.4. Correlation chart of variables included in the predator analysis for Spanish orchards. Scatterplot of total abundance (number of individuals per 24 trees) of Araneae, Coleoptera, Dermaptera, Diptera, Heteroptera, Neuroptera, Opiliones, total dry body mass (BodyMass, mg) and total energy use (EnergyUse, J h^{-1}), cover of woody habitats (WoodyHab, m^2) in a 20 m radius from the orchard edge, cover (%) of different land use types (see Table S3.1) in the surrounding of the orchard (1 km radius), landscape heterogeneity (Shannon's Diversity Index, SHDI) and total plant species richness (TotPlant). Lower panels show scatterplots with a smoother added to visualize the patterns, panels in the middle show a histogram of each variable and upper panels contain Spearman's correlation coefficients (r) with *P*-values (red for $P < 0.05$).

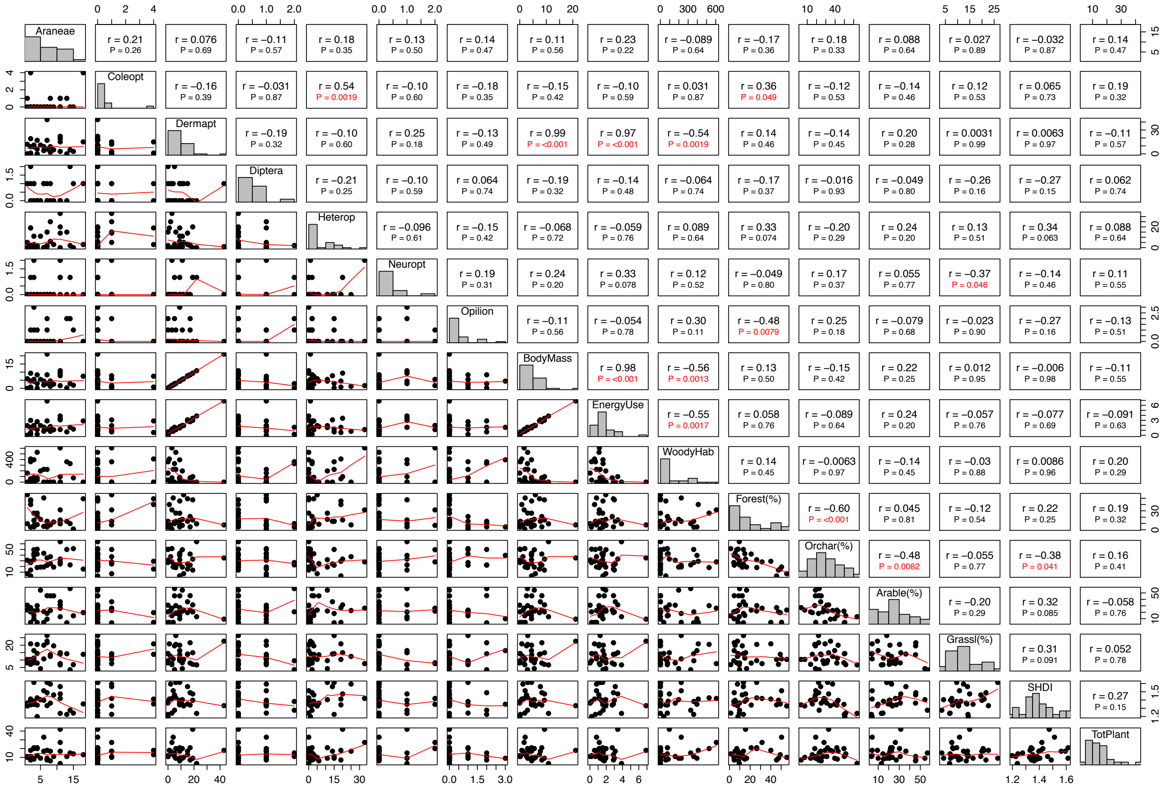

Figure S3.5. Correlation chart of variables included in the predator analysis for German orchards. See caption of Figure S3.4 for details.

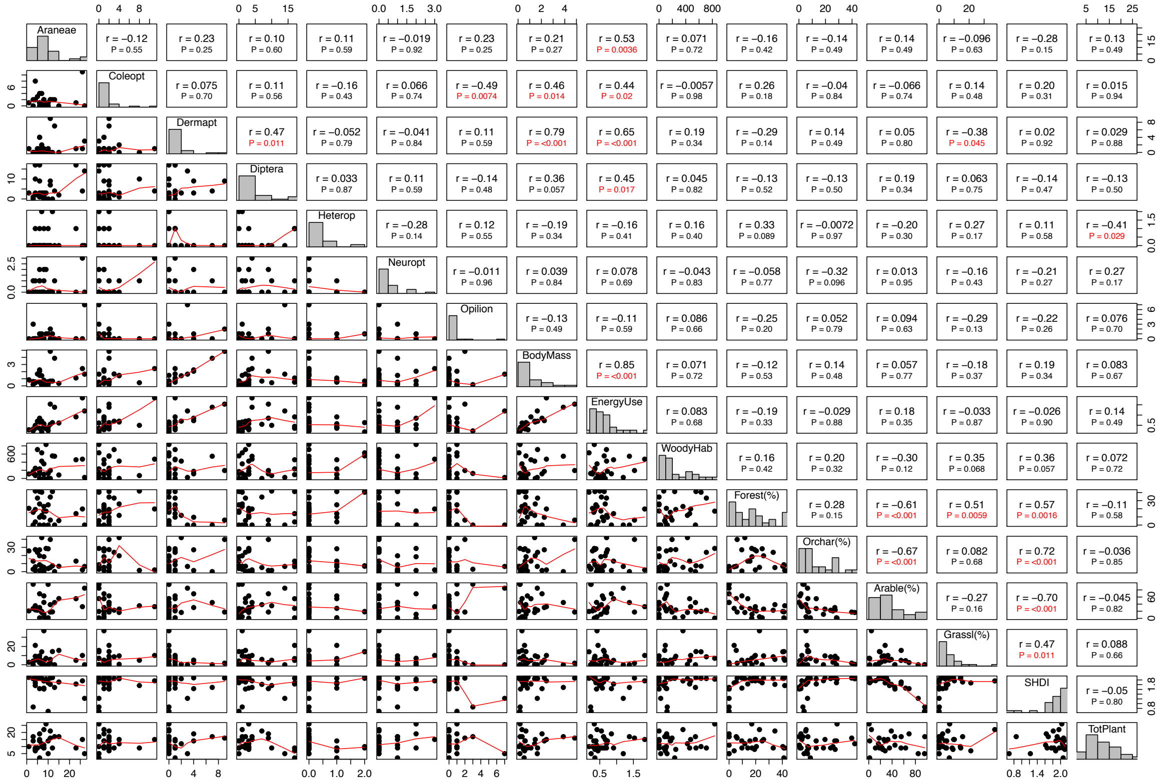

Figure S3.6. Correlation chart of variables included in the predator analysis for Swedish orchards. See caption of Figure S3.4 for details.

4. PUBLICATION III: EARWIGS AND WOOLLY APPLE APHIDS IN INTEGRATED AND ORGANIC APPLE ORCHARDS: RESPONSES OF A GENERALIST PREDATOR AND A PEST PREY TO LOCAL AND LANDSCAPE FACTORS

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Forficula auricularia L., female (DISC3D, 2019). © M. Heethoff, 2019.

ABSTRACT

Organic management, connective woody habitats, and landscape complexity are supposed to enhance beneficial arthropods and biological pest control in agro-ecosystems.

We studied earwigs (Dermaptera: Forficulidae) as generalist predators and aphids (Hemiptera: Aphididae) as key pests serving as earwig prey in a total of 58 commercial apple orchards differing in management (integrated production (IP) *versus* organic) in Germany and Spain. We focused on the effects of local agri-environmental structures, orchard management, and composition of the surrounding landscape on earwig populations and on tree infestation by the woolly apple aphid (WAA), *Eriosoma lanigerum*.

Surprisingly, the common earwig, *Forficula auricularia,* did not benefit from organic management in either country, and we found even slightly higher earwig abundances in IP than in organic orchards in Germany. In Spain, we found a negative impact of IP compared to organic management on abundance of the earwig *Forficula pubescens*, whereas orchard management did not affect the abundance of *F. auricularia*. The presence of woody habitats adjacent to the orchard reduced the abundance of *F. auricularia* in IP but not in organic orchards in Germany. We did not study the effects of woody habitats in Spain, where these structures were very scarce. There was no effect of high plant species richness at the orchard boundary or compositional landscape heterogeneity on earwig abundance in either country. In Germany, WAA infestation was very low and driven by landscape characteristics rather than orchard management. In Spain, WAA infestation differed strongly between management types (higher in organic orchards). There were no strong, consistent correlations between earwig abundance and WAA infestation in either country.

Our study shows that adjacent woody structures and orchard management may affect earwigs in perennial cropping systems. The consequences of orchard management, however, seem to strongly depend on earwig species. Our study suggests that woody elements may serve as sink habitats - potentially attracting earwigs by providing alternative prey and shelter - in IP (but not in organic) orchards.

Keywords: Agri-environmental structure; Biological pest control; *Eriosoma lanigerum*; *Forficula auricularia*; Integrated production; Organic farming.

INTRODUCTION

Agricultural intensification affects biodiversity and biological pest control at various scales (Geiger et al., 2010; Jonsson et al., 2012; Rundlöf et al., 2007). Increased landscape complexity, local agri-environmental structures and organic management have been promoted as potential ways to mitigate biodiversity loss and associated ecosystem services in agricultural areas (Batáry et al., 2015; Chaplin-Kramer et al., 2011; Rusch et al., 2016). Increased landscape complexity (low proportion of crop cover; Jonsson et al., 2012) affects species in agricultural landscapes differently, and its effectiveness in promoting specific taxa depends on farmland type (Concepción et al., 2012). Large-scale studies of local and landscape effects on biodiversity and biological pest control have so far focused on annual cropping systems (Bianchi et al., 2006; Dainese et al., 2016; Tschumi et al., 2016). In contrast, little is known about how the interacting effects of landscape complexity, agri-environmental structures and management in perennial cropping systems, including orchards, affect generalist predators (Lefebvre et al., 2016; Malagnoux et al., 2015b; Marliac et al., 2016) such as chrysopids, coccinellids, anthocorids and earwigs.

Earwigs as generalist predators in apple orchards

The common European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae), is an omnivorous predator. Although it is sometimes considered a pest of stone and soft fruits (Saladini et al., 2016), farmers, consultants and scientists generally agree that the common earwig contributes to biological pest control by maintaining populations of several fruit tree herbivores below economic threshold levels (Cross et al., 2015; Dib et al., 2017; Logan et al., 2017). In apple cultivation, in particular, negative effects such as fruit damage and frass accumulation at harvest (Alford, 2014) seem to be negligible compared to the biological control benefits (Solomon et al., 2000).

Aphids (Hemiptera: Aphididae) are major pests in apple orchards (Blommers 1994; Rousselin et al., 2017; Solomon et al., 2000). Different aphid species, including the rosy apple aphid, *Dysaphis plantaginea* Passerini (Dib et al., 2011; Miñarro et al., 2005), the green apple aphid, *Aphis pomi* De Geer (Carroll and Hoyt, 1984; Stoeckli et al., 2008b), and the woolly apple aphid, *Eriosoma lanigerum* Hausmann (Lordan et al., 2015a; Mueller et al., 1988; Nicholas et al., 2005), are amongst the main prey of earwigs in orchard environments (Dib et al., 2017). Other pests of fruit trees, including scale insects (Logan et al., 2017), psyllids (Sauphanor et al., 1993) and lepidopteran larvae and eggs (Unruh et al., 2016), may serve as supplementary food sources. Common earwigs mate in late autumn and overwinter as adults in underground shelters. In these shelters, females lay a first batch of eggs in late winter and a second one in May or June and nymphs hatch in early spring and late June. The highest numbers of adult earwigs can be found in mid-July and September (Alford, 2014; Solomon et al., 2000). An earlier peak of earwig numbers between May and July has been reported from

Mediterranean orchards (Lordan et al., 2015b). Earwigs release a volatile aggregation pheromone, which enables conspecifics to detect and colonize previously occupied hideouts (Lordan et al., 2014). Thus, their populations can easily be surveyed and augmented using artificial shelters, which serve as daytime refuges (Burnip et al., 2002; Dib et al., 2017; Suckling et al., 2006). Their nocturnal activity leads to a higher effectiveness in regulating fruit pests at night than during the day (Logan et al., 2017). Earwigs' overall contribution to biological pest control in orchards has been estimated to reduce insecticide sprayings in orchards by up to three applications per year (Cross et al., 2015). Earwigs are especially important in the control of woolly apple aphids (Stap et al., 1987). In combination with the parasitoid *Aphelinus mali* Haldeman (Hymenoptera: Aphelinidae), earwigs can keep infestations of this pest below the economic threshold level (Nicholas et al., 2005).

Local management and surrounding landscape

High quality local habitats, including woodland edges and permanent grasslands, as well as agri-environmental structures, including field margins, flower strips and hedgerows, provide increased plant richness, alternative prey, overwintering sites and refuge for natural enemies (Rusch et al., 2016; Simon et al., 2010; Tscharntke et al., 2007). At the landscape level, semi-natural habitats and a high proportion of uncultivated land-cover (Bianchi et al., 2006) are usually assumed to enhance predator communities and biological control. However, in some instances, forest cover has also been associated with reduced numbers of natural enemies (Sarthou et al., 2014). As far as earwigs are concerned, the presence of woody habitats and hedgerows in the orchard surroundings has been reported to enhance their abundance (Debras et al., 2007), but the amount (cover) of woody elements appears to be less important (Stutz and Entling, 2011). Earwigs' sensitivity to habitat isolation can be explained by their dispersal mode and habitat preference. Earwigs are mostly walking dispersers inhabiting semi-open habitats and forests (Bucher et al., 2010). The benefits of woody structures and hedgerows on earwigs may be overridden by intensive orchard management and associated pesticide applications (Malagnoux et al., 2015b).

Commercial apple orchards in Europe are usually managed either under integrated production (IP) or under organic management. The differences between these two types of management are mainly based on pesticide and fertilizer use as well as weed control (mostly soil tillage in organic orchards as opposed to herbicide use in IP orchards; see European Council Regulation (EC) No 834/2007). Malagnoux et al. (2015b) reported higher insecticide (but not fungicide) application frequency in IP compared to organic orchards. Some insecticides have been shown to have non-target effects on earwigs (Beers et al., 2016, 2007; Gontijo et al., 2015; Sauphanor et al., 1993). Various laboratory and field tests revealed that non-target effects strongly depend on pesticide concentration and timing of application in relation to the earwigs' life cycle (Fountain and Harris, 2015; Gobin et al., 2008a; Moerkens et al., 2009).

Landscape composition may constrain the effectiveness of agri-environmental structures and organic farming (Concepción et al., 2012; Holzschuh et al., 2008). Landscape effects on population dynamics of natural enemies and crop pests have often been analyzed within a 1 km radius, which proved to be a relevant scale to understand trophic interactions of different organisms and biological control agents (Rusch et al., 2016; Thies and Tscharntke, 1999). Compared to annual cropping systems, orchards are considered more stable habitats for natural enemies because perennial cultivation reduces disturbances such as crop rotation and plowing (Stutz and Entling, 2011). Although natural enemies in tree crops are assumed to be less dependent on landscape effects, non-crop habitat cover in the surrounding landscape has been shown to enhance biological control in these perennial systems (Eilers and Klein, 2009).

In this study, we test for the first time how local factors (plant species richness and woody habitats) and landscape composition (proportion of orchard cover within a 1-km-radius) interact with management (IP *vs.* organic) to affect earwig populations and their aphid prey in commercial apple orchards in two European countries. We expected higher earwig abundance in organic orchards due to lower management intensity and higher prey availability. We also expected increased earwig abundance in complex landscapes with a reduced proportion of crop cover and additional connective woody elements providing quality habitats.

MATERIAL AND METHODS

Study sites and study design

Our study was conducted in 58 commercial apple orchards in SW Germany (lake Constance region, Baden-Württemberg; 47°43'N, 9°23'E; 15 IP and 15 organic) and NE Spain (Lleida province, 41°37'N, 0°38'E; 8 IP and 9 organic; Girona province, 41°59'N, 2°49'E; 6 IP and 5 organic). Surveys were conducted in 2015 (both countries) and in 2016 (Germany only; the same orchards as in 2015 with the exception of one IP orchard). Annual mean temperature and annual precipitation in the study areas were 11.1 °C and 736 mm (Constance 2015), 10.7 °C and 977.8 mm (Constance 2016) (DWD, 2017); 14.4 ºC and 199.7 mm (Lleida 2015) and 14.9 ºC and 541 mm (Girona 2015) (IDESCAT, 2017).

Orchards were planted with trees grafted on dwarfing rootstocks (M9; 2.0-3.5 m height; 6-18 years old, Table 4.1). Trees were grown in rows at different spacing (minimum 3 × 1 m, maximum 4 × 5 m). Orchard size ranged from 0.7 to 4 ha. Surveys were conducted along a 40-m-long row transect per orchard. To avoid dilution effects, transect rows were at least two rows away from rows of pollinizer cultivars and orchard edges.

In Germany, all orchards were covered with hail nets from the time of flowering (May) until harvest (September-October). The studied cultivar was Braeburn. Minimum distance between orchards of different management type was 2 km. In Spain, only three orchards had hail nets. The main cultivars in Spain were Golden and Gala. Minimum distance between orchards of different management type was 1 km.

Earwig surveys

In Germany, one earwig shelter consisting of two bamboo sections was set up at a height of 120 cm on the trunk of each of five trees in the middle of each transect (about 20 m away from the orchard edge). Shelters were placed vertically with the blind end (internode) facing up as a protection against rain. Bamboo sections had a diameter of 1.7±0.7 cm (mean±SD) and a length of 28.1±7.3 cm. Shelters were installed in the first week of June 2015 and left in place for two years. They were emptied and dry-cleaned with brushes after each sampling. In 2015, sampling took place on July 27-31 after shelters had been exposed for seven weeks (40-60 % final fruit size; BBCH 74-77; Meier, 2001). In 2016, earwigs were sampled three times: May 23 - June 3 (i.e. after exposure during winter), July 25 - August 8 (after 9 weeks of exposure), and September 12-16 (after 6 weeks of exposure) (BBCH 71-74, 75-78, 79-84). In both years, earwigs were extracted from the shelters by strong beating.

In Spain, bands of corrugated cardboard (100 × 400 × 35 mm) were used as shelters. These shelters were stapled to the trunks (approx. 40 cm above ground) of uniformly distributed trees along the 40 m survey transects (n = 25-51 trees per orchard, one shelter per tree). Shelters were installed on June 1-5, 2015 and sampled once two weeks later (BBCH 73-75). Table S4.1 provides an overview of the sampling methods used in each country.

Woolly apple aphid surveys

In Germany, we checked for presence/absence of woolly apple aphids (WAA) on 30-32 randomly chosen trees along each survey transect to estimate the proportion of infested trees per orchard. We excluded trees with earwig shelters to obtain representative values of WAA infestation for each orchard and to avoid bias by experimental shelters. WAA surveys were carried out on July 15-31, 2015 (BBCH 74-77), July 26 – August 2, 2016 (BBCH 75-78) and September 12-16, 2016 (BBCH 79-84).

In Spain, we checked for presence/absence of WAA on trees of the survey transects (n=13-44 trees per orchard; mean = 33) to estimate the proportion of infested trees per orchard. The surveys were conducted on May 21-29, 2015 (BBCH 73-74), before earwig shelters were installed.

Orchard management

In both management types (IP and organic), apple growers conducted standard pesticide treatments using air-assisted sprayers, following label recommendations and advice from local plant protection consultants. We validated standard pesticide lists for each country and management type with spraying data provided by farmers or their consultants. As access to data on treatments was limited, we could only analyze the spraying data from 5 IP and 5 organic orchards in Germany, and 3 IP and 4 organic orchards in Spain (Table S4.2). We focused on substances with reported effects on earwigs and aphids. In IP orchards in both countries, several synthetic insecticides were applied against aphids and other pests. Some active compounds of these pesticides are known for harmful side effects on earwigs (Table S4.2), including organophosphates and neonicotinoids (Fountain and Harris, 2015; Malagnoux et al., 2015a). Organic growers in both countries applied only insecticides for which no or minor side effects on earwigs have been reported (Table S4.2). There was no management of WAA in organic orchards in either country but several IP farmers in Germany applied aphicides such as Pirimor® to control this pest.

Adjacent agri-environmental structures and landscape composition

Hedgerows, forest edges and other woody elements, including orchard meadows (traditional unmanaged orchards with extensive pruning strategy), were considered relevant agri-environmental structures (AES). We recorded the presence and cover (m^2) of woody structures within a radius of 20 m from the first transect-trees (those located at the orchard edge) (see Table 4.1 for orchard and landscape characteristics).

We conducted vegetation surveys within a radius of 20 m from the first transect tree in both countries during apple bloom in 2015. We surveyed entomophilous plants in 1 × 1 m quadrates in the adjacent habitat, considering plant species richness as a proxy for extra-orchard habitat quality. In Germany, overall species richness of plants was assessed in six quadrates (equally distributed in case more than one habitat type adjoined the orchard). In Spain, plant species richness was assessed in three quadrates per habitat type (e.g. fallow field, embankment, grassy pathway, hedgerow). For this reason, the total number of survey quadrates differed between orchards in Spain, and we used sample-based rarefaction to obtain a comparable number of plant species for three quadrates per orchard (Gotelli and Colwell, 2001).

We used official digital maps (Carreras and Diego, 2009; LGL, 2016; SIOSE, 2015) and Geographic Information Systems and Remote Sensing software ArcView 10.3.1 (ESRI) and MiraMon (CREAF) to quantify landscape characteristics. Landscape analysis targeted % orchard cover (excluding orchard meadows, i.e. orchards without visible row structure on aerial photographs), grassland, cropland and forest (Table 4.1) within a 1 km radius around the center of each transect.

The distinction between crop-habitats and non-crop habitats has proved as a suitable measure of effects of landscape composition on natural pest control (Bianchi et al., 2006). Amongst arable cropland in Spain, and forest cover and cropland in Germany, fruit orchards are a dominant cover type in both study regions (Table 4.1; see 'Results' for correlations between landscape variables). We thus focused on orchard cover (the proportion of intensively managed fruit orchards) as a simple and robust proxy of dominant crop-habitats in both countries, to analyze effects of landscape composition and to avoid collinearity between different cover types (Rusch et al., 2016). We additionally computed correlations between orchard cover and landscape complexity metrics (Shannon index; e.g. Chaplin-Kramer et al., 2011).

Statistical analyses

All statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016). For German earwig and aphid data, we run separate models (LM and GLM) for each sampling period. We applied a binomial distribution (accounting for overdispersion by correcting the standard errors using a quasi-GLM) for WAA presence/absence. The response variables were mean number of earwigs per tree ('earwig abundance') and proportion of trees infested by aphids. We used the factors management (IP *vs.* organic) and adjacent local woody elements ('woody AES': presence *vs.* absence) and the continuous variables 'plant species richness' and 'orchard cover' (%) in the surrounding landscape as predictors. In the full model, we allowed first level interactions among management and all other predictors.

We applied linear models (LM) for Spanish earwig data to assess effects of orchard cover, plant species richness and management on mean number of earwigs per shelter. We conducted separate analyses for each of the two earwig species that we found in Spain. Nymphs could not be unambiguously assigned to either species and were excluded from the analyses. We did not assess the effects of woody AES in Spain because they were only present in four (one IP, three organic) of the 28 orchards. To analyze Spanish aphid data, we used GLMs with binomial distribution (accounting for overdispersion by using a quasi-GLM).

We applied visual methods (quantile-quantile plots and residuals *vs.* fitted values) and Shapiro-Wilk-tests to check the distribution of the residuals. To meet the criterion of normality, we log-transformed the response variable in the earwig analyses of both countries. To prevent problems with zero values, we added a value corresponding to half the amount of the smallest mean abundance per tree (0.1 for Germany, 0.03 for Spain) to each earwig abundance value.

We used Akaike's information criterion corrected for small sample size (AICc) and F-tests to select the models with the best fit in a manual model simplification process (Pinheiro and Bates, 2000; Zuur et al., 2009). We calculated adjusted R^2 values (for LMs) and the explained deviance, comparing the difference of null deviance and residual deviance to null deviance, to assess the goodness-of-fit of GLMs (Dormann, 2013) and conducted outlier exclusion (Cook et al., 1982; Dormann, 2013) to check for influential measures. We refer to probability levels as significant for $P < 0.05$.

To test the relationship between the mean number of earwigs and the proportion of trees infested by aphids, we calculated Spearman's rank correlation coefficient (ρ). We also used Spearman's rank correlations (Figs. S4.1-2) and GLMs to check for independence of the explanatory variables included for Germany and Spain (Table S4.3). See Table S4.1 for an overview on differences in model specification and relevant factors in the two countries.

RESULTS

Agri-environmental structures and landscape composition

In Germany, plant species richness in the surroundings of the orchard ranged from 3 to 42 and did not differ between management types (Table 4.1). In Spain, plant species richness ranged from 2 to 21.1 plant species (rarefied values). It was higher in organic than in IP orchards ($t_{23.5} = 2.42$, $P = 0.02$; Table 4.1). In Germany, woody AES were present in 9 organic and 8 IP orchards in 2015, and in 9 organic and 7 IP orchards in 2016. Plant species richness was independent of presence of woody AES (Table S4.3). Woody AES were scarce in Spain (Table 4.1). Orchard cover was, by far, the most relevant agricultural land use type in both countries. Percentage of orchard cover in the surrounding landscape (radius 1 km) ranged from 3.4 - 63.7% in Germany and 0 - 97.1% in Spain. It did not differ between management types (Table S4.3). In Germany, orchard cover was negatively correlated to forest cover ($\rho = -0.60$, $P < 0.001$; Fig. S4.1) and arable cropland ($\rho = -0.48$, $P = 0.008$; Fig. S4.1). Landscape heterogeneity (Shannon index) was lower in landscapes with a high proportion of orchard cover ($\rho = -0.38$, $P = 0.041$; Fig. S4.1). In Spain, landscapes with a high cover (%) of orchards had a lower cover of arable cropland ($\rho = -0.87$, $P < 0.001$; Fig. S4.2) but were not characterized by a lower Shannon index ($\rho = 0.04$, $P = 0.851$; Fig. S4.2). Plant species richness in this country decreased with increasing orchard cover under IP but not under organic production (GLM: $F_{1,24} = 4.84$, $P = 0.038$, Table S4.3).

Table 4.1. Orchard characteristics (age and size), land use types (% cover in 1 km radius), plant species richness and local woody habitat (woody AES) cover in a 20-m radius from the edge of the orchard, in apple orchards in Germany (cultivar Braeburn) and Spain (Golden and Gala) for two management types (integrated production 'IP' *vs*. organic) in 2015 (mean±SD). Significant differences between management types within each country are shown in bold (t-tests; $P < 0.05$).

	Germany (n=30)		Spain (n=28)	
	IP	Organic	IP	Organic
Age (years)	9.7±3.7	9.9±3.0	11.4±7.3	13.3±8.3
Size (ha)	1.0±0.6	0.9±0.6	1.7±1.1	2.4±2.8
Cropland (%)	20.9±12.8	27.2±15.8	51.8±29.2	51.0±34.0
Forest (%)	19.3±17.3	19.5±15.6	1.0±2.0	2.6±3.3
Grassland (%)	11.9±5.6	14.0±6.2	0.6±0.9	1.3±2.7
Orchard (%)	34.1±16.4	27.0±11.1	41.6±30.5	32.5±31.1
Plant species richness	13.3±5.1	16.5±10.5	**8.3±3.1**	**11.7±4.3**
Woody AES present	8	9	1	3
Woody AES (m^2)	129.0±176.8	152.7±189.4	33.2±124.3	50.0±100.7

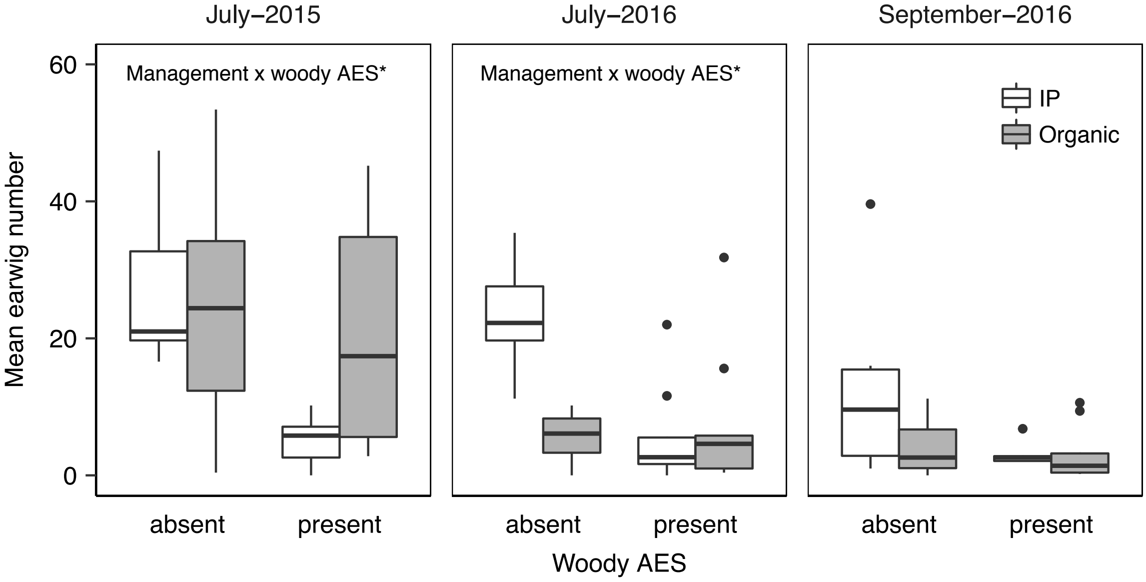

Figure 4.1. Mean number of earwigs (*Forficula auricularia*) per tree in German orchards. We tested for effects of two management types (IP *vs.* organic) and the presence or absence of woody agri-environmental structures (woody AES) in a 20-m radius in three sampling periods (July 2015 and 2016, and September 2016). Level of significance: * < 0.05, ** < 0.01; cf. Table 4.2.

Earwig surveys

In Germany we collected 5104 specimens of *Forficula auricularia*. Earwigs occurred in all orchards of both management types (IP: 2612 specimens; organic: 2492 (Table S4.4)). The survey in May 2016 yielded very low numbers (only 43 individuals, 20 of which in a single organic orchard), and was not included in the analysis. Earwig abundance differed significantly between sampling periods and between orchards with and without woody AES, depending on management (LM: Management: $F_{1,81}$ = 1.93, P = 0.169; Woody AES: $F_{1,8}$ = 8.86, P = 0.004; Sampling period: $F_{2,81}$ = 7.97, $P < 0.001$; Management × woody AES: $F_{1,81}$ = 9.27, P = 0.003; Table S4.4). Earwig abundance peaked in July and decreased in September (Table S4.4). There was no direct effect of management on earwig abundance in any of the three analyzed sampling periods. The presence of woody AES reduced the number of earwigs in IP orchards in July (Fig. 4.1, Table 4.2). Neither local plant species richness nor orchard cover in the surrounding landscape influenced earwig abundance. There was a significant interaction between management and presence of woody AES on earwig abundance in both years in July but not in September (Table 4.2).

In Spain, we collected 5056 earwigs belonging to two species: *F. auricularia* (82.2%; 1991 specimens in IP and 2165 in organic orchards) and *F. pubescens* Gené (9.6%; 2 specimens in IP and 484 in organic orchards). The remaining specimens were nymphs and could not be identified to species (Table S4.5). *F. auricularia* was present in 13 out of 14 organic orchards and in 12 out of 13 IP orchards, whereas *F. pubescens* was present in 9 organic and in 1 IP orchard. For abundance of *F. auricularia*, we did not find any effect of management, orchard cover or plant species richness, and the null-model performed best (*F* = 0.34, *P* = 0.882; comparison with the full-model, Table 4.2). On the other hand, organic management significantly increased the abundance of *F. pubescens* (Fig. 4.2, Table 4.2).

Table 4.2. Effects of management, and local and landscape factors on earwig (*Forficula auricularia* and *F. pubescens*) abundance (mean number of earwigs per tree). Predictors are management (IP *vs.* organic), woody agri-environmental structures (Germany only; woody AES were scarce in Spain), plant species richness, and % orchard cover in the landscape. Effects on mean earwig abundance per tree (log-transformed) were assessed fitting linear regressions; in Germany for each sampling period. R^2 is given as a goodness-of-fit measure. For Spain, results of the linear regression for mean earwig abundance (log-transformed) per tree are provided. Significant effects are shown in bold.

	df	*F*	*P*	Estimate±SE
GERMANY (*F. auricularia*)				
July 2015: $R^2_{adj} = 0.24$				
Intercept	1	106.22	<0.001	2.40±0.23
Management	1	1.03	0.320	0.33±0.33
Woody AES	**1**	**4.65**	**0.040**	**-0.71±0.33**
Management × woody AES	**1**	**5.84**	**0.023**	**1.12 ±0.47**
Residuals	26			
July 2016: $R^2_{adj} = 0.19$				
Intercept	1	36.6	<0.001	1.61±0.27
Management	1	2.29	0.143	-0.57±0.38
Woody AES	1	3.63	0.068	-0.71±0.38
Management × woody AES	**1**	**4.63**	**0.041**	**1.14±0.53**
Residuals	25			
Sept 2016: $R^2_{adj} = 0.09$				
Intercept	1	17.30	<0.001	1.00±0.24
Management	1	3.67	0.066	-0.65±0.34
Residuals	26			
SPAIN				
F. auricularia: $R^2_{adj} = -0.15$				
Intercept	1	0.49	0.490	1.21±1.72
Management	1	0.43	0.520	-1.60±2.44
Plant species richness	1	0.12	0.732	-0.05±0.15
Orchard cover	1	0.90	0.354	-0.02±0.02
Management × plant species richness	1	0.55	0.467	0.15±0.20
Management × orchard cover	1	0.05	0.047	-0.01±0.02
Residuals	21			
F. pubescens: $R^2_{adj} = 0.28$				
Intercept	1	86.23	<0.001	-1.26± 0.28
Management	**1**	**9.38**	**0.005**	**1.20 ±0.39**
Residuals	25			

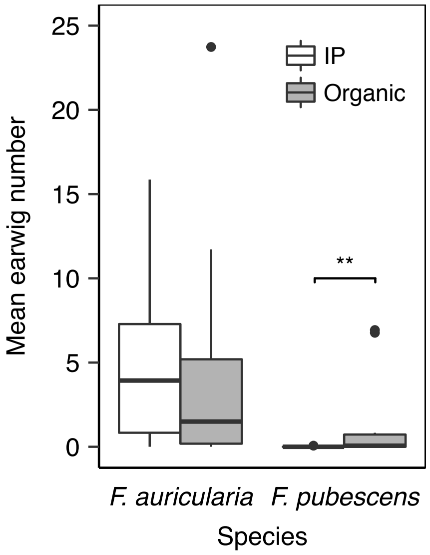

Figure 4.2. Mean number of earwigs (*Forficula auricularia* and *F. pubescens*) per tree in Spanish orchards for two management types (IP vs. organic). Level of significance: ** < 0.01; cf. Table 4.2.

Woolly apple aphid surveys

In Germany, tree infestation by WAA differed between survey periods and management types (GLM: Management: $F_{1,80}$ = 2.77, P = 0.100; Survey period: $F_{2,80}$ = 0.75, P = 0.475; Woody AES: $F_{1,80}$ = 4.47, P = 0.038; Management × woody AES: $F_{1,80}$ = 3.41, P = 0.038; Table S4.4). It was highest in July in 2016 and lowest in July in 2015 (Fig. 4.3a). In separate analyses for each survey period, neither management type nor the presence of woody AES affected the proportion of infested trees. However, higher orchard cover in the surrounding landscape resulted in higher infestation levels (Table 4.3). We found a significant negative correlation between earwig abundance and aphid infestation in July 2016, when WAA infestation was high (ρ = -0.43, P = 0.019). The correlation between earwigs and WAA in other months was negative but not significant (July-2015: ρ = -0.26, P = 0.171, September-2016: ρ = -0.23, P = 0.229).

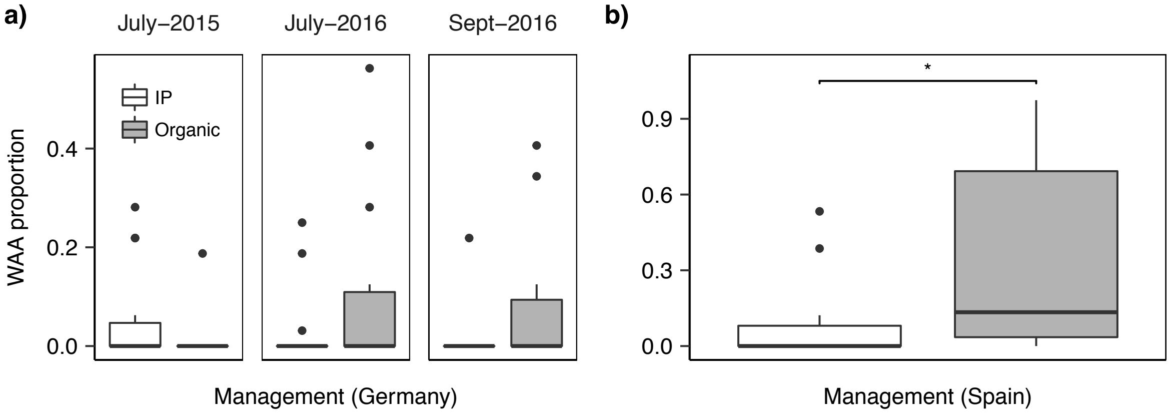

Figure 4.3. Proportion of trees (Germany: 30-32 per orchard; Spain: 13-44 trees per orchard) infested by woolly apple aphids in apple orchards with different management types (IP *vs.* organic) for (a) three sampling periods (July 2015 and 2016, and September 2016) in Germany and (b) one sampling period (May 2015) in Spain.

In Spanish orchards, tree infestation by WAA was higher in organic orchards and was not affected by any other of the examined predictors (Fig. 4.3b, Table 4.3, Table S4.5). There was no significant correlation between abundance of *F. auricularia* or *F. pubescens* and WAA infestation (Fig. S4.2; *F. auricularia* – WAA: ρ = -0.19, P = 0.320; *F. pubescens* – WAA: ρ = 0.30, P = 0.125).

Table 4.3. Effects of management, and local and landscape factors on woolly apple aphid (WAA) infestation (proportion of infested trees per orchard). Predictors are management (IP *vs.* organic), woody agri-environmental structures (Germany only; woody AES were scarce in Spain), plant species richness and % orchard cover. For both countries, effects on woolly apple aphid infestation were assessed fitting GLMs with quasi-binomial distribution (logit-link) for each sampling period. The explained deviance (dev. expl.) is given as a goodness-of-fit measure. Significant effects are shown in bold.

	df	*F*	*P*	Estimate±SE
GERMANY				
July 2015: 8 out of 30 orchards with WAA presence; 22.8 % dev. expl.				
Intercept				-5.63±1.10
Orchard cover	**1**	**7.10**	**0.013**	**0.06±0.03**
Residuals	28			
July 2016: 9/29; 18.1 % dev. expl.				
Intercept				-3.35±1.29
Management	1	1.03	0.321	0.64±0.66
Plant species richness	1	0.43	0.517	0.03±0.04
Orchard cover	1	0.33	0.574	-0.02±0.03
Woody AES	1	1.28	0.268	1.04±0.99
Residuals	24			
Sept 2016: 8/29; 35.4 % dev. expl.				
Intercept				-3.39±1.15
Management	1	1.22	0.280	0.70±0.68
Plant species richness	1	2.53	0.125	0.05±0.03
Orchard cover	1	2.71	0.113	-0.06±0.04
Woody AES	1	1.28	0.270	1.03±0.97
Residuals	23			
SPAIN: 17/28; 20.5 % dev. expl.				
Intercept				-2.47±0.70
Management	**1**	**7.04**	**0.013**	**1.89±0.80**
Residuals	26			

DISCUSSION

Orchard management

We expected higher earwig abundance in organic orchards due to the reduced application of agrochemicals with non-target effects on earwigs. Malagnoux et al. (2015b) showed that intensive orchard management and frequent pesticide use can have a strong negative impact on earwig populations in apple orchards, but they faced difficulties to disentangle direct (pesticide toxicity) from indirect (food reduction) effects. Like Moerkens et al. (2009), we did not detect a direct effect of management on abundance of the common earwig *F. auricularia*. This species was well established in both organic and IP orchards, suggesting that it can do well under both management types in both countries. On the other hand, the higher sensitivity of the Mediterranean earwig species *F. pubescens* to integrated pest management is in accordance with findings by Malagnoux et al. (2015b) who found lower abundances of *F. pubescens* in IP compared to organic orchards in France. Although earwigs are nocturnal and therefore their activity does not directly coincide with the timing of pesticide application, intensive management can be expected to alter living conditions for earwigs, and apparently does so for *F. pubescens*. Despite strong application regulations, several active compounds, such as chlorpyrifos and flonicamid (Table S4.2) used in commercial apple orchards in Germany and Spain, are known to have non-target effects on earwigs depending on dose and application time (Fountain and Harris, 2015; Malagnoux et al., 2015b). Organic management, on the other hand, can deteriorate living conditions of earwigs through tillage (Moerkens et al., 2012). Earwigs depend on undisturbed nesting sites in the soil during winter and spring, and there is evidence that optimized timing of tillage, i.e. before nesting starts in autumn and after nymphs hatch in spring, may reduce negative impacts of tillage on earwigs (Moerkens et al., 2012; Sharley et al., 2008). The negative effects of tillage in organic orchards could have counteracted the positive effects of reduced agrochemical inputs in our study. However, some studies indicate that *F. auricularia* does not overwinter within the orchards, thus, limiting the effects of tillage in organic orchards (Romeu-Dalmau et al., 2016). In Spain, *F. pubescens* may have benefited from increased prey availability due to higher WAA infestation in organic orchards, or it may have directly suffered from agrochemicals that were only applied in IP orchards (Table S4.2).

Given the absence of strong management effects on WAA infestation in Germany, our data provides no indication that higher prey abundance in organic orchards could directly enhance earwig populations in organic compared to IP orchards. However, because earwigs are generalist predators, other groups of prey should also be considered to elucidate whether prey availability regulates earwig populations in apple orchards. WAA showed similar (and low) abundance in German orchards of both management types. The observed higher proportion of WAA at an increased cover of fruit orchards (%) in the landscape indicates a higher infestation pressure by WAA in landscapes dominated by a single crop (mostly apple). This finding is in accordance with the 'resource concentration hypothesis' (O'Rourke and Petersen, 2017) and congruent with the low mobility of WAA (dispersal of first instar nymphs between trees) combined with a strong dependence on apple as a host plant (Lordan et al., 2015a).

Woody agri-environmental structures

We were surprised to find lower earwig abundances in IP orchards with adjacent woody AES. Dib et al. (2017) found larger earwig populations at the orchard edge adjacent to a hedgerow compared to the center. They argued that hedgerows can be considered source habitats for earwigs and other natural enemies (Debras et al., 2007). Similarly, abundance of earwigs in experimental cherry orchards was reported to be lower in isolated habitats with no direct connection to woody elements (Bucher et al., 2010). Trees adjacent to the forest had earwig densities more than four times higher and lower aphid infestations than trees isolated from woody habitats (Stutz and Entling, 2011). Our results suggest a different response of earwigs. An explanation could be that our orchards were more mature (5-17 years old) than the newly established orchards studied by Bucher et al. (2010) and Stutz & Entling (2011), where initial colonization of the new habitat and absence of intensive management practices may have caused higher earwig abundances in orchards with adjacent woody habitats. In organic orchards we found no differences in earwig abundance between orchards with and without woody AES, suggesting that earwig populations in these orchards are well established and find suitable refuge sites within the orchard. By contrast, earwig abundance declined in IP orchards when woody AES were present. A possible explanation for this finding is that earwig populations may survive in these orchards but tend to use adjacent woody structures when they are available.

Despite their limited flight activity, earwigs were found to move 8-29 m per month (Crumb et al., 1941; Moerkens et al., 2010). Earwigs collected in a recapture experiment in French orchards showed even larger foraging ranges. Individuals were detected 150 m away from the orchard, in adjacent apricot orchards (Debras et al., 2007). If earwigs in IP orchards are attracted to high quality surrounding habitats that provide alternative foraging opportunities at high population densities they might have easily moved to the woody boundaries. Competition as a trigger for migration is nevertheless questioned by Moerkens et al. (2009), who found very few adult earwigs when monitoring remigration to the ground. Limitations in dispersal ability on a landscape scale may help to explain that we did not detect any effects of orchard cover.

Another explanation for lower earwig abundances in IP orchards with adjacent woody habitats could be differing top-down regulation by insectivorous birds (Gunnarsson et al., 2009; Piñol et al., 2010), which strongly depend on woody habitats in the surroundings of orchards (García et al., 2018). Nevertheless, the regular use of anti-hail nets in commercial orchards in Germany might have impeded predation by insectivorous birds, which can be negatively affected by the nets (Brambilla et al., 2015).

Conclusion

Our study demonstrates that - despite intensive management practices - the common earwig *F. auricularia* is well established in commercial orchards in Germany and Spain. Other earwig species, such as *F. pubescens* in Spain, appear to be more sensitive to local management as they were more abundant in organic than in IP orchards. Contrary to previous reports, the presence of adjacent woody elements decreased earwig abundance in IP orchards, but not in organic ones. We suggest that, depending on the environmental conditions in the orchard, earwigs may use these semi-natural structures as temporary habitats.

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SUPPLEMENTARY MATERIAL

Table S4.1. Summary of study design in Germany and Spain and analyses conducted for earwigs and woolly apple aphids

Table S4.2. Applied pesticides and their side effects on earwigs

Table S4.3. Tests for independence of explanatory variables

Table S4.4. Mean earwig abundance and proportion of aphid infestation in Germany

Table S4.5. Mean earwig abundance and proportion of aphid infestation in Spain

Figure S4.1. Correlation chart for German data

Figure S4.2. Correlation chart for Spanish data

Table S4.1. Summary of study design in Germany and Spain and analyses conducted for earwigs and woolly apple aphids (WAA); AES: agri-environmental structure. We allowed for first level interactions between management and all other variables, including the term (Orchard cover)^2 in the initial model. In Germany, we analyzed data subsets for each sampling period but also report the effects of sampling period (full dataset). Factors and interactions with a significant effect are shown in bold.

Country	Target group	Sampling period	Exposition time	Sampling method	Number of orchards	Sampled trees per orchard	Response variable	Predictors	Model type
Germany	Earwigs	Jul 27-31, 2015 Jul 25 - Aug 8, 2016 Sep 12-16, 2016	7 weeks 9 weeks 6 weeks	Shelters	15 IP, 15 ORG 15 IP, 14 ORG[a] 14 IP, 14 ORG[b]	5	Mean number of earwigs per tree	**(Sampling period)** **Management x woody AES** **Management** **Woody AES** Orchard cover Plant species richness	LM
	WAA	Jul 15-31, 2015 Jul 26 – Aug 2, 2016 Sep 12-16, 2016		Visual survey	15 IP, 15 ORG 15 IP, 14 ORG[a] 15 IP, 14 ORG[a]	30 in 2015 32 in 2016	Proportion of infested trees	(Sampling period) Management Woody AES **Orchard cover** Plant species richness	GLM (binomial)
Spain	Earwigs	Jun 14-19, 2015	2 weeks	Shelters	13 IP[b] 14 ORG	25-51	Mean number of earwigs per tree	**Species x management** **Species** Management Orchard cover Plant species richness	LM
	WAA	May 21-29, 2015		Visual survey	14 IP 14 ORG	13-44	Proportion of infested trees	**Management** Orchard cover Plant species richness	GLM (binomial)

[a]2016: one IP orchard less due to change in management, [b]earwig traps lost in one IP orchard

Table S4.2. Applied pesticides and their side effects on earwigs (IOBC toxicity class* for active compound indicated if available). The permission and application status is indicated for both countries and management types (IP vs. organic (ORG)). Sources: spraying reports, farmer/expert interviews, official spraying recommendations (FÖKO, 2017, 2016; LTZ, 2017).

		Spain		Germany		Non-target effect on earwigs		
Active substance	Commercial product name (examples)	IP	ORG[†]	IP	ORG[†]	IOBC*	IOBC-reference	Other references
Acetamiprid	Mospilan® SG (Cheminova)	(+)	-	(-)	-			Harmful to adults (Malagnoux et al., 2015)
Azadirachtin	NeemAzal-T/S® (Trifolio-M GmbH)	(+)	+	(-)	+	3, 4	(Sauphanor et al., 1995)	
Bacillus thuringiensis	XenTari® (Biofa) / Dipel® ES (Cheminova)	(+)	(+)	(-)	+	1	(Sterk et al., 1999)	Safe (Colvin and Cranshaw, 2009; Fountain and Harris, 2015)
Chlorpyrifos	Inaclor 25 PM (Sipcam Inagra) / DurasbanTM 75 WG (Dow	+	-	(-)	-			Harmful (Fountain and Harris, 2015; Malagnoux et al., 2015)
Deltamethrin	Proteus® O-TEQ (Bayer)	+	-	(-)	-			Safe (Malagnoux et al., 2015), slightly harmful (Colvin and Cranshaw, 2009)
Flonicamid	Teppeki® (ISK Biosciences Europe)	+	-	+	-			Harmful for nymphs (Fountain and Harris, 2015)
Indoxacarb	Steward® (Stähler)	(+)	-	(+)	-			Harmful to males (Fountain and Harris, 2015), harmful (Shaw and
Kaolin	Surround® WP (Stähler)	(+)	(+)	(+)	+			Harmful (Markó et al., 2008)
Methoxyfenozide	Gladiator® (Dow AgroSciences) / Runner® (Bayer)	(+)	-	+	-			Harmful to nymphs (Fountain and Harris, 2015); safe to adults (Shaw
Phosmet	Imidian® WP (BASF Agro)	+	-	-	-	4	(Sterk et al., 1999)	Organophosphates harmful (Malagnoux et al., 2015), slightly
Pirimicarb[‡]	Pirimor® (Syngenta)	(+)	-	+	-			
Pyrethrine + oil	Spruzit® Neu (Progema GmbH)	-	-	(-)	(+)			Slightly harmful to adults (Peusens and Gobin, 2008)
Spirodiclofen	Envidor® (Bayer)	(+)	-	(+)	-			Harmful to nymphs (Fountain and Harris, 2015)
Thiacloprid	Calypso® (Bayer) / Proteus O-TEQ (Bayer)	(+)	-	+	-			Harmful (Fountain and Harris, 2015; Shaw and Wallis, 2010)

- not permitted in apple orchards during study time; (-) not applied; (+) applied rarely (1-2 orchards); + applied regularly (>5 orchards)

*1 (harmless), 2 (slightly harmful), 3 (moderately harmful), 4 (harmful); [†]depending on certification organisation, there can be some restrictions in pesticide use (e.g. for mineral oil in Demeter orchards); [‡]targets woolly apple aphids

Table S4.3. Tests for independence of explanatory variables in earwig and aphid analyses based on linear models and GLM. Response variables are orchard cover in the surrounding landscape (1 km) and plant species richness; AES: agri-environmental structure. Significant effects are shown in bold.

	Germany (n=30, 2015)			Spain (n=28)		
	df	*F*	*P*	df	*F*	*P*
Orchard cover*						
Management	1	0.41	0.530	1	2.04	0.166
Woody AES	1	0.44	0.514			
Plant species richness	1	0.71	0.410	1	0.16	0.695
Management x woody AES	1	0.92	0.347			
Management x plant species richness	1	0.54	0.471	1	2.03	0.167
Woody AES x plant species richness	1	0.47	0.500			
Residuals	23			24		
Plant species richness†						
Management	1	1.15	0.296	1	0.15	0.699
Woody AES	1	1.30	0.266			
Orchard cover	1	1.18	0.288	1	0.46	0.506
Management x woody AES	1	0.20	0.657			
Management x orchard cover	1	1.74	0.201	1	**4.84**	**0.038**
Woody AES x orchard cover	1	0.70	0.413			
Residuals	23			24		

*log(y+1.7) transformed, Gaussian error distribution

†Germany: total plant species richness, negative binomial errors; Spain: log-transformed rarefied plant species richness, Gaussian error distribution

Table S4.4. Mean number of earwigs (FA, *Forficula auricularia*) per tree, total number of earwigs (in brackets), and mean proportion of trees infested by woolly apple aphids (WAA) in German orchards (mean±SD) with two management types (IP *vs*. organic) and with (+) and without (-) woody agri-environmental structures (AES).

	IP		Organic	
	woody AES -	woody AES +	woody AES -	woody AES +
July 2015	n=7	n=8	n=6	n=9
FA	27.1±11.9 (949)	5.2±3.8 (209)	24.7±19.1 (742)	21.6±16.5 (970)
WAA	0.05±0.10	0.07±0.10	0	0.02±0.06
July 2016	n=6	n=8	n=6	n=9
FA	23.2±8.4 (695)	5.7±7.5 (265)	5.6±3.8 (169)	7.6±10.2 (341)
WAA	0	0.06±0.10	0.06±0.11	0.12±0.21
Sept 2016	n=6	n=7	n=6	n=9
FA	13.0±14.4 (388)	3.0±1.7 (106)	4.2±4.4 (127)	3.2±4.0 (143)
WAA	0	0.03±0.08	0.04±0.05	0.10±0.16

Table S4.5. Mean number of earwigs (*Forficula auricularia* and *F. pubescens*) per tree, total number of earwigs per management type (in brackets), and mean proportion of trees infested by woolly apple aphid (WAA) in 2015 in Spanish apple orchards with two management types (IP *vs.* organic).

	IP	Organic
Earwigs		
F. auricularia adults	4.89±10.64 (1991)	4.72±10.64 (2165)
F. pubescens adults	0.01±0.10 (2)	1.06±3.56 (484)
Nymphs	0.13±0.49 (52)	0.79±1.58 (362)
WAA	0.08±0.17	0.33±0.38

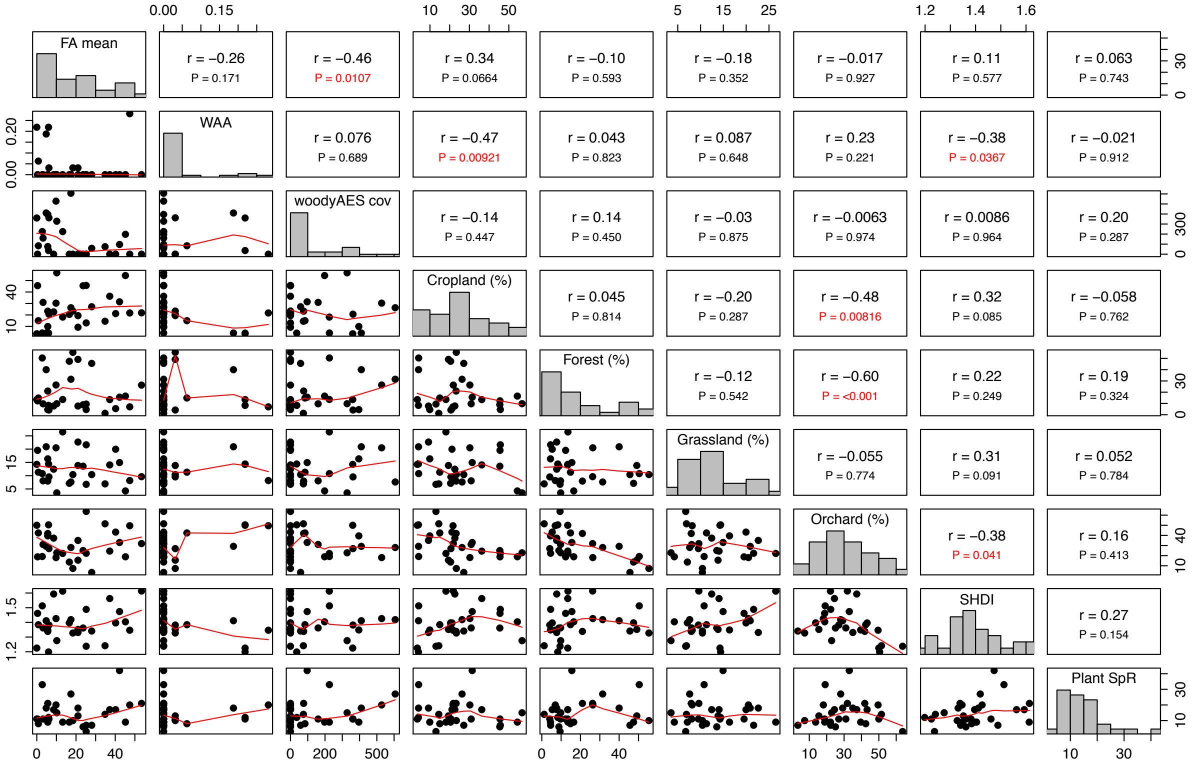

Figure S4.1. Correlation chart of variables included in the earwig analysis for German orchards in July 2015 (n=30). Scatterplot of mean abundance of earwigs per tree, *Forficula auricularia* (FA mean), proportion of trees infested by woolly apple aphids (WAA), cover (m^2) of woody habitats in a 20 m radius from the orchard edge (woodyAES cov), cover (%) of different land use types in the surrounding of the orchard (1 km radius), landscape heterogeneity (Shannon's Diversity Index, SHDI) and plant species richness (Plant SpR). Lower panels show scatterplots with a smoother added to visualize the patterns, panels in the middle show a histogram of each variable and upper panels contain Spearman's correlation coefficients (r) with *P*-values (red for *P* < 0.05).

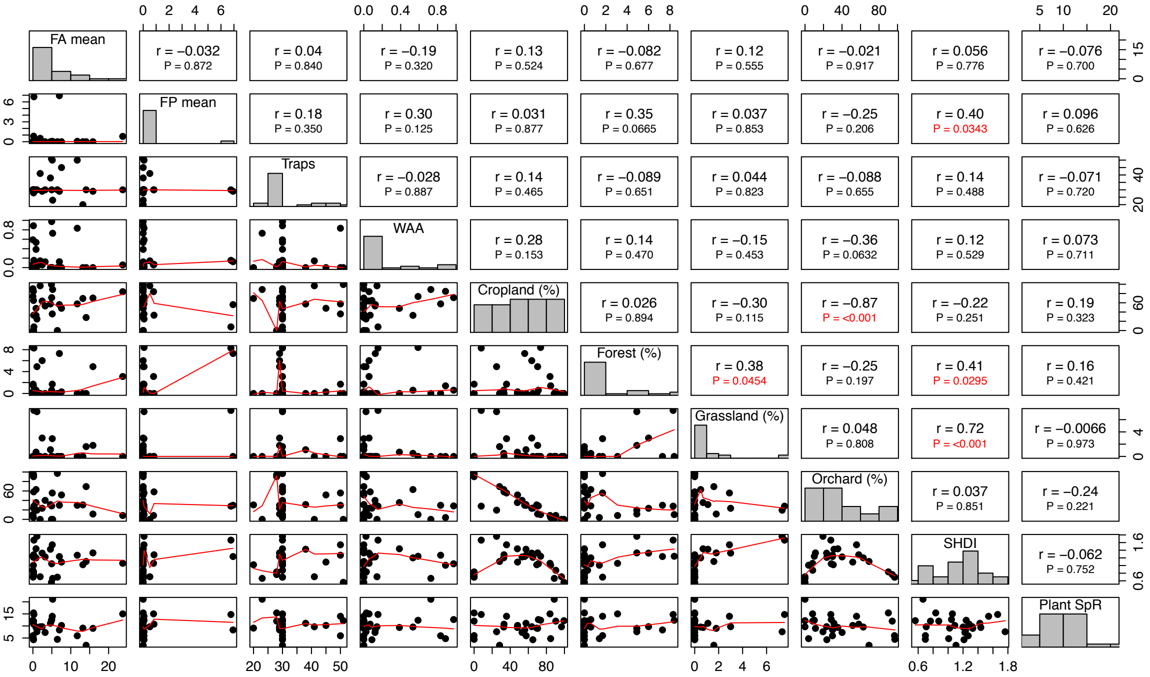

Figure S4.2. Correlation chart of variables included in the earwig analysis for Spain. Scatterplot of mean earwig abundance per tree for *Forficula auricularia* (FA mean) and *F. pubescens* (FP mean), proportion of trees infested by woolly apple aphids (WAA), cover (%) of different land-use types in the surrounding of the orchard (1 km radius), landscape heterogeneity (Shannon's Diversity Index, SHDI) and plant species richness (Plant SpR). Lower panels show scatterplots with a smoother, panels in the middle show a histogram of each variable and upper panels contain Spearman's correlation coefficients with *P*-values (red for $P < 0.05$).

5. GENERAL DISCUSSION

In this chapter I discuss the main findings of the three publications, following a short summary of the main results that answer the initial research questions:

(Q1) What landscape elements, local habitat features and management practices support beneficial arthropods (natural enemies and pollinators) across Europe? (a) What factors enhance ecosystem services (pollination and pest control)? *Organic management had a positive influence on natural enemy abundance, and on species richness of beneficial arthropods. Focusing on ecosystem services, positive effects of AES were restricted to pollinators. They benefit from enhanced local flower cover and reduced land-use intensity (lower orchard cover in the landscape).* (b) How does diversity of beneficial arthropods translate into seed set, fruit damage, and final fruit yield? *Higher natural enemy abundance in organic orchards translated into higher fruit production. Higher flower cover enhanced flower visitation and pollination by wild pollinators.* (c) Are there trade-offs between ecosystem services and final fruit yield? *Yes – organic management enhanced pest pressure, which led to lower yield in organic orchards; however, the lower yield was partly compensated by enhanced natural enemy abundance and a higher flower visitation rate of wild pollinators in organic orchards.*

(Q2) What local and landscape factors influence abundance patterns in communities of predatory arthropods in apple orchards? (a) Do predator communities differ between management types and countries? *Effects of management intensity on predator community composition in the two studied management types differ between regions.* (b) How do individual predator taxa differ in their response to local and landscape factors? *Organic management benefited spiders, beetles, earwigs, flies and bugs, but not in all countries. The effects of local habitat and landscape composition were inconsistent among predatory arthropod groups and countries. Depending on the region and/or the management type, woody habitat enhanced earwig abundance and plant species richness reduced bug abundance. Predation potential (energy use) was higher in organic orchards but only in one country.*

(Q3) How do earwigs and their prey react to local and landscape factors?

Organic management enhanced earwig abundance of Forficula pubescens in Spain. The presence of semi-natural woody habitats reduced abundance of F. auricularia in IP (but not in organic) orchards in Germany. A high proportion of fruit orchards in the landscape enhanced tree infestation by woolly apple aphids.

Synthesis

Only very few studies have so far tested trade-offs between a large-set of different factors such as biological control, pollination, biodiversity, crop yield, organic management and local floral resources. According to the Oxford English Dictionary, a 'trade-off' describes 'a balance achieved between two desirable but incompatible features; a compromise' (OED, 2019). Theoretically, trade-offs in apple orchards can be manifold: for example, enhanced biodiversity and abundance of arthropods may come at the cost of higher pest pressure leading to lower crop yield but could also increase biological control by enhancing species richness and abundance of predatory arthropods or by attracting natural enemies by providing alternative food resources. Herbs in the understorey of orchards may compete with the crop for nutrients and water, reducing productivity and final yield and enhancing susceptibility of crop plants to fungal diseases or pests. Meanwhile, a higher abundance of flowering plants may enhance pollination of the crop by supporting pollinators with floral resources throughout the growing season. Sutter et al. (2018) showed that local agricultural management is the most important predictor of arable crop yield in high-input conventional production systems whereas pollination and biological pest control have a much lower relevance for final yield. They found that sown perennial flower strips and hedgerows enhance pollinators and natural enemies but their study also suggests that minimising trade-offs is a key to environmentally friendly food production (Sutter et al., 2018). A recent study on interactions and trade-offs between local and landscape factors, their effects on ecosystem services and crop yields in IPM apple orchards in Australia suggests that local plant species richness in orchard understories supports natural enemies and pollinators as well as their services if orchards are isolated from woody habitats. Positive effects flower strips were, however, stronger in crop interiors, rather than at edges (Saunders et al., 2013). Our study proves that agricultural management, which was not included in the mentioned studies, is more import to explain trade-offs between ecosystem services, disservices and final yield than specific local and landscape factors. Tschumi et al. (2018) raised concerns that agricultural management practices to support beneficial arthropods in annual crop systems lead to a parallel increase in disservices. I share this concern based on higher pest pressure of rosy apple aphids (publication I) and higher tree infestation by woolly apple aphids (publication III) in organic apple orchards. In annual crop systems, reduced yield in organic vs. conventional production systems has been identified as a major driver for higher diversity of bumblebees, lepidopterans, syrphids and epigeal arthropods in organic systems (Gabriel et al., 2013). In apple production, disservices and lower yield associated with organic management (publication I and III) were partly compensated by enhanced natural enemy abundance (publication I and II) and higher rates of flower visitation by pollinators (publication I), and species richness of beneficial arthropods was uncorrelated with fruit production (publication I).

Despite lower yields and the importance of diversity in farming practices within each type of management (Puech et al., 2014), the implementation of organic management can enhance sustainable food systems by enhancing natural enemies, reducing pesticide use, N-surplus, and greenhouse gas emissions (Inclán et al., 2015; Muller et al., 2017; Seufert et al., 2012). Studies in apple orchards show that it can moreover enhance biodiversity and abundance of beneficial arthropods, pollination services and (depending on country) the predation potential of predator communities in apple orchards (Dib et al., 2016; Happe et al., 2019; Samnegård et al., 2018). In an international comparison, Seufert et al. (2017) found a high degree of consistency in the regulation of organic practices at national and international level. My research results suggest that predatory arthropods may be sensitive to country-specific differences in management intensity in both management types (publication II) and that a more fine-tuned analysis of management effects may be essential to explain variation in arthropod communities between management types in different countries (publication II and III).

The application of agrochemicals, a key factor of agricultural management, often incorporates a strong negative impact on biodiversity, pollinators and biological control (Geiger et al., 2010). The concentration of the applied substance as well as the timing of application in relation to arthropod life cycle is highly relevant in order to reliably assess side effects of specific pesticides on natural enemies (Fountain and Harris, 2015; Gobin et al., 2008b; Müller, 2018). Several authors refer to site-specific treatment frequency levels in order to explain variability in arthropod abundance (Lefebvre et al., 2016; Malagnoux et al., 2015b; Mickaël et al., 2015). However, I shared the experience of Saunders et al. (2018) that most growers refused to provide spray records (including details on number and timing of insecticide sprays and the concentrations of active compounds). To better understand the two management categories and to characterize management intensity in each country, I compiled a standard list of pesticide applications for each country and management type (see appendices of publication II and III), validated by farmer interviews and spraying reports. In the analyses, pesticide applications are included in the management factor and they cannot be separated from other agricultural practices inherent to each management type. For some predator groups in apple orchards, specific management practices such as tree row management (straw mulching, tillage and herbicide application) and the diversity of management practices within management types can be more relevant than the mere distinction in wider management categories (Marliac et al., 2016; Miñarro et al., 2009). For instance, tilling, fertilization, growth regulators and weed control may influence predator communities (Malone et al., 2017; Puech et al., 2014).

Two highly relevant other results are apparent from the trade-off analysis (publication I): a positive effect of high flower cover on flower visitation by wild pollinators, and the importance of low land-use intensity for diversity of beneficial insects. The relevance of flower provision for pollinators is well known (Goulson et al., 2015; Nayak et al., 2015; Wratten et al., 2012). Given the importance of low land-use intensity for beneficial arthropods (publication I), its low impact on natural enemies (publication I-III) comes at a surprise. The inclusion of wild pollinators in the group of beneficial arthropods (publication I) could partly explain the effect of reduced land-use intensity at the landscape scale. For example, Holzschuh et al. (2008) showed that wild bees are sensitive to the amount of organic crop in the surrounding landscape. The cover of apple orchards in our study regions is mainly composed by IP orchards (Samnegård et al., 2018), which may have led to a reduced habitat quality for wild pollinators at the landscape scale. However, other authors show that not only wild bees but also bugs, beetles and spiders profit from a low land-use intensity (Hendrickx et al., 2007; Martins et al., 2015).

Potential drivers for inconsistency in the arthropods' response to local and landscape factors

A closer look on the results of publication I (Table 2.1) reveals the need to study local and landscape effects on predators and their prey in each country separately: responses of arthropods, their services and disservices to local and landscape factors were highly variable and partly opposed between countries. For example, aphid infestation by rosy apple aphids in Germany was higher in IP than in organic orchards, contrary to the other countries. Similar patterns in aphid abundance were reported by Martin et al. (2015) who found higher aphid abundances in conventional than in organic winter wheat fields early in the season. They concluded that fertilization (soil nitrogen availability) is a major factor in driving higher initial aphid population build-up (Butler et al., 2012). Apart from regional differences in management, the taxonomic identity of predators and their trophic interactions have to be considered as potential drivers for inconsistency in responses to local and landscape factors. In a recent review on conservation biological control, Begg et al. (2017) point out that the response of natural enemy populations to conservation measures is inconsistent because various ecological and behavioural processes influence it at multiple scales. Biological control agents form part of local food webs and trophic cascades (Gagic et al., 2011; Gurr et al., 2017). Additionally, the same environmental or management factor has often diverging effects on ecosystem services and biodiversity due to species-specific variations in life history (Liere et al., 2017; Shackelford et al., 2013).

Seasonal and diurnal variation in predator communities

For all studies, we conducted sampling at standardised tree phenology in all three regions. However, communities of predatory arthropods (publication II) may have changed during the two months of sampling, relating to region-specific predator and prey voltinism (Stoeckli et al., 2012; Tobin et al., 2008). In Publication III, a significant difference in management effects between sampling periods becomes evident when sampling date is included in the analysis but these differences are expected from earwigs' seasonal abundance patterns in temperate (Alford, 2014; Solomon et al., 2000) and in Mediterranean orchards (Lordan et al., 2015b) and were not in the focus of our study.

Apart from seasonal differences, there is also diurnal variation in abundance patterns of some predator groups. Earwigs, for instance, are nocturnal foragers (Logan et al., 2017) and woody habitats may serve as earwig refuges during the day leading to lower acceptance of artificial shelters within the orchard. In publication III, a negative effect of the presence of woody habitats on earwig abundance was only evident in IP but not in organic orchards. Therefore, I assume that woody habitats are not generally more attractive for earwigs as daytime shelters than artificial shelters. In consequence, I thus consider nycthemeral variation a negligible factor to explain the observed differences in earwig abundance.

Research transfer & outreach

Growers are often well aware of the importance of biological control and pollination for their production (Page and Bellotti, 2015). To support biodiversity and ecosystem services, some apple growers in this study added privately funded semi-natural hedgerows or patches of flowering plants as conservation measure. However, apart from organic management, the acceptance of EU-funded AES in the study regions was low: in Spain, woody habitats were only present alongside four out of 28 orchards, and in all three countries we had difficulties to find orchards with sown flower strips or planted hedgerows that had been funded by EU subsidies. The low acceptance is surprising, considering that AES targeted at areas out of production (e.g. field margins, flower strips and hedgerows) have proved to be effective tools for conservation of biodiversity (Batáry et al., 2015). Kreiser (2018) identified deficits in EU financing as the main cause for the reluctance of growers to implement costly or labour-intensive AES such as those aimed at areas out of production. The author highlights the importance of enhanced funding in the EU's Common Agriculture Policy, which is currently negotiated for the period 2021-2027. Stronger financial support beyond compensation for production losses would encourage the implementation of more targeted AES such as sown flower strips providing specific food plants and valuable resources for pollinators and natural enemies (Begum et al., 2006; Wäckers and van Rijn, 2012; Wratten et al., 2012). In addition, the set of acknowledged AES needs to improve constantly; for instance, the high value of small-scale agriculture for wild bees and pollination (Happe et al., 2018b; Hass et al., 2018) and the vital contribution of organic management to enhancing biological control (Muneret et al., 2018) need a stronger recognition in policy and practice.

The results of this study support the importance of organic management across climatic regions and across taxonomic groups of predatory arthropods. However, it remains challenging to derive generalised recommendations to improve AES-habitats for apple production in Europe. A closer look at the local set of predator groups and available management options (restricted by national regulations) will help to identify suitable management measures for predatory arthropods in apple orchards in each context.

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7. APPENDIX

CONTRIBUTIONS TO THE RESEARCH CHAPTERS

Publication I – Management trade-offs on ecosystem services in apple orchards across Europe: direct and indirect effects of organic production

Ulrika Samnegård, Georgina Alins, Virginie Boreux, Jordi Bosch, Daniel García, Anne-Kathrin Happe, Alexandra Maria Klein, Marcos Miñarro, Karsten Mody, Mario Porcel, Anselm Rodrigo, Laura Roquer-Beni, Marco Tasin and Peter A. Hambäck

Author's contributions: AMK, AKH, JB, KM, LRB, PAH, US, and VB conceived the ideas for the paper and designed the studies; US, GA, VB, AKH, MP, AR, DG, MM, MT and LRB collected the data; US and PAH analyzed the data and led the writing of the manuscript. All authors contributed to the development of ideas and drafts and gave final approval to publication.

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Publication II – Predatory arthropods in apple orchards across Europe: responses to agricultural management, adjacent habitat, landscape composition and country

Anne-Kathrin Happe, Georgina Alins, Nico Blüthgen, Virginie Boreux, Jordi Bosch, Daniel García, Peter A. Hambäck, Alexandra Maria Klein, Rodrigo Martínez-Sastre, Marcos Miñarro, Ann-Kathrin Müller, Mario Porcel, Anselm Rodrigo, Laura Roquer-Beni, Ulrika Samnegård, Marco Tasin, Karsten Mody

Author's contributions: JB, NB, DG, AKH, PAH, AMK, KM, MM, AR, LRB and MT conceived the ideas for the paper and designed the studies; GA, JB, LRB, VB, DG, AKH, PAH, MM, AKM, MP, MT and US collected the data; AKH analyzed the data and led the writing of the manuscript with substantial input from PAH and KM. All authors contributed to the development of ideas and drafts and gave final approval to publication.

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Publication III – Earwigs and woolly apple aphids in integrated and organic apple orchards: responses of a generalist predator and a pest prey to local and landscape factors

Anne-Kathrin Happe, Laura Roquer-Beni, Jordi Bosch, Georgina Alins, Karsten Mody

Author's contributions: KM and AKH conceived the ideas and designed methodology for Germany, GA, JB and LR for Spain; AKH, JB and LR collected the data; AKH and KM planned data analyses; AKH analyzed the data; AKH wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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PROJECT INFORMATION & FUNDING

My studies form a part of the European EcoFruit research initiative, promoted by the BiodivERsA network to develop management schemes for ecosystem services linking scientific advancements to policy and practice. It was funded through the 2013-2014 BiodivERsA/FACCE-JPI joint call (agreement BiodivERsA-FACCE2014-74), with the German Federal Ministry of Education and Research (PT-DLR/BMBF) (grant 01LC1403) as a national funder in Germany. I am obliged to BMBF for the funding of my research position.

Without the strong cooperation in a consortium of 17 scientists in Germany, Spain and Sweden, and the support of regional grower associations, production advisors and local research institutes, this thesis and the three publications it is based on, would not exist: throughout the EcoFruit project, local stakeholders were engaged in the research process. During two workshops, we discussed the expectations of growers, their advisers, and local institutes for fruit organic and integrated production. Several methods, such as sampling of earwigs, pest surveys and grower interviews were improved based on stakeholder suggestions. On request of the organic growers' association FÖKO e.V., we additionally included 14 organic orchards of a typical organic cultivar, Topaz, in Germany. Results on this cultivar are not included in the studies included in this thesis but will be presented during a follow-up workshop with all German stakeholders.

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Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit entsprechend den Regeln guter wissenschaftlicher Praxis selbstständig und ohne unzulässige Hilfe Dritter angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommenen Gedanken sowie sämtliche von Anderen direkt oder indirekt übernommenen Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher bei keiner anderen Hochschule zu Prüfungszwecken eingereicht.

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