Vertebrates and insects as pest and bio-control agents in agricultural landscapes of the Judean Foothills in Israel

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Summary

Agricultural expansion and land use change are leading drivers of biodiversity loss worldwide. Today, agricultural land covers about 38% of the Earth's total ice-free land, and agriculture is the primary user of Earth's freshwater resources. Fragments of semi-natural and natural habitats in agricultural landscapes are primary habitats for many beneficial organisms. These organisms may move from natural habitats to croplands at times when crops provide massive plant resources and can therefore enhance agro-ecosystem services such as biological pest control. Natural habitats in agricultural landscapes may also promote pest organisms or crop diseases which influence crops negatively, but little is known about such ecosystem dis-services mediated by the availability of natural habitats to agriculture. When managing agricultural landscapes to conserve biodiversity and ecosystem services, we need to understand if the availability of semi-natural and natural habitats increases ecosystem dis-services to avoid risking higher costs than benefits. Unfortunately, the simultaneous effects of surrounding habitats and other landscape structures on agro-ecosystem services, dis-services and their interactions are largely unknown.

In the first part of my thesis (chapter I) I investigated which vertebrates are using almond orchards and sunflower fields and studied their impact on crop seed predation in relation to the availability of natural (shrub land) and semi-natural habitat (shrub land mixed with planted forest) in an agricultural landscape of Israel. I selected 20 almond and 20 sunflower study sites with varying percentages of natural (0–61%) and semi-natural (0–70%) habitats within a 1000 m radius of their surroundings. I observed birds, trapped rodents, counted seeds and noted feeding marks to obtain seed predation rates at each study site. Furthermore in almond crops, I physically excluded birds, rodents and both to determine their relative and combined influence on seed predation.

In the second part (chapter II) I tested how natural and semi-natural habitat surrounding almond orchards in Israel influence almond pest predation by the almond wasp (*Eurytoma amygdali* Enderlein) (dis-service). I also focused on the abundance of their parasitoids (service) and how these habitats influence granivorous birds. These birds either consume almonds before harvest (dis-service) or after harvest, when overwintering almonds "mummy nuts" provide potential pest breeding habitat (service). For this study, I chose 17 almond orchards with varying percentages of surrounding natural and semi-natural habitat. I harvested almonds to count almond wasps and their parasitoids, collected nuts and mummy nuts with bird-feeding marks and conducted bird observations to identify bird species and their abundance.

In the third part (chapter III) I concentrated on birds as important seed predators and investigated their impact on sunflower seed predation. Birds are known for using elevated landscape structures to perch and hide. High trees in agricultural landscapes may therefore drive seed predation. I examined if the presence, the distance and the percentages of high trees (tree height >5 m) and the percentages of natural habitat surrounding sunflower fields increase seed predation by birds. I chose to use two datasets, one collected at the field scale and one at the landscape scale. At the field scale I assessed seed predation across a sample grid of an entire sunflower field. At the landscape scale I assessed seed predation at the field margins and interiors of 20 sunflower fields. I estimated seed predation as the percentage of removed seeds from sunflower heads. Distances of sample points to the closest high tree and percentage of natural habitat and of high trees in a 1 km radius surrounding the fields were additionally measured.

In my first study I found that neither vertebrate abundance nor species richness (birds and rodents) was influenced by the percentage of natural habitat. However, bird species richness increased with increasing percentage of semi-natural habitat. Seed predation across both crops was not influenced by natural or semi-natural habitat but increased significantly with increasing abundance and species richness of birds. This was also reflected by the exclusions of birds, rodents and both to the almond crop, leading to lowest seed predation when both groups were excluded.

In the second study, natural habitat did not influence any targeted ecosystem services or dis-services in almond orchards. Almond wasp predation was positively influenced by semi-natural habitat. Parasitoid abundance was not influenced by the surrounding habitats, but bird abundance was negatively influenced by semi-natural habitats. Granivorous bird abundance did not show an effect on bird seed predation of harvestable almonds or mummy nuts.

The results of my third study show that seed predation increased with decreasing distance to the closest high tree at the field and landscape scale with a threshold of 50 m. However the percentage of high trees and natural habitat did not increase seed predation.

Synthesis and applications

Natural habitat did not influence the agro-ecosystem dis-service of seed predation by birds and rodents and infestation rates of almond wasps. However, semi-natural habitat can support insect almond pests and can have different impacts on different services and dis-services. The high trees, which can be found in the semi-natural habitat of my study region are mainly planted and introduced trees which are not native in the area. Therefore, protecting natural habitats for conservation or to enhance agro-ecosystem services meditated by beneficial organisms like natural pest enemies and pollinators is not necessarily coupled with disadvantages for farmers. Sunflower seed predation by birds can be reduced when avoiding sowing sunflowers within a radius of 50 m to high trees. To provide more detailed management recommendations concerning vertebrate and invertebrate dis-services their feeding behaviour, metabolic needs, behaviour patterns and local abundances should be taken into account and farmers need to be aware of different services and dis-services and their connection to different habitats to plan for sustainable agriculture.

Zusammenfassung

Die Intensivierung der Landwirtschaft sowie Veränderungen in der Landnutzung sind treibende Kräfte des weltweiten Biodiversitätsverlustes. Etwa 38% der gesamten eisfreien Landfläche wird landwirtschaftlich genutzt und sie ist der Hauptnutzer der Süßwasserressourcen der Erde.

Fragmente von naturnahen und natürlichen Habitaten in Agrarlandschaften sind primäre Habitate für viele Nützlinge. Diese Nützlinge können von natürlichen Habitaten in landwirtschaftliche Flächen übertreten und somit Ökosystemleistungen wie die biologische Schädlingsbekämpfung verbessern. Allerdings können dieselben Habitate auch Schädlinge oder Pflanzenkrankheiten fördern, und somit den Nutzpflanzenanbau z.B. durch erhöhte Samenprädation negativ beeinflussen (Ökosystem Fehlleistungen). Bis heute ist wenig über den Zusammenhang zwischen Ökosystem Fehlleistungen und der Verfügbarkeit von natürlichen Habitaten bekannt. Wenn Agrarlandschaften auf eine Weise bewirtschaftet werden, die Biodiversität und Ökosystemtleistungen fördert, sollte auch beachtet werden, ob die Verfügbarkeit von naturnahen und natürlichen Habitaten auch Ökosystem Fehlleistungen fördert, um höhere Kosten als Nutzen zu vermeiden. Bis heute ist der Einfluss von Agrarflächen umgebenden Habitaten und anderen Landschaftsstrukturen auf Ökosystemleistungen, Ökosystem Fehlleistungen und deren Wechselwirkungen weitgehend unbekannt.

Im ersten Teil meiner Dissertation (Kapitel I) habe ich untersucht, welche Wirbeltiere Mandel- und Sonnenblumenfelder nutzen und welche Auswirkungen diese auf die Samenprädation in Bezug auf die Verfügbarkeit von natürlichen und naturnahen Habitaten haben. Ich wählte 20 Mandel- und Sonnenblumenfelder in einer Agrarlandschaft in Israel als Untersuchungsflächen. Untersuchungsflächen waren umgeben von unterschiedlichen Anteilen natürlicher (0-61%) und naturnaher (0-70%) Habitate in einem 1000 m Radius. In jedem Studienfeld beobachtete ich Vögel, fing Nagetiere und nahm Fraßspuren auf, um Samenprädationsraten festzustellen. Innerhalb der Mandelstudienfelder führte ich außerdem Ausschlusexperimente durch, in welchen ich physisch Vögeln oder Nagetieren oder beiden den Zugang zu Mandeln verwährte um ihren relativen und kombinierten Einfluss auf die Samenprädation zu bestimmen.

Im zweiten Teil (Kapitel II) wurde von mir untersucht, wie natürliche und naturnahe Habitate, welche Mandelfelder umgeben, die Samenprädation der Mandelwespe (*Eurytoma amygdali* Enderlein) und das Vorkommen ihrer Parasitoide beeinflussen. Außerdem untersuchte ich welchen Einfluss granivore Vögel auf die Mandelernte haben, da sie entweder Mandeln vor der Ernte fressen (Fehlleistung) oder nach der Ernte überwinternde Nüsse (mummy nuts) fressen.

Diese überwinternden Nüsse sind potentielle Habitate für Schädlinge, daher wäre die Prädation dieser Nüsse eine Ökosystemleistung. Für diese Studie wählte ich 17 Mandelfelder mit unterschiedlichen Anteilen von natürlichen und naturnahen Habitaten in der umgebenden Landschaft. Zusätzlich erntete ich Mandeln um die Anzahl von Mandelwespen und ihren Parasitoiden zu bestimmen, untersuchte Mandeln und überwinterte Nüsse auf Vogelfraßspuren und führte Vogelbeobachtungen durch um Vogelarten und ihre Abundanzen zu ermitteln.

Im dritten Teil (Kapitel III) konzentrierte ich mich auf Vögel als wichtige Samenprädatoren und untersuchte deren Auswirkungen auf die Sonnenblumenernte. Vögel sind dafür bekannt, dass sie hohe Strukturen in der Landschaft als Aussichtspunkte und Verstecke nutzen. Hohe Bäume in der Agrarlandschaft können somit die Samenprädation durch Vögel beeinflussen. Daher untersuchte ich, ob das Vorkommen, die Distanz und die Anteile hoher Bäume (Baumhöhe > 5 m) und die Anteile der natürlichen Habitate in der Umgebung der Sonnenblumenfelder, zu erhöhter Samenprädation durch Vögel führen. Ich entschied mich dazu zwei Ansätze der Datenaufnahme zu verwenden, einen auf der Feldebene, einen auf der Landschaftsebene. Auf der Feldebene sammelte ich Daten zur Samenprädation mit Hilfe eines Rasters über die Fläche eines ganzen Sonnenblumenfeldes. Auf der Landschaftsebene, erhob ich Daten zur Samenprädation an Feldrändern und im Inneren von 20 Sonnenblumenfeldern. Die Samenprädation wurde von mir als prozentualer Anteil der entfernten Samen je Sonnenblume bestimmt. Außerdem wurden die Distanz zum nächsten hohen Baum, der Flächenanteil natürlichen Habitats und der Anteil hoher Bäume in 1 km um die Felder bestimmt.

Die Ergebnisse meiner ersten Studie zeigen, dass weder die Abundanz noch der Artenreichtum von Vögeln und Nagetieren durch den Anteil an natürlichem Habitat in der umgebenden Landschaft beeinflusst werden. Allerdings erhöhte sich der Artenreichtum von Vögeln mit zunehmendem Anteil von naturnahem Habitat. Samenprädation in Mandeln und Sonnenblumen wurde nicht direkt von natürlichen oder naturnahen Habitaten beeinflusst, nahm jedoch deutlich mit zunehmendem Artenreichtum und zunehmender Abundanz von Vögeln zu. Dies spiegelte sich auch in den Ausschlussexperimenten wieder, da der Ausschluss von Vögeln, Nagern oder beiden zu niedrigerer Samenprädation führte.

Auch in der zweiten Studie hatte natürliches Habitat keinen Einfluss auf die untersuchten Ökosystemleistungen oder Fehlleistungen. Samenprädation durch die Mandelwespe wurde positiv durch das Vorkommen naturnahen Habitats beeinflusst. Die Abundanz von Parasitoiden wurde nicht von umgebenden natürlichen oder naturnahen Habitaten beeinflusst. Die

Vogelabundanz wurde jedoch durch naturnahes Habitat negativ beeinflusst. Die Abundanz von granivoren Vögeln zeigte keinen Einfluss auf Samenprädation an erntereifen und überwinternden Mandeln.

Die Ergebnisse meiner dritten Studie zeigen, dass Samenprädation an Sonnenblumensamen stärker ausgeprägt ist je näher der nächste hohe Baum ist. Dies gilt für einen Radius bis 50 m. Der Anteil von hohen Bäumen und natürlichem Habitat in der umgebenden Landschaft führte nicht zu einer erhöhten Samenprädation.

Synthese und Anwendungen

Die Agrarökosystem Fehlleistungen Samenprädation durch Vögel, Nagetiere und Mandelwespen wurden nicht durch natürliches Habitat beeinflusst. Daher ist der Schutz natürlicher Habitate für die Erhaltung oder zur Verbesserung der Agrarökosystemleistungen von Nützlingen, wie natürliche Schädlingsbekämpfung und Bestäubung, nicht notwendigerweise mit Nachteilen für die Landwirte verbunden. Allerdings kann naturnahes Habitat Schädlinge unterstützen und unterschiedliche Auswirkungen auf verschiedene Leistungen und Fehlleistungen haben. Samenprädation an Sonnenblumen durch Vögel kann reduziert werden wenn Sonnenblumenfelder weiter als 50 m entfernt von hohen Bäumen angebaut werden. Die hohen Bäume in den naturnahen Habitaten meines Untersuchungsgebietes sind eingeschleppte Arten und daher nicht natürlich vorkommend. Um detailliertere Bewirtschaftsungs-Empfehlungen für die Unterbindung von Fehlleistungen durch Wirbeltiere und Wirbellose geben zu können, ist es wichtig, ihr Fraßverhalten, Stoffwechselbedürfnisse, Verhaltensmuster und lokale Abundanzen zu berücksichtigen. Landwirte müssen sich verschiedener Leistungen und Fehlleistungen bewusst sein um nachhaltige Landwirtschaft planen und betreiben zu können.

General Introduction

"The ecosystem services concept"

The human population has increased from three to seven billion people in the past 50 years, and agricultural areas now cover almost 40% of the total earth’s ice-free terrestrial land. As the global population continues to increase and is estimated to reach nine billion by 2050, the pressure on natural and semi-natural habitats is growing (Roberts, 2011) also due to agricultural intensification. While in 1700 95% of terrestrial ice-free areas were covered by natural and semi-natural habitats, in 2000 more than half of these areas have been transformed to agricultural areas. As a consequence, natural and semi-natural habitats have declined substantially and got fragmented in many landscapes (Foley *et al.*, 2005; Ellis *et al.*, 2010), leading to a strong decline of biodiversity (Pimm & Raven, 2000).

Habitats with high biodiversity do not just inhabit a diverse number of species but also their functions, which are often interactions between different species (Scherber *et al.*, 2010). These so-called ecosystem functions can be defined as the capacity of natural processes and components to provide goods and services, directly or indirectly, that satisfy human needs and can be grouped into four categories: regulation functions, habitat functions, production functions and information functions (de Groot *et al.*, 2002). All of these functions are important in sustaining functional ecosystems (Hector & Bagchi, 2007). Some ecosystem functions have a direct benefit for humans and are termed ecosystem services. These ecosystem services are generated from numerous interactions occurring in complex ecosystems with high biodiversity (Harrison *et al.*, 2014). The relationships and links between biodiversity and the provision of ecosystem services are complex and still involve many uncertainties, hence further research is necessary (Balvanera *et al.*, 2013; Harrison *et al.*, 2014). Ecosystem services have been defined as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life” (Daily, 1997). Ecosystem services can be classified into four main categories: provisioning, supporting, cultural, and regulating services (MEA, 2005). Agricultural ecosystems are highly dependent on some of these ecosystem services since they are managed to optimize the provisioning ecosystem services of food, fiber, and fuel. Furthermore, in the process of managing the provisioning of these ecosystem services they rely on supporting services like soil fertility, nutrient cycling, water provisioning and genetic diversity and regulating services like pollination, dung burial, natural control of plant pests and water purification (Zhang *et al.*, 2007) (Fig. A).

There are three dimensions to ecosystem services research. (1) The characterization and explanation of interdependencies between humans and natural systems (Balmford *et al.*, 2011; Collins *et al.*, 2011), (2) ecosystem services related to species loss and hence linked to biodiversity conservation (Gómez-Baggethun *et al.*, 2010), (3) the implications of changes to ecosystem services for human well-being (Fig. A) (de Groot, 1987; Daily *et al.*, 1997; Costanza *et al.*, 1998). These three dimensions are considered the foundation of the ecosystem service concept (Costanza, 2000; Wilson & Howarth, 2002; Chan *et al.*, 2006). Therefore the ecosystem service concept is of an interdisciplinary nature (Collins *et al.*, 2011), and ecosystem services have become a topic in social sciences and economics.

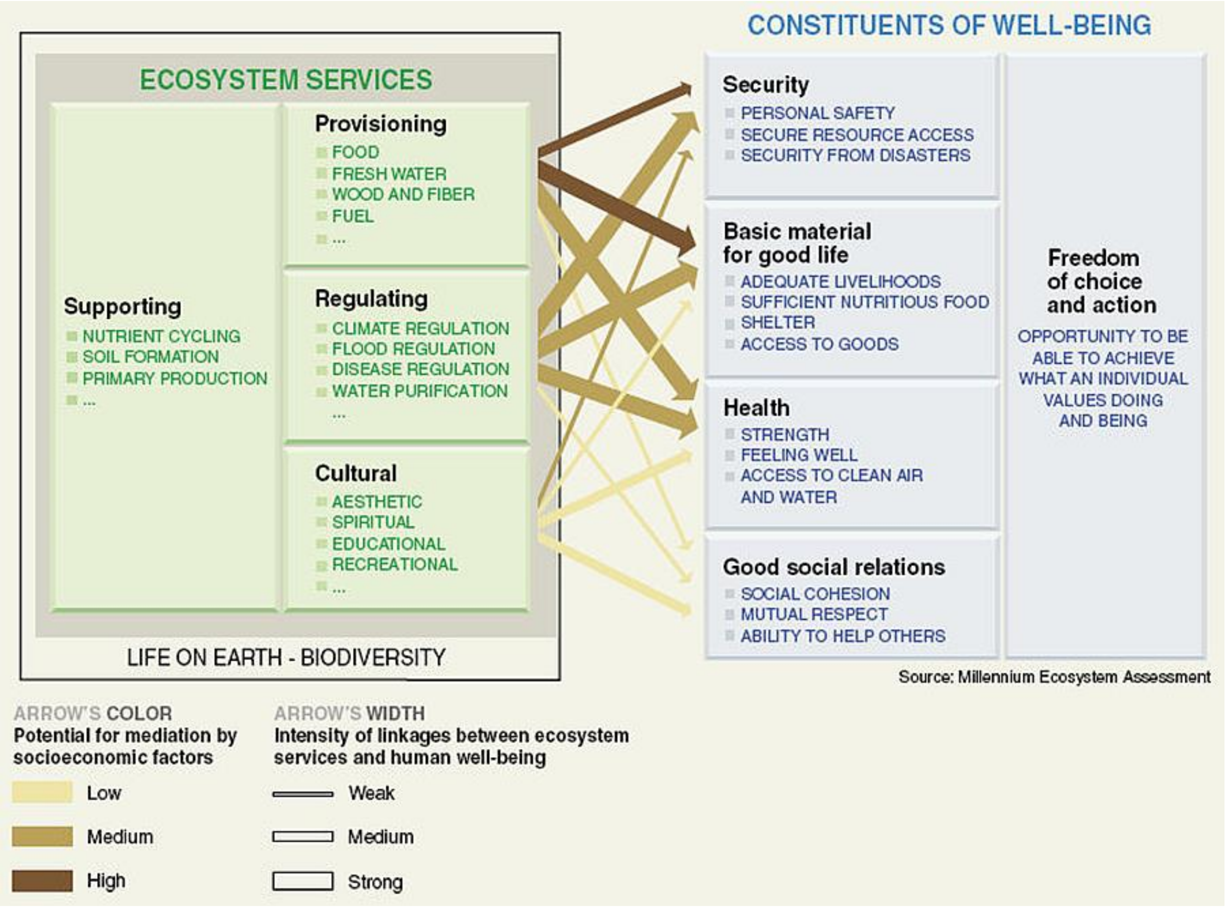


Figure A: Ecosystem services and their influences on constituents of human well-being. Modified after MEA, 2005.

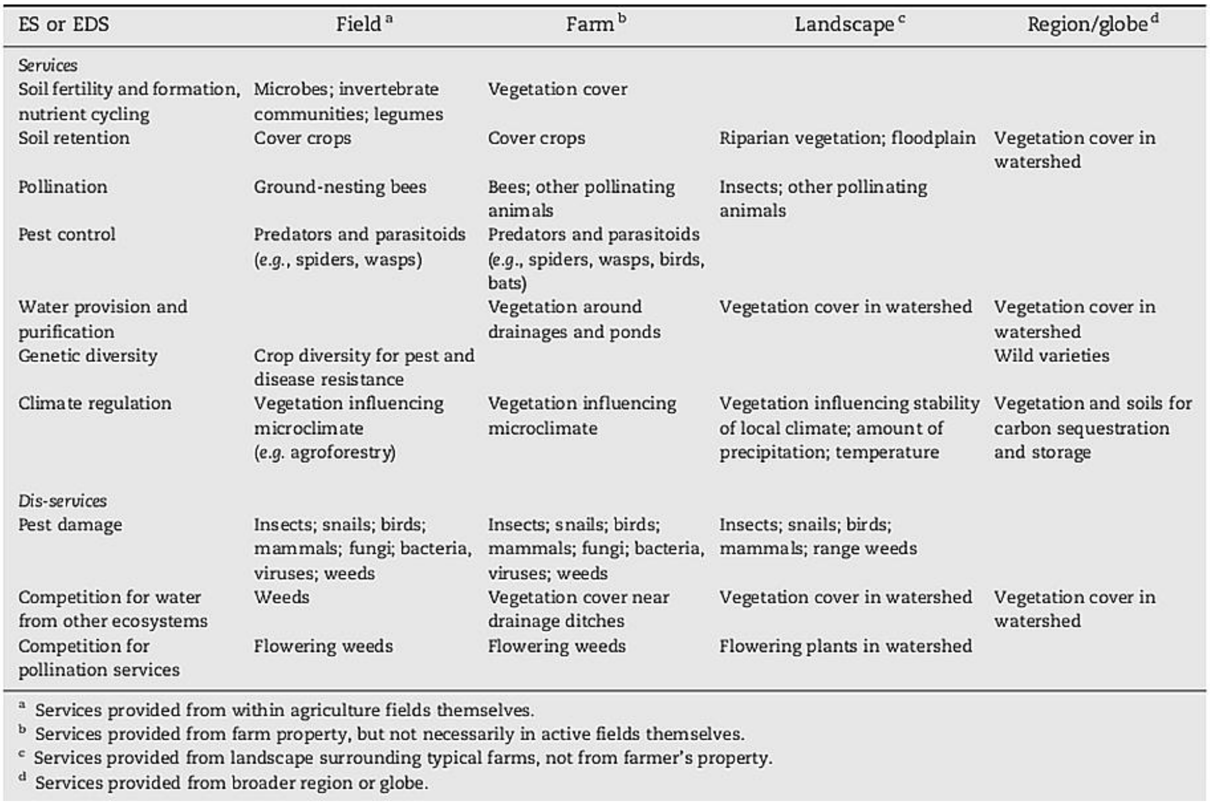
Ecosystem services have an estimated value of 125 to 145 trillion US $ per year and the loss of ecosystem services due to land use change between 1997 to 2011 is estimated 4.3 to 20.2 trillion US $ per year (Costanza *et al.*, 2014). This numbers can give an impression of the value of ecosystem services, but should be considered carefully since calculated values of ecosystem services may vary depending on the valuation method (Spangenberg & Settele, 2010). Lately ecosystem services have also been directly linked to sustainability since the notion of sustainability can provide a framework for using the ecosystem service concept as tool for considering and managing societal obligations to humans and the natural environment (Abson *et al.*, 2014). Abson *et al.* (2014) found that the ecosystem service concept can become a transformative tool for sustainability into transdisciplinary research, but since the ecosystem service concept has been promoted as a management tool, there is a need to more fully consider the role of normative knowledge in both the conceptualization of ecosystem services as a scientific concept and as a means of guiding the enhancement of both, systems knowledge and transformative knowledge.

Ecosystem services, ecosystem dis-services and their influence on agriculture

One important ecosystem service is natural biological pest control by wild vertebrates and invertebrates. These natural pest control services are freely available without causing costs like pesticides, that might be ineffective (Bianchi *et al.*, 2006; Motzke *et al.*, 2013). It is increasingly acknowledged that beneficial insects (naturally available bio-control agents from nature, hereafter referred to as bio-control agents) provide valuable services and the interest in developing strategies to conserve them is growing (Bianchi *et al.*, 2006; Kremen & Chaplin-Kramer, 2007). Natural habitats support bio-control agents, by providing habitats and resources over an entire season (Dennis & Fry, 1992; Thies & Tscharntke, 1999; Bianchi *et al.*, 2006). These bio-control agents often move from natural habitats to agricultural fields to temporally access prey resources concurrently providing natural pest control. Therefore, crop fields with a higher percentage of natural habitats in their surrounding landscape can experience low pest abundance through high pest control (Veres *et al.*, 2013).

Natural and semi-natural habitats are known to be important for beneficial organisms, providing ecosystem services like natural pest control and pollination. Hence, habitat and biodiversity loss caused by agricultural intensification can negatively influence agro-ecosystem services (Tscharntke *et al.*, 2005) and have negative impacts on human well-being (Díaz *et al.*, 2006).

Table A: The main ecosystem services and ecosystem dis-services to agriculture, where they can be found and who are the suppliers. Modified after Zhang et. al., 2007.



ES or EDS	Field[a]	Farm[b]	Landscape[c]	Region/globe[d]
Services				
Soil fertility and formation, nutrient cycling	Microbes; invertebrate communities; legumes	Vegetation cover		
Soil retention	Cover crops	Cover crops	Riparian vegetation; floodplain	Vegetation cover in watershed
Pollination	Ground-nesting bees	Bees; other pollinating animals	Insects; other pollinating animals	
Pest control	Predators and parasitoids (*e.g.*, spiders, wasps)	Predators and parasitoids (*e.g.*, spiders, wasps, birds, bats)		
Water provision and purification		Vegetation around drainages and ponds	Vegetation cover in watershed	Vegetation cover in watershed
Genetic diversity	Crop diversity for pest and disease resistance			Wild varieties
Climate regulation	Vegetation influencing microclimate (*e.g.* agroforestry)	Vegetation influencing microclimate	Vegetation influencing stability of local climate; amount of precipitation; temperature	Vegetation and soils for carbon sequestration and storage
Dis-services				
Pest damage	Insects; snails; birds; mammals; fungi; bacteria, viruses; weeds	Insects; snails; birds; mammals; fungi; bacteria, viruses; weeds	Insects; snails; birds; mammals; range weeds	
Competition for water from other ecosystems	Weeds	Vegetation cover near drainage ditches	Vegetation cover in watershed	Vegetation cover in watershed
Competition for pollination services	Flowering weeds	Flowering weeds	Flowering plants in watershed	

[a] Services provided from within agriculture fields themselves.
[b] Services provided from farm property, but not necessarily in active fields themselves.
[c] Services provided from landscape surrounding typical farms, not from farmer's property.
[d] Services provided from broader region or globe.

Studies focusing on the positive effects of biodiversity on agricultural production often neglect the possible negative effects that may co-occur. Vice versa, if negative effects are known the positive effects are often not accounted for (Shapiro & Báldi, 2014). This creates an imbalance between accounting for benefits and damages that nature causes to societies (Shapiro & Báldi, 2014). Natural habitats can, besides their positive effects, promote organisms that have a negative effect on crop production either directly by consuming parts or whole crop plants (herbivores, frugivores, granivores) or indirectly by transmission of diseases (specifically, fungal, bacterial and viral diseases) (Dunn, 2010; Keesing *et al.*, 2010; Blitzer *et al.*, 2012). Crop pests decrease crop productivity and in the worst case can result in complete crop loss (Zhang *et al.*, 2007). These so termed ecosystem dis-services (Table A) are frequently overlooked (Ghazoul, 2007), but with the growing human demand for food (Hobbs, 2007; Dias, 2010; Godfray *et al.*, 2010), predation of crops by pest species is of vital concern.

It is well known that insect pests negatively influence crop production (Eilers and Klein, 2009; Cini et al., 2012; El-Wakeil and Volkmar, 2012) but also seed or fruit predation by vertebrates cause crop yield reductions (Moran & Keidar, 1993; Ahmad *et al.*, 2011; de Mey *et al.*, 2012).

For example, birds are found to be agricultural pests by feeding on crop seeds (Fig. B) like almond (Emlen, 1937), sunflower (Ahmad *et al.*, 2011), and rice (de Mey *et al.*, 2012).

Figure B: left side: Eurasian Jay (*Garrulus glandarius* L.) in a sunflower field perching on a sunflower head, right side: Eurasian Jay feeding on sunflower seeds. Photos by Noam Weiss.

Furthermore, non-crop plants can reduce agricultural productivity by competing for resources (Stoller *et al.*, 1987). Water consumed by wild plants can reduce water available to agricultural plants (van Wilgen *et al.*, 1998; Zavaleta, 2000) and competition for pollination between flowering weeds and non-crop plants can reduce crop yields (Free, 1993).

Ecosystem services and dis-services can be closely linked when involving interactions of different trophic levels, services and dis-services that can influence each other (Fig. C). Pest insects provide dis-services by destroying crops but their natural parasitoids provide a service by reducing numbers of pest insects (Schmidt *et al.*, 2003). For sustainable agricultural planning, combined studies of ecosystem services and dis-services and the effect of different habitats on these functions are necessary, and should ideally lead to useful management strategies in agricultural areas to support ecosystem services without increasing dis-services (Lavandero *et al.*, 2006; Isaacs *et al.*, 2009).

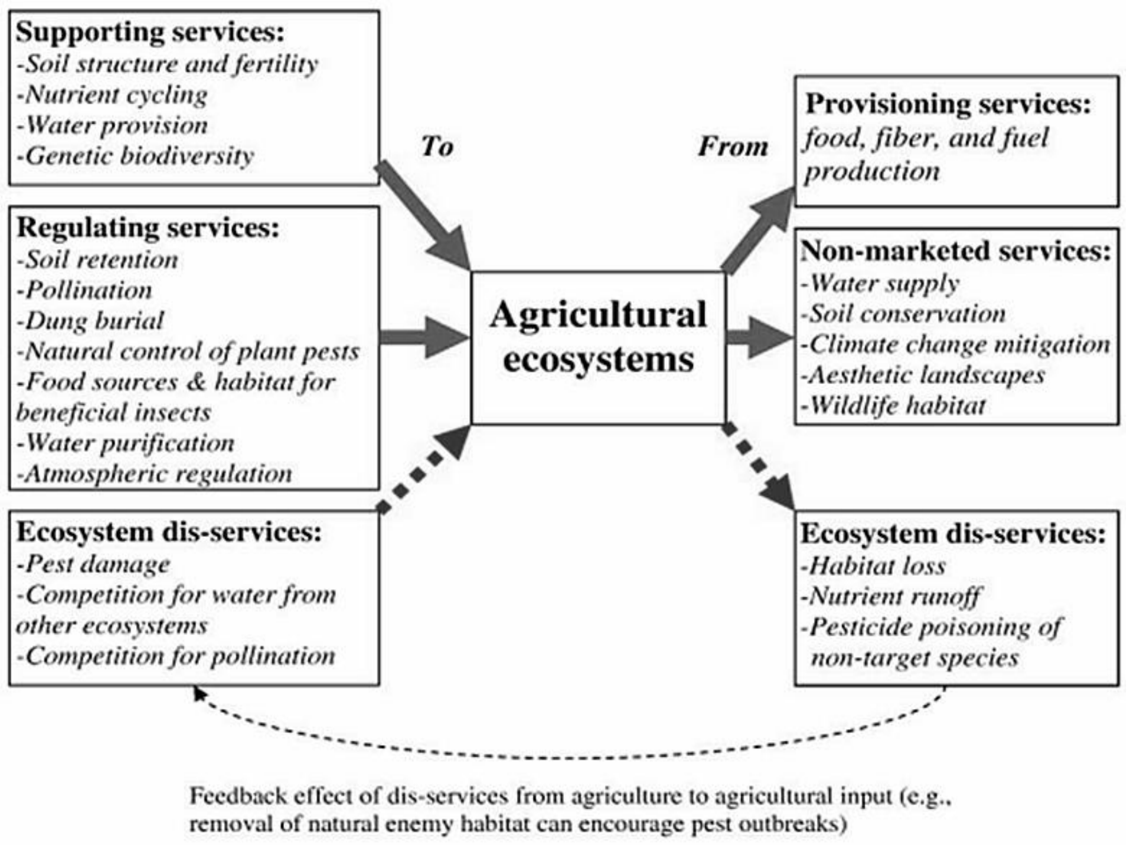


Figure C: Ecosystem services and dis-services to and from agriculture. Solid arrows indicate services, whereas dashed arrows indicate dis-services. Modified after Zhang et. al., 2007.

Some animal groups can provide services as well as dis-services, depending on the species, ecosystem or time. For example, insectivorous birds might have a negative effect on beneficial insects and frugivorous and granivorous birds might destroy large quantities of fruit or seed harvests (Linz *et al.*, 2011; de Mey *et al.*, 2012), thereby providing a dis-service.

However, insectivorous birds can provide an ecosystem service by reducing the negative impact of insect pests to agriculture such as the coffee berry borer in coffee plantations (Johnson *et al.*, 2010; Karp *et al.*, 2013) or caterpillars in apple orchards (Mols & Visser, 2007). Ecosystem services by granivorous birds are mostly unknown, but there is evidence that granivorous birds contribute to weed control by consuming large quantities of weed seeds (Kelly & McCallum, 1990) and also pest insects (Wenny *et al.*, 2011). Yet limited knowledge exists on the factors that influence seed predation by vertebrates. Largely unexplored are the relationships between natural and semi-natural habitats surrounding production areas with regards to abundance and richness of vertebrate crop predators and seed predation rates.

The relevance of this topic for Israel

In Israel, agriculture is an important source of income. Most of the consumed vegetables and fruits in Israel are also produced within the country. However export of fruits and vegetables to other countries is important for Israel economically (Tubi, 2005). Therefore, great effort is made to make agriculture as lucrative as possible. The prevention of pest outbreaks (e.g. insects, diseases) in agricultural fields is one of the main issues for farmers and the Ministry of Agriculture (personal communication with Yoav Motro, Ministry of Agriculture in Israel). Hence the monetary amounts that are currently invested by farmers to buy insecticides, fungicides etc. are extremely high (personal communication with farmers of the study area). But in recent years, the “organic movement” also arrived in Israel and increasing numbers of consumers aim to buy food that is produced without chemical pest suppressors. A company in Israel called bio bee was founded to match these needs (http://www.biobee.com/). Bio bee breeds different species of bio-control agents, mainly against pest insects, which can be applied directly in the fields and on plants of concern. This method of biological pest control is reported by farmers to be effective and the demand for more bio-control agents against other pests is growing. Furthermore, farmers are highly interested in gaining knowledge on how to enhance the surrounding of their fields to support naturally occurring bio-control agents (personal communication with the farmers). Unfortunately many pests still have to be controlled with chemical inputs, because no suitable agents have been found yet or breeding them commercially is just not feasible. This increases the costs of agricultural production by reducing yield and by the additional agro-chemical inputs (Ghazoul, 2007). One of the crops of Israel is the almond and one of its main pests is the almond wasp (*Eurytoma amygdalii* Enderlein). The larvae of the wasp are destroying large amounts of the almond harvest in Israel, by feeding on seeds before harvest. In spring the adult wasp lays an egg in an almond, which is just at the beginning of its development. The larva of the wasp grows in the almond shell, feeds on the seed and overwinters in the almond. The adult wasp emerges in the next spring to mate and lay new eggs (Plaut, 1971; Kouloussis & Katsoyannos, 1994). Infested almonds are not useable for the farmers and worse, if they remain on the trees after harvest, the next generation of almond wasps develops within them. Invertebrates which could be bio-control agents of the almond wasp have not been identified yet. However, seed eating birds and rodents, which live in the almond orchards or their surroundings, might break this circle by feeding on infested almonds and thus destroying the nut-destroying wasps. But whilst granivorous birds could act as bio-control agents after harvest, they can also act as a pest while feeding on healthy non-infested almonds before harvest. Birds are known to attack agricultural crops like almond (Emlen, 1937), sunflower, maize (Ahmad *et al.*, 2011; Linz *et al.*, 2011) and rice (de Mey *et al.*, 2012). In sunflower fields in Israel, birds are considered to be one of the main pests and farmers suffer high losses because of birds feeding on sunflower seeds (Nemtzov, 2003). Furthermore, farmers in Israel fear wildlife will spill over from natural habitats surrounding their fields to the crop plants (Batáry *et al.*, 2010; Kleijn *et al.*, 2011) and that this wildlife might act as pest. Scientific evidence for almond and sunflower in Israel on this matter is missing and the real impact of semi-natural and natural habitat on agriculture is unknown. Natural habitat in my study area contains open shrub land with different grasses, herbs and shrubs but no high trees; while semi-natural habitat is a mixture of shrub land with planted, mostly not native high trees (higher than 5 m) like eucalyptus species or planted forests of mostly different pine species.

To improve our knowledge about pests and bio-control agents (parasitoids, predators), how their abundances are connected to the surrounding of the fields and if the provisioning of services and dis-services changes along a landscape gradient and within the year, I conducted a series of studies in almond orchards and sunflower fields of the Judean Foothills in Israel. I investigated the influences of birds (Fig. D), rodents and invertebrates on almond and sunflower seed predation, if they act as pests or bio-control agents and the impact of the landscape (natural and semi-natural habitat) on services and dis-services.

Figure D: Bird data collection in an almond orchard. Photo by Jessica Schilde.

General approaches and main research questions

The overall goals of my dissertation were to study the effects of landscape context on vertebrate-invertebrate-plant interactions and to explore the potential functional consequences of these effects on crop production. Since the results of my study were meant to improve our knowledge of the sustainable use of the ecosystem service of natural pest control and how to avoid the dis-service of seed predation in agro-ecosystems, I applied the following approaches. One approach included real-world field experiments where I collected data about bird and rodent abundances and species richness in almond orchards and sunflower fields in different seasons of the year over several years, by using observation and trapping methods. I collected invertebrate data by collection and storing almonds and seed predation rates in sunflower by counting absent seeds. To add experimental evidence from controlled environments about seed predation, I conducted an exclusion experiment in the almond orchards excluding birds and / or rodents from almond access (Fig. E).

Figure E: Exclusion experiment in almond orchard. Black polygal wrapping on trunk against rodents, bird net covering a branch against birds and red and white ties are marking the tree. Photo by J. Schäckermann.

My research included two aspects of functional biodiversity:

1) Ecological understanding of factors that determine diversity patterns of pests and bio-control agents by:

- Identification of pests and bio-control agents and habitats used.
- Measuring changes in species richness, abundance and composition in almond orchards and sunflower fields, along a gradient of natural and semi-natural habitat towards man-made habitats in the surrounding of the orchards and fields.

2) Finding functional consequences of changing community composition of pests and bio-control agents by:

- Measuring seed predation caused by vertebrates and invertebrates.
- Measuring vertebrate and invertebrate pest control services provided by bio-control agents.
- Evaluating if ecosystem dis-services can turn to services for agricultural production (seed predation versus removal of overwintering nuts by vertebrates).
- Evaluating interactions between services and dis-services and their potential combined effects on crop production.

Specifically I addressed the following research questions:

1) Which species of pests and bio-control agents (predators, parasitoids) and their hosts inhabit almond orchards and sunflower fields and their surroundings? What are their abundances?
    a. For vertebrate species?
    b. For invertebrate species?
2) How does a gradient of decreasing natural and semi-natural habitats influence
    a. Vertebrate species?
    b. Dis-services?
    c. Invertebrate species?
3)
    a. Do services / dis-services interact?
    b. Can dis-services turn into services when considering different seasons?
    c. What are the predictors of disservices?

Summary of aims and methods

Chapter I aims to answer questions **(1a), (2a, b).** The motivation for this study was to find scientific evidence for the claim of farmers that vertebrates, like birds and rodents, have a severe negative impact on almond and sunflower yields in Israel. Furthermore, I investigated if the fear of farmers, that natural and semi-natural habitats surrounding their fields attract higher numbers of vertebrate seed predators was justified. Therefore I studied which vertebrates have a negative impact on crop seed predation and if their impact is related to the percentage of natural and semi-natural habitat (landscape gradient) in the surrounding of the fields. In 2010 I selected 20 almond and 20 sunflower study sites with varying percentages of natural and semi-natural habitat in their surroundings within a 1000 m radius. To answer questions **(1a)** and **(2a)** I observed birds, trapped rodents, counted seeds, noted feeding marks and related these to the landscape gradient. In the almond orchards I conducted an exclusion experiment to answer question **(2b)** and I determined the influence of birds and rodents on seed predation. Therefore, I physically excluded birds, rodents, birds and rodents in combination and set up a control without vertebrate exclusion.

Chapter II aims to answer question **(1b)**, **(2b, c)**, **(3a, b)**. I investigated if the main pest to almond in Israel, the almond wasp, is influenced by the surrounding natural or semi-natural habitats and / or if these habitats influence parasitoids of the almond wasp. Additionally, the role of granivorous birds in almond orchards was surveyed and their connections to surrounding habitats were investigated. I chose 17 almond orchards with varying percentages of surrounding natural and semi-natural habitat. To answer question **(1b)** and **(2b, c)** I harvested almonds and identified invertebrate pests and parasitoids in almonds. To answer question **(3a)** I looked for relations between the pests and parasitoids. To answer question **(3b)** I observed birds and identified bird feeding marks on leftover nuts form the previous year and on nuts from the recent year and studied their impact on harvestable nuts before harvest (recent year, dis-service) and on leftover nuts from the previous year which are known to be breeding habitats for the almond wasp (service).

Chapter III addresses questions **(2b)** and **(3c)**. I studied how birds as seed predators of sunflowers and therefore pests are influenced by the presence, abundance and distance of high trees which function as bird perches. I suspected that high introduced, non-native trees have a negative influence on harvest since they might attract birds, but scientific evidence was missing. I chose a single sunflower field in 2010 for a field scale study and 20 sunflower fields in 2012 for a landscape scale study. I assessed seed predation across the whole field in 2010 with help of a grid system and on margin and interior sampling points in all fields in 2012. I furthermore measured distances to the next high tree from each sampling point and measured the percentage of high trees and natural habitat in the surrounding of the field. I then related the seed predation with the different landscape variables.

Article overview

(In accordance with the guideline for cumulative dissertations in Sustainability Science [January 2012], in the following termed “the guideline”)

Overview of articles included in this cumulative Ph.D. thesis

Title of Ph.D. thesis: Vertebrates and insects as pest and bio-control agents in agricultural landscapes of the Judean Foothills in Israel

Papers included:

[1] Schäckermann, J., Mandelik, Y., Weiss, N., Wehrden, H. von & Klein, A.-M. (2015a) Natural habitat does not mediate vertebrate seed predation as an ecosystem dis-service to agriculture. Journal of Applied Ecology, 52, 291-299. doi: 10.1111/1365–2664.12402.

[2] Schäckermann, J., Pufal, G., Mandelik, Y. & Klein, A.-M. (2015b) Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape. Ecological Entomology, 40, 12-21. doi: 10.1111/een.12244.

[3] Schäckermann, J., Weiss, N., Wehrden, H. von & Klein, A.-M. (2014) High trees increase sunflower seed predation by birds in an agricultural landscape of Israel. Frontiers in Ecology and Evolution, 2, doi: 10.3389/fevo.2014.00035.

Authors' contributions to the articles and articles publication status (according to §16 of the guideline):

Article #	**Short title**	**Specific contributions of all authors**	**Author status**	**Weighting factor**	**Publication status**	**Conference contributions**
[1]	Natural habitat does not mediate seed predation	JS: literature review, JS, NW: data collection JS, HW: data analysis JS, AMK, YM, HW: question of the paper, writing of the paper JS, AMK, YM: research design	Co-author with predominant contribution	1.0	Published in Journal of Applied Ecology (IF= 4,754)	GfÖ 2012 ISEES 2013
[2]	Agro-ecosystem services and dis-services are differentially influenced by the landscape	JS: literature review, data collection JS, GP: data analysis JS, AMK, YM, GP: question of the paper, writing of the paper JS, AMK, YM: research design	Co-author with predominant contribution	1.0	Published in Ecological Entomology (IF= 1,967)	
[3]	High trees increase seed predation by birds	JS: literature review, data collection JS, HW: data analysis JS, AMK, HW, NW: question of the paper, writing of the paper JS, AMK, NW: research design	Co-author with predominant contribution	1.0	Published in Frontiers in Ecology and Evolution (IF= not yet available)	ICCB 2011 GfÖ 2011
			Sum:	3.0		

Publication status

IF=ISI Web of Science - Impact Factor (2013)

Explanations

Specific contributions of all authors

JS = Jessica Schäckermann, AMK = Alexandra-Maria Klein, HW = Henrik von Wehrden, YM = Yael Mandelik, GP = Gesine Pufal, NW = Noam Weiss

Author status

According to §12b of the guideline:

Single author [Allein-Autorenschaft] = Own contribution amounts to 100%.

Co-author with predominant contribution [Überwiegender Anteil] = Own contribution is greater than the individual share of all other co-authors and is at least 35%.

Co-author with equal contribution [Gleicher Anteil] = (1) own contribution is as high as the share of other co-authors, (2) no other co-author has a contribution higher than the own contribution, and (3) the own contribution is at least 25%.

Co-author with important contribution [Wichtiger Anteil] = own contribution is at least 25%, but is insufficient to qualify as single authorship, predominant or equal contribution.

Co-author with small contribution [Geringer Anteil] = own contribution is less than 20%.

Weighting factor

According to §14 of the guideline:

Single author [Allein-Autorenschaft]	1.0
Co-author with predominant contribution [Überwiegender Anteil]	1.0
Co-author with equal contribution [Gleicher Anteil]	1.0
Co-author with important contribution [Wichtiger Anteil]	0.5
Co-author with small contribution [Geringer Anteil]	0

Conference contributions (acronym, society, date, venue, website)

GfÖ 2011, Annual Meeting of the Ecological Society of Germany, Switzerland and Austria, 05. – 09.09.2011, Oldenburg (Germany), *www.gfoe-2011.de*. Talk.

GfÖ 2012, Annual Meeting of the Ecological Society of Germany, Switzerland and Austria, 10. – 14.09.2012, Lüneburg (Germany), *www.gfoe-2012.de*. Talk.

ICCB 2011. Biennial Meeting of the Society for Conservation Biology – A global community of conservation professionals.05-09.12.2011, Auckland (New Zealand), *www.conbio.org/images/content_conferences/ICCB2011_Abstracts_Electronic.pdf*. Talk.

ISEES 2013, Annual meeting of the Israel Society of Ecology and Environmental Sciences. 07-09.10.2013, Rehovot (Israel). *www.isees.org.il/DMPageEng.aspx?MenuId=47&ItemId=1256&mytabsmenu=xxx*. Talk.

Declaration (according to §16 of the guideline)

I avouch that all information given in this appendix is true in each instance and overall.

Jessica Schäckermann

Chapter I

Natural habitat does not mediate vertebrate seed predation as an ecosystem dis-service to agriculture

Jessica Schäckermann, Yael Mandelik, Noam Weiss, Henrik von Wehrden & Alexandra-Maria Klein

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Natural habitat does not mediate vertebrate seed predation as an ecosystem dis-service to agriculture

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Summary

1. Spillover of beneficial organisms from natural habitats to croplands can improve agro-ecosystem services, but wildlife can also negatively influence agricultural production. When managing agricultural landscapes to conserve biodiversity, we need to understand whether the availability of natural habitats increases ecosystem dis-services such as vertebrate seed predation to avoid risking higher costs than benefits.

2. We studied whether vertebrates and their impact in crop seed predation are related to the percentage of natural (chaparral) and semi-natural habitat (planted forest with native and exotic trees) in an agricultural landscape of Israel. We selected 20 almond and 20 sunflower study sites within a landscape with varying percentages of natural (0–61%) and semi-natural (0–70%) habitats within a 1000 m radius of their surroundings. We observed birds, trapped rodents (in almond), counted seeds and noted feeding marks to obtain seed predation rates, at each site. Within the almond crops, we physically excluded birds, rodents and both to determine their relative and combined influence on seed predation.

3. Neither vertebrate abundance nor species richness was influenced by the percentage of natural habitat. However, bird species richness increased with increasing percentage of semi-natural habitat.

4. Seed predation across both crops was not influenced by natural or semi-natural habitat but increased significantly with increasing abundance and species richness of birds. This was also reflected by the exclusions of birds, vertebrates and both to the almond crop, leading to lowest seed predation when both groups were excluded.

5. *Synthesis and applications*. Natural or semi-natural habitat did not influence the agro-ecosystem dis-service of seed predation by birds and rodents. Policymakers should consider promoting agri-environment schemes that include the conservation of natural habitats and the management of semi-natural habitats adjacent to cropland to enhance agro-ecosystem services meditated by beneficial organisms such as natural pest enemies and pollinators without fearing increased vertebrate seed predation. In order to provide more detailed management recommendations tackling the reduction of vertebrate dis-services, their feeding behaviour, metabolic needs, behaviour patterns and local abundances should be taken into account.

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Key-words: almonds, birds, chaparral, ecosystem services, Israel, landscape ecology, rodents, sunflowers

Introduction

The global demands on ecosystem services in agricultural landscapes increase in an effort to mitigate the increasing yield gap in agricultural production (Bommarco, Kleijn & Potts 2013) caused by the growing human population (Godfray *et al*. 2010). The challenge is to increase multiple agro-ecosystem services simultaneously without promoting dis-services to agriculture (Zhang *et al*. 2007; Boreux *et al*. 2013). Most studies focus on the positive effects of biodiversity on agricultural production while largely neglecting the possible negative effects that may co-occur. Limited knowledge exists on negative impacts of wildlife conservation in agricultural landscapes on crop yield (Eilers *et al*. 2011; Ango *et al*. 2014). In order to meet production demands while conserving biodiversity in agricultural landscapes, we need to understand negative influences caused by wildlife to crop production, and how they are mediated.

Natural and semi-natural habitats are important for organisms that are beneficial to agriculture, providing ecosystem services such as biological pest control and pollination (Bianchi, Booij & Tscharntke 2006; Mandelik *et al*. 2012). These habitats provide food, nesting sites and refuges for natural pest enemies (Thies & Tscharntke 1999; Bianchi, Booij & Tscharntke 2006) and for pollinators (Mandelik *et al*. 2012). Therefore, crops surrounded with a higher percentage of natural and semi-natural habitats experience higher rates of ecosystem services than crops surrounded with lower proportions of these habitats (Veres *et al*. 2011). In addition to the positive effects, natural habitats also promote negative effects by, for example, increasing wildlife animal populations consuming crop plants, competing for limited resources such as water and nutrients, or by transmitting diseases (Dunn 2010; Keesing *et al*. 2010; Blitzer *et al*. 2012; Martin *et al*. 2013). These negative effects increase the costs of agricultural production by reducing yield and/or by requiring additional agro-chemical inputs (Ghazoul 2007).

Crop seed predation is a global concern that may detrimentally affect food security (Losey & Vaughan 2006). Invertebrates are responsible for high levels of seed predation in cropland around the world (Andersen 1988; Cummings, Alexander & Snow 1999). Much knowledge accumulated on the factors that regulate their activity, how to control their populations and detrimental activity (Bianchi, Booij & Tscharntke 2006). However, in many agricultural landscapes, vertebrates are abundant and often found active within crops (Radtke & Dieter 2011; Werner *et al*. 2011; De Mey, Demont & Diagne 2012). Yet limited knowledge exists on the factors that affect seed predation by vertebrates. Largely unexplored are the relationships between natural and semi-natural habitats surrounding production areas with abundance and richness of vertebrate crop predators and seed predation rates. Establishing these links is fundamental for developing management strategies within agricultural areas supporting beneficial organisms without increasing pest pressures (Isaacs *et al*. 2009; Martin *et al*. 2013). If seed predation occurs in the pre-dispersal phase, it can greatly decrease yield. Therefore, detailed knowledge about this temporal aspect is crucial for management strategies.

In an agricultural landscape in central Israel, we studied two model crops, almond and sunflower, to test how the abundance and species richness of birds, rodents and their seed predation are related to the percentage of natural and of semi-natural habitat in the landscape. In Israel, 27 mammal, 32 bird and two reptile species are described as agricultural pests (Moran & Keidar 1993), yet there is no knowledge on how their abundance and species richness influence crop seed predation in relation to the surrounding landscape. We additionally tested the individual and combined influences of rodents and birds on crop seed predation. Since interspecific interactions of different functional groups (for example behavioural interactions between predatory and granivorous birds) can indirectly influence ecosystem services such as pest control and pollination (Brittain *et al*. 2013; Martin *et al*. 2013), we tested for the influences of all and of only granivorous birds on seed predation. Our study aims to contribute to the discussion of conserving natural and managing semi-natural habitat patches within agricultural landscapes. If birds and rodents perform a substantial level of seed predation and if they are promoted by natural or semi-natural habitats in the agricultural landscape, promoting management of those habitats to increase ecosystem services needs to be carefully considered by policymakers.

Materials and methods

STUDY AREA AND LANDSCAPE CHARACTERIZATION

The study was conducted in the Judean Foothills, a unique transient ecosystem at the interface of the humid Mediterranean ecosystem to its north and the arid ecosystem to its south (Weizel, Polak & Cohen 1978) and approximately 30 km south-west of Jerusalem. The area is characterized by a mosaic of different land-use types, natural habitats (shrubland of variable densities and succession stages, generally lacking trees higher than 5 m), crops (annual and perennial crops), semi-natural habitats (planted forests comprising mainly pines of the species *Pinus halepensis* Miller, *Pinus pinea* L., *Pinus brutia* Tenore and to a lesser extent pines mixed with planted native broad-leave species), some rural settlements and a few urban and industrial areas (Weizel, Polak & Cohen 1978; Fig. 1).

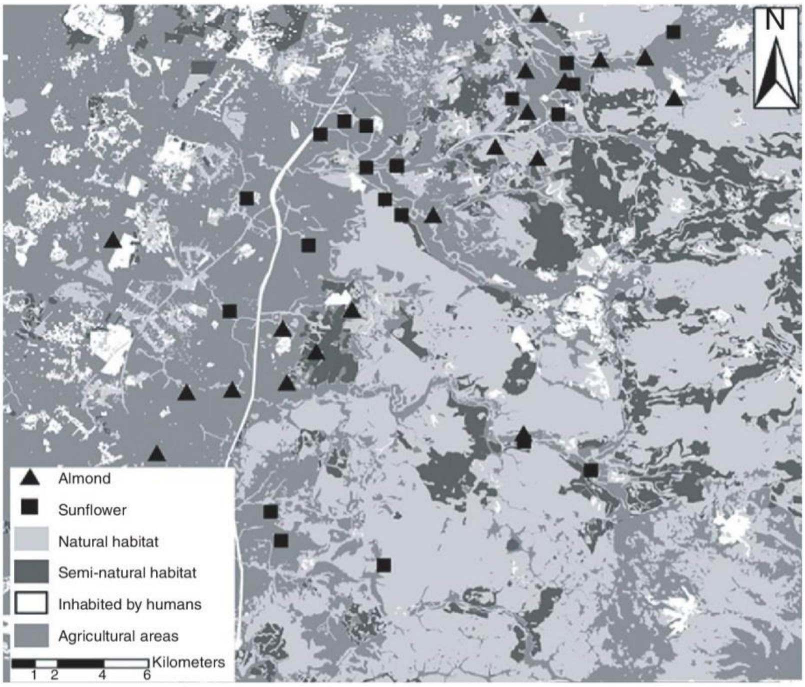

Fig. 1. Study area, land-use types and the distribution of the almond (Δ) and sunflower (□) study sites in the Judean foothills of Israel. One almond crop is not shown as it was located 15 km from the most south-west located almond study site.

STUDY CROPS

The almond tree *Prunus dulcis* Miller is a small deciduous tree, 4–10 m tall and with a trunk of up to 30 cm in diameter. Almond flowers in February and early March and is harvested between July and September. In 2010, an area of 4000–4500 ha was cultivated with almond in Israel (Ministry of Agriculture, from now on referred to as MOA). The most common almond varieties in the study area are Um Al Fahm, Kohav, Kohva, Ne Plus Ultra and Mem Dalet.

The main pest species reported by MOA are the almond wasp *Eurytoma amygdali* Enderlein, the Locust Bean Moth *Ectomyelois ceratoniae* Zeller and the Peach Twig Borer *Anarsia lineatella* Zeller. Birds in general are described as almond pests in the study region (Nemtzov 2003). We selected orchards that were similarly managed, that is trees of the dominant local varieties, planted at least three years prior to data collection, similar insecticide application (Kotanyon, Dorsban, Smash or Simbush against the locus bean moth and Metasistocks, Levaicid or Rogor against the almond wasp; applied twice a season), and drip irrigated from March until September. The size of the orchards varied between 11 and 112 ha.

The sunflower crop *Helianthus annuus* L. is an annual herb grown in Israel for seed production. It is sowed in March and harvested between July and September. In 2010, an area of around 7000 ha was cultivated with sunflowers in Israel (MOA). We interviewed farmers for information about pest species in the study area; rose-ringed-parakeet *Psittacula krameri* L. was described as a major pest consuming seeds from the sunflower heads. Other sunflower pests are various granivorous bird species, the Middle East blind mole rat *Spalax ehrenbergi* Nehring, known to destroy the roots of the sunflower plants and the cotton bollworm *Helicoverpa armigera* Hübner, with larvae developing in the flower heads facilitating fungal infections (Heth 1991). We selected sunflower fields that were similarly managed, that is using three hybrid seed production varieties (Shelly, Shemesh, Dalet Yod 3), treated with the fungicide Bayfidan and with the insecticide Endosulfan once during bloom and irrigated with a drip system from April/May until June/July. Sunflower study sites were alternated with cotton, chickpea, watermelon, corn or spring wheat within the next season or with winter wheat in double cropping systems. The size of fields varied between 5 and 44 ha.

STUDY SITE SELECTION

We selected 20 almond orchards and 20 sunflower fields (from now on referred to as crops) as study sites (Fig. 1), and we located two sampling points per site: (i) at the crop edge (sunflower: the outer most crop plant up to 5 m inside, almond: the outer most row of trees) and (ii) at the interior of the crop 150 m from the edge, to test whether vertebrates prefer to forage at the edge or also move to the interior. We used the edge closest to natural habitat, flowering strip or planted forest (proximity to natural habitat was given priority when more options were available). Minimal distance between the edge sampling points of different sites of each crop was 1000 m to minimize the risk of overlapping bird and rodent communities and to minimize spatial autocorrelation. Two almond and eight sunflower study sites were too narrow to allow an interior sampling point; therefore, data were only collected at edges. We measured geographic coordinates at edge sampling points using GIS (ArcGIS, version 9.2.; ESRI, Redlands, CA, USA). From these sampling points at crop edges, we used 1000 m radii to calculate the percentages of (i) natural habitat and (ii) semi-natural habitats for each study site. A radius of 1000 m was shown to be an appropriate scale in other vertebrate landscape studies (e.g. Eilers & Klein 2009; Guerrero *et al.* 2012). Land cover data were obtained from the archive of the Hebrew University of Jerusalem. For each crop species, study sites were selected to comprise a gradient in the percentage of natural habitat of the surrounding landscapes, ranging from zero to 51% for almond and from zero to 66% for sunflower. We additionally calculated a second gradient in the percentage of surrounding semi-natural habitat ranging from zero to 70% for almond and zero to 48% for sunflower. Crops were selected to avoid a correlation of natural and semi-natural habitat surrounding the crop systems. For correlations between explanatory landscape variables, see Table S1 (Supporting information).

BIRD OBSERVATIONS

Birds were only observed when crop seeds were attractive to them in order to correlate bird abundance and species richness with crop seed predation. Observations were done twice per study site, in April and May 2010 in almond and in May and June 2010 in sunflower. The fixed radius point count method was used to assess bird communities (Bibby, Burges & Hill 1992). This fixed distance sampling technique requires only a small area for bird surveys within patches (Petit *et al.* 1995). For each study site, we observed the two sampling points with an observation radius of 50 m each by using binoculars (Swarovski, Habicht 10X42WB). Observation duration of one point count was 5 min per sampling point for each of the two sampling days per study site (total of 20 min per study site for sites with an interior sampling point and 10 min for sites without an interior sampling point). Observations took place in the morning between 05:00 and 09:00 am, with temperatures between 10 and 23 °C, covering the period of highest bird activity. Observation time was altered across study sites to minimize temporal bias (Perfecto *et al.* 2003). Observation started 3 min after the observer was settled to allow the birds to return to their normal activity. Bird species and numbers were counted. Flying birds that did not land in the observation radius were excluded. In addition to visual counts, bird voices were recorded for 5 min for each point count to confirm species identification with a ZOOM handy recorder H2 on a SD card and voice tapes were analysed (windows XP media player; Microsoft Corporation, Redmond, WA, USA).

RODENT TRAPPING

Rodents were trapped for three nights from April to May 2010 in almond, corresponding to the time of year where almonds are vulnerable to seed predation. Rodents were trapped at each of the two sampling points in each site using 15 baited Sherman live traps (H.B. Sherman Traps, www.shermantraps.com) placed in two transects at a distance of 1–2 m (distance between transects was 3–5 m) and baited with peanut snacks, carrot and supplied with cotton balls (to protect from hypothermia). Each study site was sampled for a total of 90 traps during the entire trapping period. All rodent species in the study region are nocturnal (Mendelssohn & Yom-Tov 1993), and we therefore opened the traps shortly before dusk between 04:00 and 05:00 pm. We inspected the traps in the morning between 05:00 and 09:00 am. Trapped rodents were transferred into a net and marked on the nape with colour codes using lacquer pens to identify retrapped individuals, which were excluded from the analysis. Trapped rodents were identified to species level in the field and released in the respective study site directly after marking. Prior to the experiment, we tested the marking on house rats *Rattus norwegicus* Berkenhout and Tristram's jird *Meriones tristrami* Thomas under field conditions and observed that the markings hold for at least four days. Rodents do not climb sunflower plants and do not act as pre-dispersal but as post-dispersal seed predators only (J. Schäckermann, personal observation); we therefore did not collect rodent data in sunflower.

ESTIMATING SEED PREDATION

Percentage of seed predation was assessed in 2010 and 2011 with exclusion experiments in ten of the 20 almond crops as this experiment was time-consuming and had to be conducted in a narrow time window. Five crops were surrounded by a high percentage (>20% in a 1000 m radius) and five crops by a low percentage (<5% in a 1000 m radius) of natural habitat. In each crop, we randomly chose 16 trees, eight at each sampling point and marked a single branch on each of the trees with coloured ties to assess seed predation. Selected branches were at least 30 cm above ground to avoid rodent climbing and at least 60 cm long to ensure fruit set. At each sampling point, we used four treatments, two trees per treatment: (i) rodent exclusion; we covered the trunk of two trees with smooth plastic tape (polygal 54 cm wide) to prevent rodents climbing on the tree (laboratory test trial with house rats and Tristram′s jird indicate high effectiveness), (ii) bird exclusion; we covered the marked branch of two trees each with bird netting (intermas gardening Birdnet, www.intermas.com) to prevent birds from accessing the almonds on the covered branches, (iii) bird and rodent exclusion (trunk cover and bird netting as described) and (iv) non-treated control trees with free access to almonds. Bird exclusion using nylon netting is commonly used in other studies (Greenberg *et al.* 2000) and does not restrict access to invertebrates. We counted almonds at the beginning of the experiment in early May and at the end of the experiment in mid to end July prior to commercial harvest, and the difference was used to calculate the percentage of seed predation. This is the period where almonds are most attractive to seed predators (Emlen 1937).

Since birds were considered the only pre-dispersal vertebrate seed predators on sunflowers, we assessed overall seed predation. In 2010, we estimated sunflower seed predation by counting the number of missing seeds in 50 randomly chosen sunflower heads at both sampling points in each study site. Seeds can be missing through (i) seed predation by birds, (ii) touching of neighbouring flower heads (the only observed way of mechanical removal) with seeds falling to the ground and (iii) no seed development. Seeds removed by predators can be distinguished from non-developed seeds because only seeds removed after full development leave 'pockets' (palea adhered to the anthodium), while these 'pockets' are missing when unfertilized florets do not develop seeds (Schäckermann *et al.* 2014). Seed predation per flower head was estimated by calculating the proportion of the missing seeds (excluding non-developed and fallen seeds) out of the total number of seeds.

STATISTICAL ANALYSES

Statistical analyses were conducted using R (R Development Core Team 2010, version 2.12.0). Prior to the main statistical analyses we tested the effect of year on the bird and seed predation data in a simple linear model and as a fixed factor in the generalized linear model but did not find any significant effect. Furthermore we performed generalized linear mixed models (GLMM) with crop identity as fixed factor and study site as random factor to test for differences between the two crop systems with respect to abundance and species richness of all birds and of granivorous birds. All bird response variables did not differ between almond and sunflower crops (Table S2). We therefore pooled the data of the two crop systems and included crop identity (almond, sunflower) as random effect in the models. As only two rodents were caught in almonds we did not further analyse the abundance and richness of rodents.

Correlations between explanatory variables were tested with a correlation matrix (for vertebrate variables see Table S3, Supporting information, and for study site and landscape variables see Table S1, Supporting information).

We subsequently analysed the effects on seed predation and vertebrate variables across both crops (observation, trapping and seed count data) with GLMM and PQL in all models. Vertebrate variables included abundance and species richness of all birds and of granivorous birds only and were always analysed separately as response variable as well as explanatory variable. We then analysed the relative and combined effects of birds and rodents on seed predation in almond (exclusion experiment) with GLMM and applied penalized quasi-likelihood (PQL) (see details on model specifications and variables in Table 1). As this experiment was conducted in 2010 and 2011, we also ran the same model for both years separately. Results separated per year were similar to the pooled data of both years, and we therefore present the pooled data only. Model specifications with random effects, explanatory variables and the error distribution are given in Table 1.

Results

THE EFFECT OF LANDSCAPE VARIABLES ON WILDLIFE VERTEBRATES AND SEED PREDATION

In almond, we observed a total of 795 bird individuals of 32 species including 357 individuals (45%) and 11 species (34%) of granivorous birds. In sunflower, we observed 620 bird individuals of 33 species including 422 individuals (68%) of 13 species (39%) of granivorous birds. We trapped only one Tristram's jird and one house mouse *Mus musculus* L. in almond (Table S4, Supporting information).

Abundance of all birds and of granivorous birds was not significantly correlated with increasing percentage of natural habitat (Table 2). Bird species richness increased with increasing percentage of semi-natural habitat. The number of bird species, but not of granivorous bird species, was significantly higher at the edge compared to the interior of the study sites. Abundance of all birds and granivorous birds was not significantly different between the edge and the interior of the study sites (Table 2). None of the bird response variables were related to the age or size of the study sites (data not shown).

The percentage of seed predation was not related to the percentage of the surrounding natural or semi-natural habitat (natural: $t = -0{\cdot}2145$, $P = 0{\cdot}8318$; semi-natural: $t = 0{\cdot}3413$, $P = 0{\cdot}7356$). Seed predation was significantly higher in the edge than in the interior of the study sites ($t = -3{\cdot}1233$, $P = 0{\cdot}0042$).

VERTEBRATES AS DRIVERS FOR SEED PREDATION

The percentage of seed predation across the two crop species increased with increasing abundance and species richness of all birds and of granivorous birds (Fig. 2a–d, Table 3). In the vertebrate exclusion experiments in almond, compared to the exclusion of both birds and rodents, percentage of seed predation increased significantly when rodents were excluded but birds had access to almonds, birds were excluded and rodents had access to almonds and birds and rodents had access to almonds (Fig. 3).

Discussion

THE INFLUENCE OF NATURAL AND SEMI-NATURAL HABITATS ON WILDLIFE VERTEBRATES AND CROP SEED PREDATION

We found an effect of semi-natural habitat on vertebrates (bird species richness), but did not find any effect of natural habitat on vertebrates or seed predation. Semi-natural

Table 1. Model specifications in GLMM, testing (a) single and combined effects of birds and rodent exclusions on seed predation in almond, and testing effects (b) on seed predation and vertebrate variables across the almond and sunflower system

Response variables	Random effect	Error distribution	Explanatory variables
(a) Seed predation and vertebrates across almond and sunflower			
Vertebrate variables	Crop identity, Study site, (Sampling point)	Quasi-Poisson	Percentage natural habitat Percentage semi-natural habitat Size of study sites Age of study sites Sampling point
Seed predation (crops combined)	Crop identity, Study site, (Sampling point)	Quasi-Poisson	Vertebrate variables (separately) Percentage natural habitat Percentage semi-natural habitat Sampling point
(b) Vertebrate exclusion experiment in almond			
Seed predation (almond)	Study site Sampling point Tree	Quasi-Poisson	Treatment

Separate models were conducted for each explanatory variable. Vertebrate variables include abundance and species richness of all birds, granivorous birds and are analysed separately.

Table 2. Results given here are derived from generalized linear mixed models, testing abundance and species richness of birds against natural habitat, semi-natural habitat and sampling point (edge, interior). DF in natural and semi-natural habitat for bird variables were 37. DF in sampling point for bird variables were 28. Significant relationships are highlighted in bold

	Estimate	SE	*t*-Value	*P*-value
Natural habitat				
Abundance of all birds	0·0028	0·0044	0·6338	0·5301
Species richness of all birds	0·0014	0·0031	0·4422	0·6609
Abundance of granivorous birds	−0·0028	0·0061	−0·4650	0·6447
Species richness of granivorous birds	−0·0016	0·0029	−0·5581	0·5801
Semi-natural habitat				
Abundance of all birds	0·0040	0·0051	−0·7796	0·4406
Species richness of all birds	0·0073	0·0032	2·2581	**0·0299**
Abundance of granivorous birds	−0·0012	0·0083	−0·1441	0·8862
Species richness of granivorous birds	0·0025	0·0037	0·6855	0·4973
Sampling point				
Abundance of all birds	−0·1977	0·1166	−1·6959	0·1010
Species richness of all birds	−0·1602	0·0638	−2·5124	**0·0180**
Abundance of granivorous birds	−0·1346	0·1525	−0·8823	0·3851
Species richness of granivorous birds	−0·1116	0·0864	−1·2925	0·2068

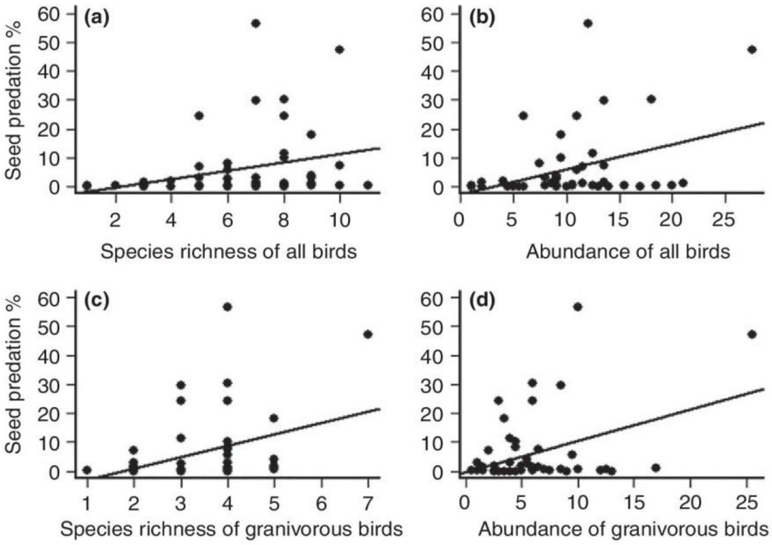

Fig. 2. Mean percentage of seed predation per study site (almond and sunflower) in relation to (a) abundance of all birds, (b) abundance of granivorous birds, (c) species richness of all birds and (d) species richness of granivorous birds. For statistics, see Table 3.

Table 3. Results given here are derived from generalized linear mixed models, testing abundance and species richness of birds against seed predation as a response variable (in percentage). Degrees of freedom for all bird variables were 20. Significant relationships are highlighted in bold

Explanatory variable	Estimate	SE	*t*-Value	*P*-value
Abundance of all birds	0·1390	0·0460	3·0070	**0·0070**
Species richness of all birds	0·3680	0·0930	3·9548	**0·0008**
Abundance of granivorous birds	0·1690	0·0580	2·8988	**0·0089**
Species richness of granivorous birds	0·5217	0·2227	2·3419	**0·0296**

habitat in our study area is interspersed with high exotic trees, far exceeding the average height of the natural vegetation (shrubland). These high trees may provide protection for birds and are places for resting and searching for food (perches), with consequences for seed predation (Miller & Cale 2000; Schäckermann *et al.* 2014). The rose-ringed parakeet (Fig. S1, Supporting information) is known to use high trees to perch (Ahmad *et al.* 2011). Therefore, the positive relationship of bird species richness with semi-natural habitat but not with natural habitat may be explained by absent perches in the natural habitat.

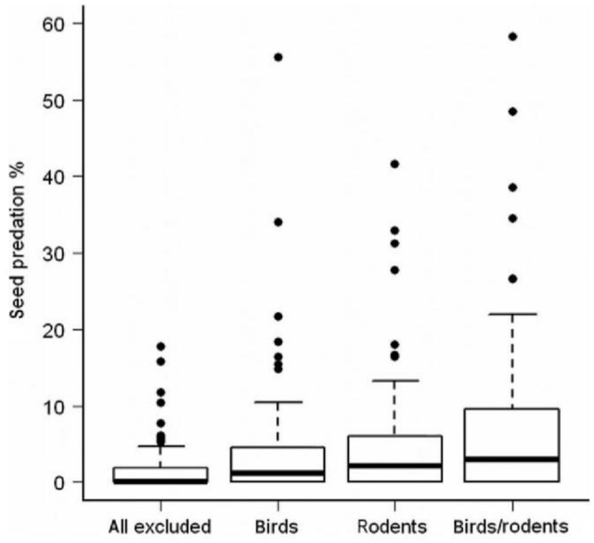

Fig. 3. Mean percentage of seed predation per study site (almond) presented in boxplots (median, upper and lower quartile, maximum, minimum and outliers) of the four different exclusion treatments in almond. Statistics comparing 'all excluded' with birds (rodents excluded, birds had access to almonds) ($t = 3{\cdot}1528$, $P = 0{\cdot}0018$); rodents (birds excluded, rodents had access to almonds) ($t = 3{\cdot}6572$, $P = 0{\cdot}0003$); and birds/rodents (both groups had access to almonds) ($t = 4{\cdot}9933$, $P < 0{\cdot}0001$).

The higher bird species richness but not abundance at crop edges compared to interiors may indicate that some species move from the surrounding habitats to crops only for foraging (Blitzer *et al.* 2012). Isolation from surrounding habitats might filter some species and prevent their entry deeper into crops. Consequently, only a subset of species remains active in the interior. Many species feed on crop edges and may only move to the interiors when food resources become limited (Kollmann & Buschor 2002). The fact that no differences were found in abundance may indicate that remaining species are active in higher numbers in crop interiors than edges due to decreased competition.

It was unexpected that seed predation was not related to the percentage of natural habitat as the bird and rodent species found are known to use shrubland as primary habitat (Mendelssohn & Yom-Tov 1993). Indirect effects such as predation risk (Whittingham & Evans 2004), alternative foraging resources or water availability may be more important for vertebrate foraging behaviour than landscape variables. Here, the main predation risk for birds and rodents is birds of prey. In particular when perches are available, birds of prey were found in high numbers in agricultural areas (Pearlstine, Mazotti & Kelly 2006). In our study area, birds of prey have been observed using agricultural areas for hunting rodents, especially during crop cultivation activities (Darawshi, Motro & Leshem 2006). Birds and rodents may therefore devote more time to predator avoidance than for foraging. Future long-term research studies are necessary to understand the mechanisms leading to changes in foraging behaviour of birds and rodents. Data on foraging behaviour of important vertebrate pest species would also lead to more targeted management recommendations for agricultural landscapes.

BIRDS AND RODENTS AS DRIVERS FOR CROP SEED PREDATION

Seed predation by birds has been reported in almond (Emlen 1937; Eilers & Klein 2009) and sunflower crops (Werner *et al.* 2011). We found that bird abundance and species richness was positively correlated with seed predation across both crop species. But the effect of granivorous birds on seed predation was weaker than that of all bird species. This might be explained by possible interspecific interactions between different bird species, which change their normal predation behaviour. Interspecific interactions were described to alter the behaviour of organisms and therefore indirectly change the provisioning of ecosystem services (Greenleaf & Kremen 2006; Brittain *et al.* 2013). Furthermore, different granivorous species vary in their food preferences; not all granivorous bird species consume nuts and some are specialized, on seeds of annual herbs (i.e. goldfinch, *Caduelis carduelis* L., European Serin, *Serinus serinus* L.). Our data collection took place when almond seeds were sensitive to bird seed predation, but the diet and feeding behaviour of some granivorous bird species change over the year, depending on changes in metabolic requirements and on nesting (foraging smaller areas) or flocking behaviour (foraging in higher densities). Some granivorous birds may have used almond trees for resting or hiding from predators only (Whittingham & Evans 2004). In addition, birds are highly mobile and forage over large areas while flocking; therefore, feeding events which are not regular could have happened outside our data collection. Emlen (1937) and Hasey & Salmon (1993) found that crows were the main seed predators in California almond crops. In our system, crows were present only in some sites with varying abundances. We observed hooded crows *Corvus cornix* L. picking single sunflower seeds and consumed them outside of the crop, while the rose-ringed parakeet consumed many seeds without moving (J. Schäckermann, personal observations). Even though both are granivorous birds, their actual contribution to seed predation may vary considerably mediated by their predation activity. Hence, feeding behaviour, metabolic needs, nesting or flocking behaviour as well as local abundances of bird species in agricultural areas should be taken into account when predicting their impact on seed predation. Our finding that exclusion of birds from almond branches decreased seed predation confirms that birds are significant seed predators in almond crops, even though not mediated by natural habitat.

Although we caught almost no rodents (two individuals of two species) in almond, they were obviously feeding on almonds as indicated by the results of the exclusion experiment and by feeding marks which we frequently found in the almond crop (J. Schäckermann & N. Weiss, personal observations). In almond, herbicides are regularly applied (to avoid competition for water between the crop and herb plants), leaving bare ground which is generally avoided by rodents (Simonetti 1989). Herb layers usually provide shelter for rodents, while open ground leads to increased predation pressure (Simonetti 1989). High predation risk for rodents, as in the open ground of the almond crop, may reduce their movements between trees but increase their foraging duration at individual trees. This may explain the relative lack of rodent captures in the traps (placed between trees), despite significant consumption of almonds (exclusion experiment). Similar behavioural patterns were found in other risk-mediated foraging patterns of rodent studies in Israel (Mandelik, Jones & Dayan 2003). Hence, when managing crop seed predation rate by rodents, the physical structure of the agricultural habitat should be taken into account, especially the provision of sheltered vs. exposed movement paths along crops. When excluding both birds and rodents from almond branches, we still found some seed predation (Fig. 3). Invertebrates are known seed predators (Andersen 1988; Cummings, Alexander & Snow 1999) and could access almonds which were excluded from birds and rodents. We observed ants of several species feeding on almonds (J. Schäckermann, personal observation). Therefore, invertebrates seem to be seed predators in almonds and responsible for a small amount of seed predation.

SYNTHESIS AND APPLICATIONS

Natural and semi-natural habitat did not mediate crop seed predation by wildlife vertebrates in almond and sunflower in Israel. Policymakers can therefore consider promoting agri-environmental schemes that conserve natural and manage semi-natural habitats adjacent to crops sensitive to vertebrate seed predation in our study region to increase pollination and pest control services without enhancing vertebrate pests. Similar studies should be conducted in other study regions to understand to which landscapes and regional conditions these recommendations can be transferred. As birds and other vertebrates also deliver ecosystem services to agriculture by, for example, removing overwintering and infested fruits, thereby controlling pest populations (Dix *et al.* 1995; Mols & Visser 2007), the conservation and management of natural and semi-natural habitats in agricultural landscapes to protect vertebrates should be further considered and studied. Gilroy *et al.* (2014), for example, recently concluded that agri-environmental schemes on farmland (land sharing) are most effective for bird conservation when large blocks of natural habitats are available in these landscapes (land sparing). Conserving natural and managing semi-natural habitats in agricultural landscapes to mitigate yield gaps (Bommarco, Kleijn & Potts 2013) requires information of potential benefits (ecosystem services) and costs (ecosystem dis-services) for different habitats and ecosystems. Therefore, considering trade-offs and interactions of multiple ecosystem services and dis-services are crucial to inform land managers and policy-makers to enable sustainable management and maximize yields without compromising biodiversity.

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Data accessibility

The data are available at the Dryad archives http://dx.doi.org/10.5061/dryad.6r8p3 (Schäckermann *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Rose-ringed parakeet feeding on sunflower.

Fig. S2. House mouse in Sherman live trap.

Table S1. Correlation matrix of the explanatory landscape variables.

Table S2. Wildlife abundance and species richness in relation to crop systems.

Table S3. Correlation matrix of the response vertebrate variables.

Table S4. Bird and rodent species list for almond and sunflower.

For supporting online material see Appendix Chapter I

Chapter II

Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape

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INSECTS AND ECOSYSTEM SERVICES SPECIAL ISSUE

Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape

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Abstract. 1. The simultaneous influence of specific habitats on agro-ecosystem services, dis-services, and their interactions are largely unknown. Natural and semi-natural habitats surrounding cropland may support ecosystem services and dis-services and their net balance is important to guide decision-making in agriculture.

2. It was tested how natural and semi-natural habitats surrounding almond orchards in Israel influence: pest control services by parasitoids, pest predation dis-services by the Almond wasp, and seed predation dis-services by granivorous birds. The latter could provide sanitation services when consuming almonds infested by Almond wasps after harvest.

3. Seventeen almond orchards were surveyed, surrounded by varying percentages of natural and semi-natural habitats. We harvested almonds to identify Almond wasp infestation and parasitoid abundance, monitored bird-feeding marks, and observed birds.

4. Almond wasp predation was positively influenced by semi-natural habitat and highest at orchard edges. Parasitoid abundance was not influenced by natural or semi-natural habitats. Granivorous bird abundance was negatively influenced by semi-natural habitats but did not influence bird seed predation of harvestable or overwintered almonds.

5. Natural habitats did not influence the studied ecosystem services or dis-services in almond orchards in Israel. Therefore, protecting natural habitats for conservation is not necessarily disadvantageous for farmers. Semi-natural habitats increased insect pests, but no direct link to services or dis-services by birds was observed. Therefore, a more holistic approach by accounting for several services and dis-services and their connection to different habitat types to manage agriculture more sustainably is advocated.

Key words. Almond, Almond wasp, birds, natural habitat, parasitoids, seed predation, semi-natural habitat.

Introduction

Agricultural landscapes often consist of a mosaic of multiple habitats e.g. croplands, forest plantations, and different types of natural and semi-natural habitats (Tscharntke *et al.*, 2005). Natural and semi-natural habitats are important for many beneficial organisms that provide agro-ecosystem services (Tscharntke *et al.*, 2005). Here, we define natural habitats as habitats that comprise vegetation structures and species that are either naturally grown or resemble the composition that would be expected native to the specific region. Semi-natural habitats consist of planted forests in different densities with native and exotic species but do not include cultivated plants (but self-seeded wild almond trees) (Fig. 1). Natural and

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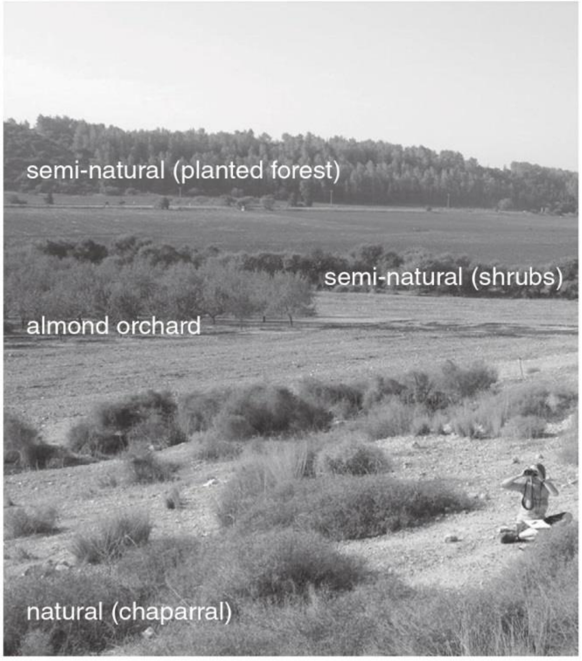

Fig. 1. Examples of semi-natural and natural habitats surrounding an almond orchard in the Judean foothills of Israel.

semi-natural habitats can offer refuges for natural pest enemies all year (Dennis & Fry, 1992; Bianchi *et al.*, 2006; Tscharntke *et al.*, 2007; Chaplin-Kramer *et al.*, 2011), and abundant forage resources for pollinators (Holzschuh *et al.,* 2009; Mandelik *et al.*, 2012). Therefore, crop fields with a higher percentage of natural and semi-natural habitats in their surrounding landscape might experience higher pest control and pollination than crop fields surrounded with a lower proportion of natural and semi-natural habitats (Eilers & Klein, 2009; Veres *et al.*, 2013). However, these habitats might also promote dis-services such as pest species and disease carriers that influence crop production negatively, either directly by consuming parts or whole crop plants or indirectly by transmitting diseases (Dunn, 2010; Keesing *et al.*, 2010; Blitzer *et al.*, 2012). Insect pests, for example, are well known to influence crop production negatively (Eilers & Klein, 2009; Cini *et al.*, 2012; El-Wakeil & Volkmar, 2012). Less is known about the dis-services provided by vertebrates; granivorous birds were found to have severe negative influences on crop production by destroying large amounts of crop seeds in sunflower fields (Schäckermann *et al.*, 2014), and birds and rodents are the main almond consumers in orchards in Israel (Schäckermann *et al.*, 2015). Vertebrate crop pests may decrease productivity and in the worst case can result in complete crop loss (Zhang *et al.*, 2007). These ecosystem dis-services are frequently overlooked (Ghazoul, 2007), but with growing human food demand (Hobbs, 2007; Dias, 2010; Godfray *et al.*, 2010), predation of crops by pests is a main concern.

To date, the majority of studies focused on a single service or dis-service, for example by studying how to support beneficial insects, how to enhance wild pollinators or how to handle a specific pest (Holzschuh *et al.*, 2009; Linz *et al.*, 2011; Klein *et al.*, 2012). However, in agricultural systems, ecosystem services and dis-services are closely linked when they involve interactions at different trophic levels. Pest insects provide dis-services by destroying crops, but their natural parasitoids provide a service by reducing the numbers of pest insects (Schmidt *et al.*, 2003). Some animal groups can provide both services and dis-services, depending on the species, the ecosystem or the season. For example, insectivorous birds might have a negative influence on beneficial insects and frugivorous and granivorous birds might destroy large quantities of fruit or seed harvests (Linz *et al.*, 2011; de Mey *et al.*, 2012), thereby providing dis-services. However, insectivorous birds can provide an ecosystem service by reducing the negative impact of insect pests to agriculture such as the coffee berry borer in coffee plantations (Johnson *et al.*, 2010; Karp *et al.*, 2013) or caterpillars in apple orchards (Mols & Visser, 2007). Ecosystem services by granivorous birds are mostly unknown but there is evidence that they may contribute to weed control by consuming large quantities of weed seeds (Kelly & McCallum, 1990) and also consume pest insects (Wenny *et al.*, 2011). For farmers, it is important to know about possible services and dis-services to manage agriculture in the most profitable way, but little is known about the links between multiple services and dis-services. Combined studies of ecosystem services and dis-services, and the influence of different habitat types on these functions are necessary and should ideally lead to useful management strategies in agricultural areas to support ecosystem services without increasing dis-services (Lavandero *et al.*, 2006; Isaacs *et al.*, 2009).

We studied how a limited set of ecosystem services and dis-services provided by insects and birds in almond orchards were affected by the surrounding landscape composition. The study was conducted in an agricultural system in central Israel comprising agriculture, natural, and semi-natural habitats. Here, farmers voice a growing concern about crop damages mediated by natural habitats, possibly leading to a conflict between agriculture and biodiversity conservation (J. Schäckermann, pers. comm. with farmers). In Israel, an important insect pest is the Almond wasp *Eurythoma amygdalii* Enderlein whose life cycle largely relies on almond orchards for forage resources, overwintering, and breeding habitats (Plaut, 1971). A high abundance of granivorous birds was observed in almond orchards before but also after harvest (reports of local bird watchers, Society for Protection of Nature in Israel, hereafter SPNI) and most birds in almond orchards are generally considered to be almond pests (Nemtzov, 2003). However, their role as ecosystem service providers has so far not been investigated.

To address landscape influences on ecosystem services and dis-services in almond orchards, we tested how surrounding natural and semi-natural habitats influence pest infestation dis-service by the Almond wasp *E. amygdalii*, the pest control service provided by their natural parasitoids, and the abundance of granivorous birds. They might either provide sanitation services by consuming infested almonds that remain in the orchard after harvest (mummy nuts) or crop predation dis-services by consuming almonds prior to harvest. The aim of the present study was to contribute to the discussion about the management of natural and semi-natural habitats within agricultural landscapes in Israel. If these natural and semi-natural habitats promote services or dis-services to adjacent agricultural crops, then the management of these habitats should be incorporated into planning by policymakers, landscape planners, and farmers for sustainable agricultural strategies and practices.

Materials and methods

Study region and landscape characterisation

The study was conducted in the Judean Foothills, a dry Mediterranean ecosystem in central Israel, approximately 30 km southwest of Jerusalem (Weizel *et al.*, 1978). The Judean Foothills are characterised by a mosaic of different land-use types. The main difference between natural and semi-natural habitat is the availability of high trees in varying abundances in semi-natural habitat areas but no high trees in natural habitats (Fig. 1). Natural habitats in these areas are defined by open shrubland with different native grasses, herbs, and shrubs of variable densities and succession stages (chaparral) and trees higher than 5 m are absent. Semi-natural habitats are planted forests of variable densities with native and exotic species such as pines *Pinus halepensis* Mill., *Pinus pinea* L., *Pinus brutia* Tenore, Eucalyptus, and wild-seeded almond, with variable degrees of understory re-growth comprising native shrubland species. Additional land use types are agricultural fields (annual and perennial crops), some rural settlements, and a few urban and industrial areas (Weizel *et al.,* 1978).

Orchard selection

Prior to orchard selection, we determined specific farming practices common in the study region to choose 17 similarly managed orchards as study sites (Fig. 2). Similar management included that the most important local varieties were planted, trees were at least 3–27 years old and productive, treated with insecticides twice per season, and irrigated with a drip system from March until September. The size of the orchards varied between 11 and 112 ha. At each orchard, we selected one sampling point at the orchard edge, and one in the orchard interior, 150 m from the edge. We chose the edge closest to the natural habitat or semi-natural habitat; when both habitat types occurred around the orchard, the edge closest to natural habitat was chosen. Along the edge of the orchard, we chose the halfway point of the edge as a sampling point. The minimal distance between edge sampling points at different orchards was 1000 m to minimise the risk of overlapping bird communities and to avoid spatial autocorrelation. Two almond orchards were too narrow to allow for an interior sampling point; therefore, data were only collected at their edges. We measured the geographical coordinates at the edge of the sampling points using GIS (ArcGIS, version 9.2., Esri, Redlands, California). For each edge sampling point, we calculated the percentages of natural and semi-natural habitat within a 1000-m radius; this radius was shown to be appropriate in other vertebrate landscape studies (Eilers & Klein, 2009; Guerrero *et al.*, 2012). Land cover data were obtained from the archive of the Hebrew University of Jerusalem and corroborated in the field by validating the landscape data and recording changes (Gidi Pisanty, Hebrew University). The selected orchards constituted a gradient of the percentage of natural and semi-natural habitats in the surrounding landscape, ranging from 3% to 51% and from 0% to 70%, respectively.

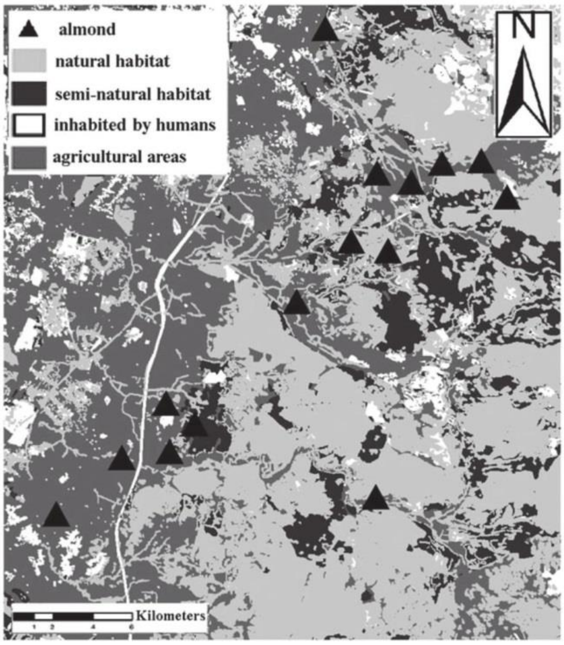

Fig. 2. Study region, land use types, and the distribution of the almond orchards (Δ) in the Judean foothills of Israel.

Study crop and its associated fauna

The almond tree *Prunus dulcis* Miller (Rosaceae) is native to Israel, the Middle East, and South Asia. It is a small deciduous tree species, up to 6 m tall in our area, and with a trunk of up to 30 cm in diameter. Almond flowers in February and March and the harvest takes place at the end of August and beginning of September in our study region.

In 2010, an area of 4000–4500 ha was cultivated with almond in Israel (J. Schäckermann, pers. comm. with Yoav Motro, Ministry of Agriculture, from now on referred to as MOA). The most common almond varieties in the study region are Um Al Fahm, Kohav - Kohva, Ne Plus Ultra, and Mem Dalet. A major pest of almond is the Almond wasp *E. amygdali* (Plaut, 1971) with infestation rates of up to 90% reported in Greece (Katsoyannos *et al.*, 1992). The Almond wasp, a specialist on almonds, overwinters in almonds remaining in the orchards after harvest (mummy nuts); the new generation hatches in spring and oviposits on a new almond. Several parasitoid species of Almond wasp were reported in Iran and Turkey, including species belonging to Pteromalidae, Eulophidae, and Torymidae families (Hym.: Chalcidoidea) (Doğanlar *et al.*, 2006; Lotf Alizadeh *et al.*, 2008), including *Adontomerus amygdali* (Hym.:

Chalcidoidea, Torymidae), but little is known about the natural enemies of the Almond wasp in Israel.

Birds in general are described as almond pests in the study region (Nemtzov, 2003) because they feed on almonds prior to harvest (crop predation dis-services). However, they might also provide a sanitation service, if they feed on almonds that are infested by the Almond wasp. If undisturbed, these infested almonds would remain in the orchards as mummy nuts and could provide the next generation of almond pests.

Insect sampling

In every almond orchard at each sampling point (edge/interior), we collected 300 almonds from 10 trees (30 almonds per tree) in July and August 2009, before harvest. One tree at the centre of the margin sample point was chosen randomly, then the following trees in the same row along the margin on its right and left. From this centre tree, we measured a distance of 150 m into the orchard, chose the tree at that point as the central interior point, and chose the remaining nine trees in a similar way as at the edge sampling point. Almonds were randomly collected from the lower half of the tree as this part was accessible to the researchers and the fruit set is similar to the upper part of the almond tree. The collected almonds were placed in a 0.5-litre translucent plastic container, one container for 30 almonds of each tree. Containers were closed with gauze to ensure air circulation and stored in a storage room with free air circulation, ambient temperature, and humidity (average of 8–32 °C and 13–94% humidity), similar to natural environmental conditions. Almonds were stored until February of the following year to ensure the development and hatching of insects. Hatched insects were then separated from the almond remnants, counted, and identified. For this study, we focused on the abundance of Almond wasps and parasitoids, which were mainly *Adontomerus* (a genus of parasitoid wasps, family: *Torymidae*) and a few other parasitoid wasps of the families Braconidae and Ichneumonidae.

Almond sampling

The percentage of Almond wasp predation rate was calculated for the 30 almonds per tree. Almond wasps create small emerging holes in each infested almond and the percentage of Almond wasp predation was therefore the proportion of almonds with Almond wasp holes of the total number of almonds ($N = 30$).

We collected and counted all visible mummy nuts (almonds that overwintered from the previous year) from the ground at each sampling point before harvest and calculated the percentage of mummy nuts with Almond wasp emergence holes (percentage of Almond wasp predation in mummy nuts). Mummy nuts of the previous year can be distinguished from almonds of the current year because of their dark grey to black colour compared with the green or light beige colour of young almonds.

We randomly collected 100 almond shells (endocarp of the almond from the current year) at each sampling point before harvest. Almond shells were classified as having bird feeding marks, other feeding marks and no feeding marks. To be able to differentiate between bird and other feeding marks, we fed rats (*Rattus norwegicus* Berkenhout), meriones (*Meriones tristrami* Thomas), house mice (*Mus musculus* L.), voles (*Microtus socialis* Pallas), Rose-ringed parakeets (*Psittacula krameri* Scopoli), and hooded crows (*Corvus cornix* L.) with almonds under lab conditions. We recorded the feeding marks that each species left on the shells, which were unique and easily distinguished as bird versus non-bird feeding marks. While bird marks looked more like a cracked nut, rodents left typical rodent chewing marks. Both destroyed the almond and made it not useable for the farmers. For almond shells, we calculated the percentage of shells with bird feeding marks from the total of the collected shells ($N = 100$).

Bird sampling

In each orchard and sampling point, birds were observed twice, between September and October 2009 (after almond harvest), with an observation radius of 50 m. The fixed-radius point count method was used to assess the bird communities (Bibby *et al.*, 1992). This fixed distance sampling technique requires only a small area for bird surveys within patches (Petit *et al.*, 1995). We used binoculars (Habicht 10×42WB, Swarovski, Optik, Absam, Austria) for species identification and counts. Observations took place between 05.00 and 09.00 hours, with temperatures between 10 and 23 °C, covering the period of highest bird activity. The time of observation was altered across orchards to minimise temporal bias (Perfecto *et al.*, 2003). The observation time at each sampling point at each day was 5 min, amounting to a total of 20 min per orchard, besides the two orchards with no interior sampling point. Observations started 3 min after the observer was settled to allow the birds to return to their normal activity. Bird species were identified, and the number of individuals per granivorous bird species (granivorous bird abundance) was counted. Flying birds that did not land in the observation radius were excluded from the dataset. In addition to visual counts, bird voices were recorded for 5 min during each point count with a ZOOM handy recorder H2 on a SD card.

Statistical analyses

Statistical analyses were conducted using R (R Core Team 2014, version 2.15.1).

To test our hypotheses, we performed generalised linear mixed models (GLMM) with a binomial or Poisson distribution, depending on the data (count or proportion) (Table 1) using the R package ‘lme4’ (Bates *et al.*, 2014). Orchard and tree (when applicable) were included as random factors and we added an observation level factor (equals N) to account for overdispersion of the data (Table 1) (Elston *et al.*, 2001). An overview of all models, their respective variables, random factors, and distribution can be found in Table 1.

Table 1. Response and explanatory variables for all generalised linear mixed effect models and the distribution of response variables.

Response variable	Explanatory variables	Random factor	Distribution
Landscape influence			
Almond wasp predation rate	Natural habitat (%) × semi-natural habitat (%) × sampling point*	Orchard + tree + observation level factor	Binomial
Parasitoid abundance	Natural habitat (%) × semi-natural habitat (%) × sampling point*	Orchard + tree + observation level factor	Poisson
Granivorous bird abundance	Natural habitat (%) × semi-natural habitat (%) × sampling point*	Orchard + observation level factor	Poisson
Influences on Almond wasp predation			
Percentage of Almond wasp predation in almonds	Parasitoid abundance + percentage of Almond wasp predation in mummy nuts†	Orchard + tree + observation level factor	Binomial
Birds providing services or dis-services			
Percentage of almonds with bird feeding marks	Granivorous bird abundance	Orchard + observation level factor	Binomial
Number of mummy nuts	Granivorous bird abundance	Orchard + observation level factor	Poisson

*Natural and semi-natural habitat were Box-Cox transformed.

†Explanatory variables were centred.

Results

Landscape influences

Almond wasps infested between 0% and 77% of almonds in the different orchards and sampling points (Fig. 3a,c). The percentage of Almond wasp predation was significantly influenced by the interaction between habitats and locations of the sampling point. Almond wasp predation was higher at the edge of orchards than in the interior, with semi-natural habitat having a stronger positive influence on Almond wasp predation than natural habitat (Fig. 3a,c, Table 2).

Overall, we found 611 parasitoid individuals with 43 individuals (7%) from the genus *Adontomerus*. Parasitoid abundance ranged from 0 to 65 individuals per orchard. Parasitoid abundance was not influenced by the percentage of semi-natural or natural habitats surrounding the orchards and we did not detect an edge effect (Fig. 3b,d, Table 2).

We observed a total of 220 granivorous birds from 20 species in all orchards and 7 species were migratory birds. We did not detect an influence of the interactions between surrounding habitat and locations of sampling points on granivorous bird abundance. However, the percentage of semi-natural habitat negatively influenced the abundance of granivorous birds (Table 2).

Influences on Almond wasp predation

We found a positive relationship between parasitoid abundance and the percentage of Almond wasp predation (Table 2). We collected a total of 719 mummy nuts from the previous year for all orchards, and 53% had emergence holes of Almond wasps. On average, we collected 24 mummy nuts at each sampling point, with an average Almond wasp predation of 54%. The percentage of Almond wasp predation of the current year was positively influenced by Almond wasp predation of the previous year (Almond wasp predation in mummy nuts) (Table 2, Fig. 4).

Granivorous birds providing services and dis-services

On average, 56% of the almond shells found on the ground in orchards had bird feeding marks, rodents accounted for 3% of the damage, and 41% of the almond shells did not show any feeding marks. We did not find a correlation between granivorous bird abundance and the number of mummy nuts. Granivorous bird abundance was also not related to the bird feeding marks on almond shells under the trees.

Discussion

Ecosystem services and dis-services in almonds responded differently to habitats surrounding the orchards. Almond predation by the Almond wasp was positively influenced by the percentage of semi-natural habitat, whereas natural habitat did not seem to influence Almond wasp predation. Semi-natural habitat might, therefore, provide some advantages to Almond wasps that are not provided by natural habitat, which could be a higher number of wild (naturally seeded) almond trees that are not sprayed with pesticides. Almond wasps depend on almonds for larval development and adult Almond wasps also require and are active around almond trees (Plaut, 1971; Kouloussis & Katsoyannos, 1994). We also observed an edge effect of Almond wasp predation, which was much more pronounced for surrounding semi-natural than natural habitats. Smaller orchards might, therefore, have a high pressure of Almond wasp predation throughout the entire orchard when surrounded by a semi-natural habitat.

Because natural habitat had no influence on insect pests, improving natural habitats for ecosystem services, for example pollination (Blitzer *et al.*, 2012), pest control (Eilers & Klein, 2009) or nature conservation issues (Batáry *et al.*, 2010; Fischer *et al.*, 2010; Tscharntke *et al.*, 2012) would not compromise almond harvest owing to higher insect predation rates in almond but might even increase it. Eilers and Klein (2009) report a positive influence of natural habitat on pest control services by invertebrates and vertebrates for California almond, providing

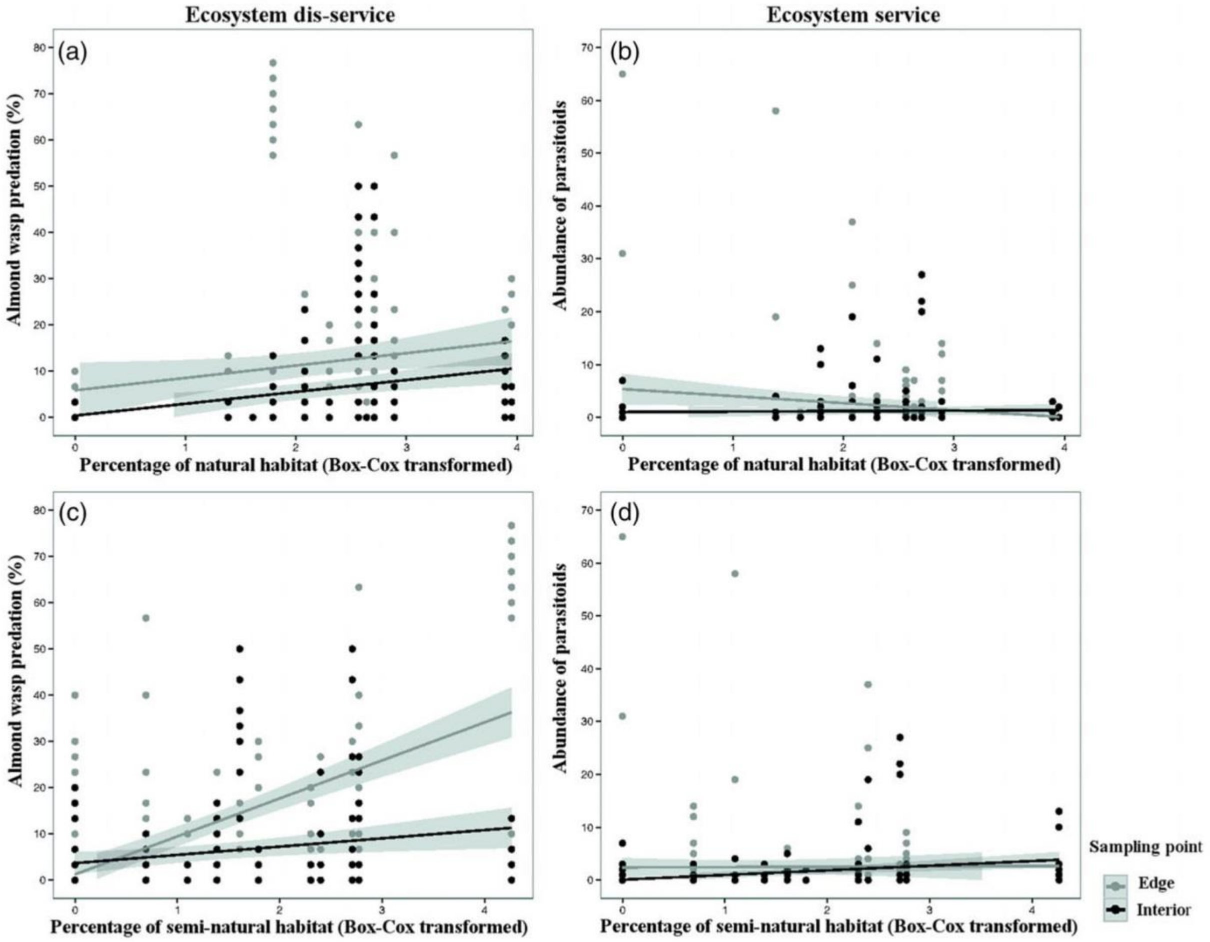

Fig. 3. The effect of natural and semi-natural habitat on ecosystem dis-services (a, c) and services (b, d) in almond orchards, depending on the location in the orchard. Shown are the percentage of Almond wasp predation (dis-service) (a, c) and the abundance of parasitoids (service) (b, d).

an incentive to increase the natural habitat surrounding almond orchards. Additionally, Klein *et al.* (2012) found a positive influence of natural habitat on wild pollinators in California orchards. In our study region, we also observed pollinators during almond bloom but the numbers of wild pollinators in the orchards were too small to find any influence of natural- or semi-natural habitats surrounding the orchards (G. Pisanty *et al.,* unpublished). A preliminary study by Mandelik and Roll (2009) suggests that wild bees prefer to forage in the natural habitats and weeded orchard margins and not in the orchards themselves. This highlights the regional differences in interactions between crop agro-ecosystems and their adjacent natural- and semi-natural habitats.

In our study sites, semi-natural habitats should be managed to reduce the impact of Almond wasps, especially at the border of almond orchards to semi-natural habitat. In our study area, we suggest that the number of wild seeded almond trees should be observed and potentially managed in agricultural planning to prevent a spillover of Almond wasps into orchards. Because trees are protected in Israel, a reduction of wild almond trees would be difficult; however, a further spreading of wild almond trees into agricultural areas could be a potential control mechanism.

Owing to the nature of our experimental approach, we could not calculate parasitism rates of Almond wasps. However, we used parasitoid abundance in collected almonds and found a positive relationship with Almond wasp seed predation, indicating a positive host–parasitoid relationship. This suggests that an increase in parasitoid abundance would increase natural pest control services if a stable host–parasitoid rate could be reached (Hassell & May, 1973).

Parasitoid numbers were generally low, and we did not detect an influence of surrounding habitat on the abundance of parasitoids. Therefore, there seems to be a need to improve suitable parasitoid micro-habitats that provide nesting and feeding resources to improve their ecosystem service of biological pest control (Lewis *et al.*, 1998; Shaw, 2006; Holzschuh *et al.*, 2009). Further research is needed to increase our knowledge about parasitoid habitat needs and to create such habitats fitting the needs of specific natural enemies such as *A. amygdali*,

Table 2. Results of generalised linear mixed models (GLMMs), testing the influences on ecosystem services and dis-services in almond orchards.

Response variable	Explanatory variable	Estimate	SE	z-value
Landscape influences				
Almond wasp predation rate	Natural habitat	0.507	0.370	1.369
	Semi-natural habitat	**1.026**	**0.299**	**3.427*****
	Sampling point (interior)	**−1.547**	**0.700**	**−2.210***
	Natural habitat : sampling point (interior)	**0.513**	**0.242**	**2.123***
	Semi-natural habitat : sampling point (interior)	**−0.481**	**0.145**	**−3.312*****
Parasitoid abundance	Natural habitat	−0.420	0.295	−1.424
	Semi-natural habitat	0.463	0.243	1.909
	Sampling point (interior)	−0.962	0.955	−1.007
	Natural habitat : sampling point (interior)	0.038	0.418	0.090
	Semi-natural habitat : sampling point (interior)	0.331	0.345	0.958
Granivorous bird abundance	Natural habitat	0.042	0.124	0.336
	Semi-natural habitat	**−0.155**	**0.078**	**−1.977***
	Sampling point (interior)	−0.259	0.494	−0.524
	Natural habitat : sampling point (interior)	−0.073	0.195	−0.376
	Semi-natural habitat : sampling point (interior)	0.163	0.132	1.235
Effects on Almond wasp predation				
Percentage of Almond wasp predation in almonds	Parasitoid abundance	**0.214**	**0.096**	**2.222***
	Percentage of Almond wasp predation in mummy nuts	**1.232**	**0.178**	**6.926*****
Granivorous birds providing services and dis-services				
Percentage of almonds with bird feeding marks	Granivorous bird abundance	0.011	0.057	0.848
Number of mummy nuts	Granivorous bird abundance	0.051	0.182	0.282

Given are estimates, their standard error and *z*-value for every explanatory variable. Significant influences are shown in bold, with $^*P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

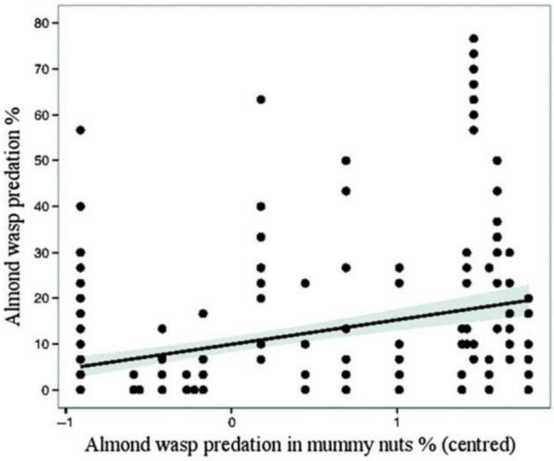

Fig. 4. The influence of Almond wasp predation of the previous year, (Almond wasp predation in mummy nuts %) on Almond wasp predation of the current year (Almond wasp predation %). Data for the previous year were collected from mummy nuts (almonds that overwintered from the previous year). Data for the current year were collected from fresh almonds on the trees.

which is a key issue for the successful application of functional agro-biodiversity (Pfiffner, 2014).

We did not find a significant influence of natural habitat on granivorous bird abundance but a negative influence of semi-natural habitat. Semi-natural habitats in our study region often include high, non-native trees, which might promote bird of prey abundance as these birds are using high landscape structures for resting and perching (Schäckermann *et al.*, 2014). Their presence might have an impact on granivorous bird abundance and foraging behaviour. Granivorous birds are mostly seen as providing dis-services in croplands and orchards by diminishing the final yield (Schäckermann *et al.*, 2014, 2015).

We propose that granivorous birds could also provide a sanitation service by consuming almonds that remain in the orchards after harvest, as these almonds provide an overwintering habitat for Almond wasps (mummy nuts) (Plaut, 1971). Indeed, we found that more than half of the mummy nuts we collected in the orchards were infested with Almond wasps and Almond wasp predation of the current year's almonds was positively related to Almond wasp predation in mummy nuts. Some farmers clear their orchards of mummy nuts after harvest to diminish the impact of Almond wasps on their yield in the following year, but there are no empirical data on the success of this strategy to date. Further research is needed to confirm the positive influence of removing mummy nuts on lower infestation rates in consecutive years. Farmers could then potentially save manpower and reduce pesticides targeting Almond wasps, if they promote granivorous birds after harvest (Kibler, 1969; Kay *et al.*, 1994; Marra & Holberton, 1998; Robb *et al.*, 2008; Lambrechts *et al.*, 2010).

In this study, we found no clear evidence for birds providing sanitation services or crop predation dis-services. We collected bird abundance data after harvest, but a change in bird abundance before and after harvest is likely. We did not collect data on the amount of mummy nuts that were consumed by birds over the course of the year, which would have given us a better estimate of the effectiveness of the sanitation service. Almonds infested with Almond wasps adhere strongly to the trees (Plaut, 1971) and are, therefore, harder to harvest with the commonly used harvest techniques, where a machine shakes the trees and almonds fall to the ground to be collected on plastic covers. This is also shown by the high percentage of mummy nuts that were infested with Almond wasps. Israel is a migration bottleneck for birds crossing to and from Africa and migrations take place in spring and autumn. If they arrive in autumn after the harvest, they feed on the remaining almonds and thereby provide the sanitation service without damaging marketable crops. To examine the sanitation service in more detail, bird feeding rates on almonds should be investigated after harvest for consecutive months and years to compare Almond wasp predation rates between several years. Furthermore, the bird species providing the ecosystem service in late autumn and winter after almond harvest should be identified and could be supported by improving their habitats, for example with feeding stations (Robb *et al.*, 2008) or water sources (Johnson, 2007).

Even although more than half of the almond shells found in orchards had bird feeding marks, we did not detect a negative relationship between granivorous bird abundance and damaged almond shells. However, almond shells on the ground are not necessarily related to almond predation rates by birds in the orchards because birds might take almonds away from the orchards and not leave shells on the ground. Also, we counted bird abundances after harvest and almond shells with bird feeding marks were collected before harvest and, as we mentioned before, bird numbers might fluctuate strongly in time as a result of migration.

Conclusions

Natural habitats did not facilitate crop seed predation by pests. Hence, when conserving or restoring natural habitats adjacent to crop fields to enhance ecosystem services or nature conservation, crop yield will not necessarily be compromised owing to higher pest predation. Semi-natural habitats positively influenced pest infestation of almonds but our results are not conclusive about the influence of natural- and semi-natural habitats on sanitation services or crop predation dis-services by birds. Therefore we, advocate that farmers should manage semi-natural habitats by, for example, controlling wild-seeded almond trees in agricultural landscapes proactively to mitigate yield gaps by considering trade-offs between services and dis-services (Bommarco *et al.*, 2013).

We could identify infestation of almonds by the Almond wasp as a major cause for yield losses, with up to 70% loss in some farms close to semi-natural habitat. Further research priorities should, therefore, aim at (i) identifying the specific benefits that semi-natural habitats provide for Almond wasps, (ii) improving habitat conditions for parasitoids of Almond wasps, (iii) evaluating and quantifying the sanitation services by granivorous birds after harvest to (iv) utilise this service to decrease Almond wasp infestation in future years.

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Chapter III

High trees increase sunflower seed predation by birds in an agricultural landscape of Israel

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High trees increase sunflower seed predation by birds in an agricultural landscape of Israel

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Natural habitats in agricultural landscapes promote agro-ecosystem services but little is known about negative effects (dis-services) derived by natural habitats such as crop seed predation. Birds are important seed predators and use high landscape structures to perch and hide. High trees in agricultural landscapes may therefore drive seed predation. We examined if the presence, the distance and the percentages of high trees (tree height >5 m) and the percentages of natural habitat surrounding sunflower fields, increased seed predation by birds in Israel. At the field scale, we assessed seed predation across a sample grid of an entire field. At the landscape scale, we assessed seed predation at the field margins and interiors of 20 sunflower fields. Seed predation was estimated as the percentage of removed seeds from sunflower heads. Distances of sample points to the closest high tree and percentage of natural habitat and of high trees in a 1 km radius surrounding the fields were measured. We found that seed predation increased with decreasing distance to the closest high tree at the field and landscape scale. At the landscape scale, the percentage of high trees and natural habitat did not increase seed predation. Seed predation in the fields increased by 37%, with a maximum seed predation of 92%, when a high tree was available within 0–50 m to the sunflower fields. If the closest high tree was further away, seed predation was less than 5%. Sunflower seed predation by birds can be reduced, when avoiding sowing sunflowers within a radius of 50 m to high trees. Farmers should plan to grow crops, not sensitive to bird seed predation, closer to trees to eventually benefit from ecosystem services provided by birds, such as predation of pest insects, while avoiding these locations for growing crops sensitive to bird seed predation. Such management recommendations are directing toward sustainable agricultural landscapes.

Keywords: ecosystem dis-service, Israel, landscape ecology, landscape structures, natural habitat, vertebrate pests

INTRODUCTION

Insects provide valuable agro-ecosystem services and the interest in developing strategies to conserve beneficial insects, for example by integrating flower patches into agricultural areas, is growing (Bianchi et al., 2006; Carvalheiro et al., 2012; Blaauw and Isaacs, 2014). Besides the positive effects of natural and semi-natural habitats, these habitats might also promote organisms that influence crop production negatively, either directly by consuming parts or whole crop plants or indirectly by transmitting diseases (Dunn, 2010; Keesing et al., 2010; Blitzer et al., 2012). Insect pests are well known to negatively influence crop production (Oerke, 2005; Eilers and Klein, 2009; Cini et al., 2012; El-Wakeil and Volkmar, 2012) but seed or fruit predation by vertebrates can also lead to losses in crop growth and production (Moran and Keidar, 1993; Ahmad et al., 2011; De Mey et al., 2012). Research was carried out to identify the bird species involved and the extent of crop yield loss and possible control methods (Moran, 2003; Linz et al., 2011; Radtke and Dieter, 2011). Important bird pests for agricultural crops are for example the Canada Goose (*Branta canadensis* L.), the Chukar Partridge (*Alectoris chukar* Gray), the Rose-Ringed Parakeet (*Psittacula krameri* Scopoli), the Ring-Necked Phesant (*Phasianus colchicus* L.) and blackbirds (Icteridae) (Moran, 2003; Radtke and Dieter, 2011; Werner et al., 2011). Crops frequently and often heavily attacked by birds comprise almond (Emlen, 1937), sunflower, maize (Ahmad et al., 2011; Linz et al., 2011) and rice (De Mey et al., 2012). Until now, several methods have been tested to reduce seed predation by birds, which can be broadly divided into population suppression, frightening and evading (Linz et al., 2011). Population suppression methods such as culling or poisoning seem to be favored by farmers (Conover, 2002) but even though they may be effective they are also expensive (Malhi, 2005).

Subramanya (1994) found that flower height and head angle of sunflowers were correlated with seed predation by the Rose-Ringed Parakeet. Also Fleming et al. (2002) and Khaleghizadeh (2011) found, that the plant morphology is correlated to seed predation. Such studies are rare and information on the feeding behavior of main seed predators is crucial to advice management practices. Seed predation in sunflower fields, caused by foraging flocks of granivorous birds has been reported from India (Subramanya, 1994) and Pakistan (Ahmad et al., 2011) but occurs in fact in every major sunflower-growing regions of the world (Linz and Hanzel, 1997) (Table S1). Therefore, the sunflower crop system is a suitable model system to investigate the drivers of crop seed predation by birds. In general, the mechanisms leading to high abundance of seed-predating birds, including the surrounding landscape, have greatly been overlooked (Martin et al., 2013). In Israel, birds are well-known pests in sunflower farming (Moran, 2003; Nemtzov, 2003). Nemtzov (2003) described the Rose-Ringed Parakeet (**Figure 1**) as a pest in sunflower farming in Israel. In addition, the Hooded Crow (*Corvus cornix* L.) was found to be a pest in sunflower fields, while none of the other investigated vertebrate species, including rodents were found feeding on sunflower seeds (Moran, 2003). Other sunflower pests in the study area are the Eurasian Jay (*Garrulus glandarius* L.) (reported by local farmers), the Middle East Blind Mole Rat (*Spalax ehrenbergi* Nehring), which is known to feed on the roots of the sunflower plants, and a moth, the Cotton Bollworm (*Helicoverpa armigera* Hübner), with larvae developing in the flower heads, facilitating fungal infections (Heth, 1991).

Seed predation, in sunflower fields of Israel shows high spatial variance similar to observations made by Stone and Mott (1986), which found seed predation by the Red-Winged Blackbird, (*Ageleaus phoeniceus* L.), in some but not in all investigated maize fields. As seed predation is highly variable between fields, we assume that differences in the surrounding of the fields, like the proportion of natural and semi-natural habitat, buildings, tree cover and other habitat structures influence the magnitude of seed predation. Sheldon and Nadkarni (2013) found that isolated high trees are highly attractive habitat structures for birds in agricultural areas. Additionally Fischer et al. (2010) found that bird species richness in landscapes with trees was twice as high as in landscapes without trees. Many bird species use trees for observing, perching, foraging and roosting (Bull et al., 1992; Sonerud, 1992; Holl, 1998; Miller and Cale, 2000) and the presence of trees adjacent to crop fields may make the crops more accessible for the birds. Hence, we hypothesize that (1) habitat structures such as high trees in the surrounding of sunflower fields will increase seed predation by birds, since these structures upgrade the landscape for birds and make perching possible and foraging therefore easier; (2) seed predation increases with decreasing distance to the closest high tree (from now on termed high tree), due to reduced foraging and perching possibilities for birds; (3) the presence of high trees within a specific range influences seed predation by birds, because birds may only be able to use these trees for foraging and perching within a specific radius dependent on their visual capabilities; (4) seed predation increases with the percentage of tree cover but not with the percentage of natural habitat in the surrounding landscape, because high trees are not part of the natural habitat in our study area.

FIGURE 1 | Rose-Ringed Parakeets (*Psittacula krameri* Scopoli) resting on a sunflower and feeding on sunflower seeds in the field used for the field-scale data.

MATERIALS AND METHODS

STUDY AREA AND LANDSCAPE CHARACTERIZATION

The study area is part of the Judean Foothills, approximately 30 km southwest of Jerusalem. The Judean Foothills are among the last remnants of a unique transient ecosystem at the interface of the humid Mediterranean ecosystem to its north and the arid ecosystem to its south (Weizel et al., 1978). The landscape is characterized by a mosaic of different land-use types; mainly natural habitats (scrublands of variable densities and stages of succession mainly lacking trees higher than 5 m, with shrubs and herbs as main plant species), agricultural fields (annual and perennial crops), semi-natural habitats (planted forests comprising mainly pines of the species *Pinus halepensis* Miller, *Pinus pinea* L., *Pinus brutia* Tenore and to a lesser extent pines mixed with planted native broad-leave species), some rural settlements and a few urban and industrial areas (Weizel et al., 1978) (**Figure 2**).

STUDY CROP SYSTEM: SUNFLOWER FIELDS

The sunflower *Helianthus annuus* L. (Asteraceae) is an annual herb and in Israel grown for seed production but not for oil. Sowing takes place in March and harvest between July and September. Prior to our study, we interviewed local farmers to get information about pest species of the study area. The Rose-Ringed Parakeet was reported as being a severe pest species consuming seeds directly from sunflower heads (see also Nemtzov, 2003; Schäckermann and Weiss, personal observations, August 2010) (**Figure 1**).

We selected similarly managed sunflower fields, concerning time of sowing, irrigation and pesticide application, of three hybrid seed production varieties (Shelly, Shemesh, Dalet Yod 3). All fields were treated with the fungicide Bayfidan and with the insecticide Endosulfan once during bloom and irrigated with a drip system from April/May until June/July, depending on the time of sowing and harvesting. The sunflower fields were alternated with cotton, chickpea, watermelon, maize or spring

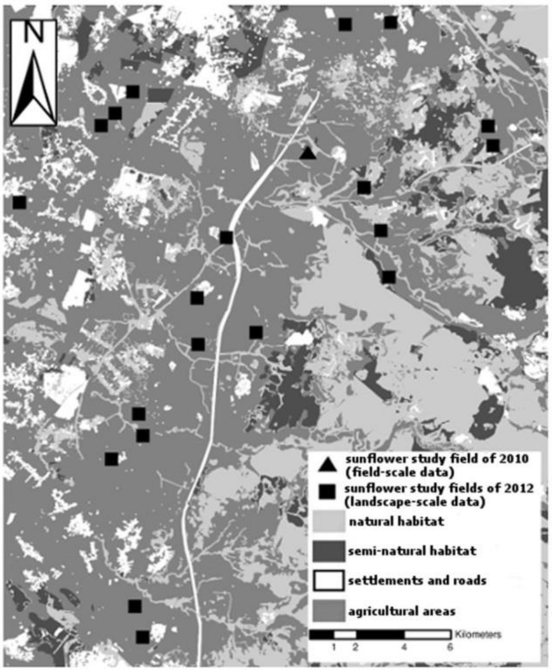

FIGURE 2 | Study area, habitat types and the distribution of the sunflower study fields at the field scale in 2010 and at the landscape scale in 2012 in the Judean foothills of Israel.

wheat in the next season or with winter wheat in a double-cropping system in the same season. The size of fields varied from 1 to 66 ha.

SUNFLOWER FIELD SELECTION

One field with high visible seed predation was chosen in 2010 for field-scale data collection using a grid system. In this field at least half of the sunflower heads at the margins showed signs of seed predation and this was reported by sunflower farmers of the study area as highly predated by birds. Within the grid-collection system, vertical and horizontal rows were selected every 50 m for the entire field. At each of a total of 140 intercept points (when vertical and horizontal rows were crossing), we estimated the percentage of seed predation per each of 50 sunflower heads (summing up to a total of 7000 sunflower heads). The estimation of the percentage of seed predation is described in Estimating Seed Predation.

In 2012, we selected 20 sunflower fields for a landscape-scale data collection to re-assess our findings from 2010 on a larger scale and to integrate landscape variables. We chose 10 fields with visible seed predation at the margins (more than 50% of the heads showed 10–100% seed predation) and 10 fields with little or no visible seed predation at the field margins (more than 50% of the heads showed 0–5% seed predation). Margins were chosen for this assessment because in 2010 we found that they suffer most from seed predation. For each field we selected two sampling points: (1) at field margin and (2) the interior of the field. Minimum distance between margin sampling points of different fields was 1 km. In each field, we used the margin with highest visible seed predation for sampling. In fields without or little seed predation we chose the margin sampling point randomly.

We measured the distances between the intercept points to the closest high tree (tree height > 5 m, single tree or a group of trees with at least one tree taller than 5 m) for all 140 intercept points of the field for the field-scale study in 2010 and for all margin and interior sampling points of all fields in 2012. We recorded the geographic coordinates at all margin sampling points of the fields in 2012 using GIS (ArcGIS, version 9.2., Esri 380 New York Street, Redlands, CA 92373-8100) and calculated in a 1 km radius surrounding the sampling point the (1) percentage of the natural habitat comprising scrubland without soil disturbance in the past 5 years (0–33%), (2) percentage of tree cover comprising high trees (0–20%), and (3) field size in ha. A 1 km radius is known to be an appropriate scale in vertebrate-focused landscape studies (Eilers and Klein, 2009; Guerrero et al., 2012). Land cover data was obtained from the archive of the Hebrew University.

ESTIMATING SEED PREDATION

We estimated sunflower seed predation of 50 randomly chosen sunflower heads at each of all 140 intercept points of the field in 2010; we therefore sampled 7000 sunflower heads in this one field. We furthermore sampled 50 randomly chosen sunflower heads each at the margin and interior sampling points in the 20 fields in 2012 (100 heads in each field and 2000 in total for 2012). We estimated seed predation per flower head by estimating the percentage of missing seeds caused by birds (seed predation estimated number of missing seeds eaten by birds/estimated number of all developed seeds in the head*100). Seeds were absent from sunflower heads through (1) seed predation by birds (**Figure 1**), (2) touching and rubbing of neighboring sunflower heads (mechanical removal), and (3) no development of seeds. Seeds removed by birds were distinguished from non-developed seeds because seeds removed after full development left "pockets" (palea adhered to the anthodium) (**Figure 3**) while these "pockets" were missing when unfertilized florets did not develop seeds. Mechanical removal was identified when complete seeds were found under the plant and this was not the case when seeds were eaten by birds.

STATISTICAL ANALYSES

We analyzed the field-scale count data from 2010 with generalized linear mixed models using a quasipoisson error distribution to account for over dispersion and penalized quasi likelihood (GLMM; packages = "nlme," "nlme4," "multcomp," "vegan"), (Script S2) (Pinheiro et al., 2007; Bates et al., 2013). We used generalized linear mixed models because of our non-normal distributed data (we did a visual test to find out if our data was normally distributed) and to fit in fixed factors as well as random factors. This approach is recommended in the literature (Bolker et al., 2009). Seed predation was used as response variable and distance from the sampling point to the closest high tree in meters as explanatory variable. For the landscape scale

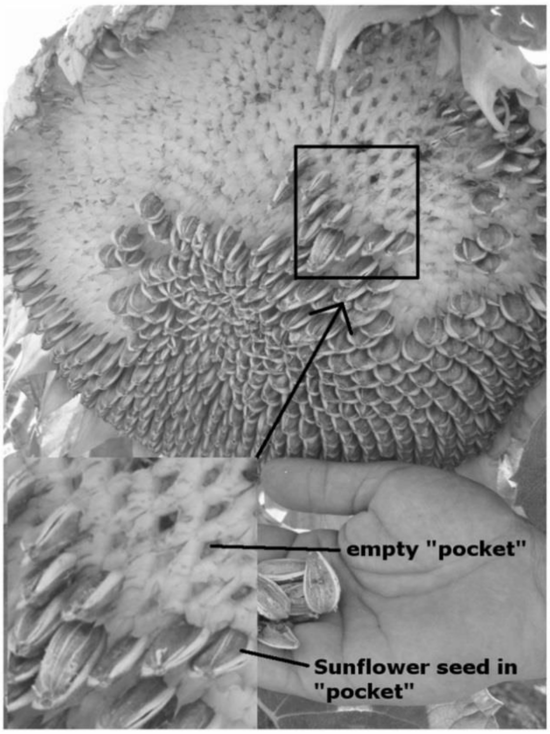

FIGURE 3 | Sunflower head with visible seed predation and empty sunflower shells from under the plant in the hand. Empty "pockets" of removed seeds and seeds in the "pockets" can be seen.

data comprising 20 fields in 2012, we also used generalized linear mixed models (Script S2). Models were analyzed using a poisson error distribution (to model the count data) or quasipoisson error distribution in case of over dispersion. Models with seed predation as response variable included the following explanatory variables as fixed factors: (1) distance from the sampling point to the closest high tree (in meters), (2) sampling point location (margin, interior), (3) percentage of tree cover in a 1 km radius surrounding the sampling point, (4) percentage of natural habitat in a 1 km radius surrounding the sampling point, (5) field size in ha. We used the additional explanatory variable (6) presence of high trees within 50 m for the landscape scale (tree or trees present (yes), no trees (no), because we detected similar patterns and a threshold of around 50 m at both the field-scale and landscape-scale analyses (**Figure 4**), when testing the effect of distance to the closest high tree on seed predation. Field and location within the fields were included as random factors if they were not included as explanatory variable (e.g., Nelder and Wedderburn, 1972). Correlations between explanatory variables were tested with a correlation matrix based on Spearman (**Table 1**). Because some of the explanatory variables were correlated, all variables were tested in separate models. In the following we present the standard results given for mixed model summaries (Zuur et al., 2009). Amongst others we give *p*-values (P) of our models. The *p*-value can be defined as the probability (therefore has a value between zero and one) how likely it is to obtain such a sample result or a more extreme, if the null hypothesis is true. The threshold used was 5% (0.05). Furthermore, we give the *t*-value (T) which measures how many standard errors the coefficient is away from zero. Generally, any *t*-value greater than +2 or less than −2 is acceptable. This is also the threshold we used for all our analyses. The higher the *t*-value, the greater the confidence we have in the coefficient as a predictor. Low *t*-values are indications of low reliability of the predictive power of that coefficient. All statistical analyses were conducted using R (R Development Core Team, 2010, version 2.12.0).

RESULTS

Seed predation at the field scale in 2010 decreased with increasing distance to the closest high tree within 50 m ($T = -2.8889$, $P = 0.0045$) (**Figure 4A**). At the landscape scale in 2012, seed predation within the field margins was higher than in the interiors of the fields (**Table 2**), therefore margins and interiors were evaluated separately. Similar to the findings at the field scale, seed predation at the margin sampling point of sunflower fields decreased with increasing distance to the closest high tree (**Figure 4B**, **Table 2**), showing the same threshold of 50 m like the field-scale data (**Figures 4A,B**). When testing the effect of the 50 m threshold at the landscape scale, seed predation at the margin sampling point of sunflower fields was higher in fields surrounded by high trees within 50 m than in fields without high trees in this radius (**Figure 5**, **Table 2**). At the margins, we found an average seed predation rate of 37%, with a maximum of up to 92% if high trees were present within 50 m. Less than 5% seed predation was observed at field margins if the closest high tree was further than 50 m away. While seed predation at the margins decreased with increasing distance to the closest high tree, it was not related to the overall percentage of tree cover in the surrounding landscape (**Table 2**). When considering the field interior sampling point only, seed predation was not related to the distance of the closest high tree (**Table 2**). Seed predation by birds at both sampling points was neither related to the percentage of natural habitat surrounding the fields nor to the field size (**Table 2**).

DISCUSSION

HIGH TREES ADJACENT TO CROP FIELDS AND SEED PREDATION

Seed predation increased strongly with decreasing distance to the closest high tree or tree group within 50 m in our study. Because birds were the main sunflower seed predators in our study area, our results agree with the findings of Hanspach et al. (2011) who found that scattered trees were key habitat structures for birds in semi-natural open areas. We observed flocks of a few hundreds of birds of the Rose-Ringed Parakeet in our study area, (Personal Observation and reports by local farmers) (**Figure 1**), one of the main bird pests to agriculture in Israel (Nemtzov, 2003). However, in other agricultural areas in Israel, flocks with up to a few thousands of birds were reported by local farmers (Personal Communication, Yoav Motro, Ministry of Agriculture and Environment).

In areas with higher bird abundance, the pressure on individual birds to locate food should be stronger, and they may therefore

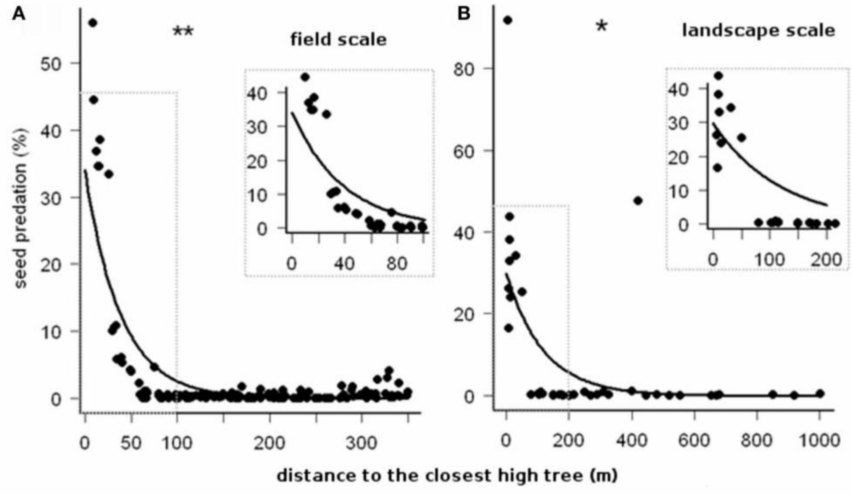

FIGURE 4 | Percentage of seed predation per field and intercept/sampling point (shown as mean seed predation per sampling point) in relation to the distance of closest high tree, (A) of the entire field sampled in 2010 and in the inset, intercept points that were not further than 100 m from the next high tree for statistics see Results. **(B)** Across all fields sampled in 2012, and in the inset only the sampling points with a high tree within 200 m ($T = -2.5025$, $P = 0.0216$). $^*p < 0.05$; $^{**}p < 0.005$.

Table 1 | Correlation matrix of the explanatory variables field size in ha, presence of high trees (higher than 5 m) within 50 m to the sampling points (at least a single tree or a group of trees was present within 50 m to the sampling point), distance to the closest high tree (single or group) in m from the sampling point, natural habitat in % surrounding the sampling point in a 1 km radius and tree cover in % surrounding the sampling point in a 1 km radius) was used to analyze correlations between explanatory variables.

	Field size (ha)	Presence of high trees (within 50 m)	Distance to high tree (m)	Natural habitat (%)	Tree cover (%)
Field size (ha)	–	0.9137	0.5021	0.8213	0.6633
Presence of high trees (50 m)	0.0259	–	0.0002	0.5105	0.0987
Distance to high tree (m)	−0.1594	0.7468	–	0.7461	0.0257
Natural habitat (%)	0.054	0.1563	−0.0773	–	0.0224
Tree cover (%)	0.1038	−0.3797	−0.4972	0.5074	–

Correlation coefficients are given on white background, p-values on light gray background. For more information see Statistical Analyses.

Table 2 | Effects on the percentage of seed predation of sunflower at the landscape scale in relation to the sampling point, presence of high trees (higher than 5 m) within 50 m to the sampling points, distance to the closest high tree or tree groups, natural habitat in % surrounding the sampling point in a 1 km radius, tree cover in % surrounding the sampling point in a 1 km radius and field size in ha.

Explanatory Variables	Sampling point	Estimate	Std. Error	*DF*	*t*-value	*p*-value
Sampling point (margin/interior)	–	**−4.2588**	**0.4882**	**1979**	**−8.7234**	**<0.0001**
Presence of high trees (50 m)	Margin	**−4.4583**	**0.6759**	**18**	**−6.5959**	**<0.0001**
Distance to high tree (m)	Margin	**−0.0080**	**0.0021**	**18**	**−3.7983**	**0.0013**
Distance to high tree (m)	Interior	−0.0013	0.0011	18	−1.1486	0.2658
Distance to high tree (m)	Margin + Interior	−0.0017	0.0046	19	−0.3735	0.7129
Natural habitat (%)	Margin	−0.0630	0.0728	18	−0.8652	0.3983
Tree cover (%)	Margin	0.1359	0.0909	18	1.4944	0.1524
Field size (ha)	Margin	−0.0234	0.0388	18	−0.6025	0.5544

Significant relationships are highlighted in bold (Std. Error is the standard Error; DF stands for Degrees of Freedom). Data was analyzed with generalized linear mixed models. For more information concerning the statistical analysis see Statistical Analyses.

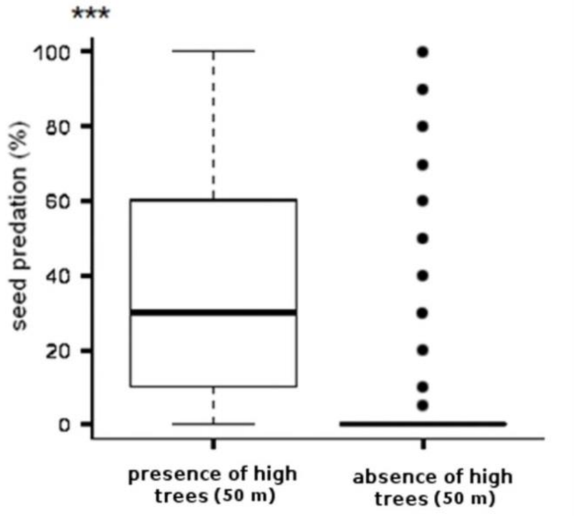

FIGURE 5 | Percentage of seed predation in the field margins presented in boxplots (median, upper and lower quartile, maximum, minimum, and outliers) of two different categories; fields with high trees or fields without high trees within a radius of 50 m. For statistics see **Table 2**. ***$p < 0.0005$.

exceed the main foraging distance of 50 m we found in our study. When comparing seed predation at the margin sampling points to the interior sampling points of the field- and at the landscape scale, we found that the margins were more affected, showing that birds live outside the sunflower fields and gradually forage toward the interior, starting at the margins. Many species tend to feed on field margins and may only move to the field interiors when food resources become limited (Kollmann and Buschor, 2002). This was also supported by our results for seed predation at the field scale throughout an entire field. Here, we found the highest seed predation at the margin intercept points of the field adjacent to a high tree or small group of trees. Hence, a field that seems highly predated at the margin does not necessarily show predation in the interior. High trees or tree groups are usually located outside the fields and therefore sunflower plants in the interior are generally further away than plants at the margin.

The dependence of seed-predating birds on high trees may also explain the high spatial variance in seed predation between different fields. If there were no high trees adjacent to the fields, we only observed very little seed predation, but there was a dramatic increase in crop seed predation by birds in crops adjacent to high trees. While birds seemed to depend on the presence of high trees to scope parts of the landscape as potential feeding areas, a higher percentage of tree cover did not cause higher seed predation in crop fields. Therefore, the high spatial variance in seed predation seems to be related to the appearance of high trees used for perching by birds. This supports findings of Fischer et al. (2010) where the number of trees was rather negligible and only the general presence of a single tree drove the overall pattern of bird richness in an Australian livestock grazing landscape. Therefore, individual trees should be taken into account in land-management planning, since at least in Israel it is not an easy option to cut trees in agricultural areas, because permissions for doing so are needed for every tree. We furthermore observed Hooded Crows picking single sunflower seeds and consume them outside of the crop fields, while the Rose-Ringed Parakeet consumed many seeds without moving at top of the sunflower heads in the fields (Schäckermann, personal observations and see also **Figure 1**). Even though the crow and the parakeet are both granivorous birds and crows have a higher body mass, their actual contribution to seed predation may vary considerably mediated by their predation activity. Therefore, different granivorous bird taxa should be considered (Notman et al., 1996). Hence, feeding behavior as well as local abundances of main bird species found in agricultural areas, that can influence the high spatial variance in seed predation between different fields, should be taken into account when predicting the impact of birds on seed predation. Even though high trees were the main perch (high structures for birds to sit on and perch) in our study, we also observed high seed predation by birds in one field with no trees in its surroundings (outlier in **Figure 5**). However, we did find electric pylons and power lines next to the field and small buildings in the area. Therefore, the availability of perches may influence seed predation in sunflowers. Future research should therefore investigate the impact of these man-made landscape structures (alone and in combination with high trees) and different habits of different seed predators. This may lead to more detailed management recommendations regarding the interaction effects of different natural and man-made landscape structures on biodiversity and ecosystem services or dis-services relationships.

NATURAL HABITAT AND SEED PREDATION BY AN INVASIVE BIRD

Natural habitats can cause services (benefits) or dis-services (negative effects) or a combination of both to agriculture (Zhang et al., 2007; Bommarco et al., 2013; Martin et al., 2013; Ango et al., 2014). In our study, natural habitats were found to be unsuitable for sunflower seed-predating birds because they did not contain trees that could be used as perching structures. Also other studies found that natural and semi-natural field margins are not suitable as breeding habitats for birds feeding on crops, but offered shelter to a broad range of bird species (for example Song Sparrow *Melospiza melodia* Wilson, Vesper Sparrow *Pooecetes gramineus* Gmelin, Savannah Sparrow *Passerculus sandwichensis* Gmelin, Red-winged Blackbird *Agelaius phoeniceus* L. and American Goldfinch *Carduelis tristis* L.) potentially useful for biological pest control (Jobin et al., 2001). High natural trees rarely occur in our study area in Israel, but introduced high-grown Eucalyptus trees can be frequently found. In our study area, high Eucalyptus trees are often located close to settlements, probably grown to spend shade in summer (Schäckermann, personal observations). Because it is known that many bird species prefer high landscape structures for perching (Bull et al., 1992; Sonerud, 1992; Holl, 1998; Miller and Cale, 2000), the presence of trees taller than 5 m improves the habitat quality, especially for birds originated in forest areas, like the Rose-Ringed Parakeet, one of the main seed predators on sunflower in Israel. Furthermore, Rose-Ringed Parakeets depend on cavities as nesting sites (Strubbe and Matthysen, 2007). In our study area, Rose-Ringed Parakeets used holes in buildings as nesting places (Weiss, personal observation) and crops they used as food resources are often planted close to settlements. Knowing that the Rose-Ringed Parakeet, which is an invasive bird in Israel and an agricultural pest, uses an introduced tree species for perching indicates, that humans can unintentionally create suitable habitats for pest bird species. Ornithologists and nature conservationists in Israel are concerned that the high numbers of Parakeets negatively influence the population density of native cavity-nesting birds, by occupying their nesting sites and reducing their breeding success (Weiss, communication with local conservationists and ornithologists). Birds of concern are the Hoopoe (*Upupa epops* L.), Syrian Woodpecker (*Dendrocopos syriacus Hemprich and Ehrenberg*) and European Scops Owl (*Otus scops* L.). Research about the effects of the introduced Rose-Ringed Parakeet on native cavity-nesting bird species and other invasive birds showed, that there are complex interactions between invasive birds, these interactions had an effect on native cavity-nesting birds (Orchan et al., 2013) showing, that a complex interaction network between native and invasive bird species exists. Globally invasive species have enormous ecological and economic costs and are an important threat to biodiversity (Wilson, 1992; Pimentel et al., 2005; Shine et al., 2009). There are many hypotheses on why birds established and/or are becoming invasive (e.g., Case, 1996; Blackburn and Duncan, 2001; Duncan et al., 2003; Cassey et al., 2004; Blackburn et al., 2009). Nevertheless, more knowledge is needed about the impact of invasive bird species on the environment and economy in the invaded range.

CONCLUSIONS, RECOMMENDED MANAGEMENT PRACTICES AND FUTURE RESEARCH

To minimize the negative impact of birds to crop harvest, a shift in management practices considering landscape structures such as high trees seems necessary and habitat management is recommended to potentially control populations of birds acting as agricultural pests (MacLeod et al., 2011). Our results show that farmers should avoid growing crops, which are susceptible to seed predation by birds, adjacent to high trees (tree height > 5 m) and if possible decide to grow crops which are not likely to suffer from seed predation by birds closer to high trees. Crops that are susceptible to bird seed predation should not be adjacent to high trees, to reduce seed predation. The location and shape of fields should therefore be planned according to surrounding conditions.

Also bird population suppression methods like culling or poisoning, which are used by agricultural producers (Conover, 2002), could be replaced by advanced crop planning, taking into account high trees and other natural and man-made landscape structures that can be used as perches. Distances of these structures to the fields should be taken into account, to include spanned distances between fields and target bird species in the planning. Hence future research should aim to understand the habitat requirements of bird pests and their foraging behavior, since effective management and conservation of avian communities require our understanding of temporal patterns of bird abundance and their implications (Best, 2001). This will help finding solutions to reduce crop seed predation harming agriculture and the environment. By spreading our results across farmers, high-quality habitats for bird pests adjacent to agricultural fields susceptible to bird seed predation can be reduced with the long-term conservation goal to control or even reduce the populations of bird pests. Since natural pest control concerns not only single fields but whole agricultural landscapes, farmers in the same region need to work jointly to implicate landscape management to promote ecosystem services while reducing ecosystem dis-services.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fevo.2014.00035/abstract

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For supporting online material see Appendix Chapter III

General Discussion

Summary of Results

In Chapter I, I investigated which species of vertebrates can be found in almond and sunflower fields and if their impact on crop seed predation is related to the percentage of natural and semi-natural habitat surrounding the crops. In almond orchards, I observed 795 individual birds of 32 species, including 357 individuals and 11 species of granivorous and hence potentially seed predating birds. In sunflower fields, I observed 620 individual birds of 33 species including 422 individuals of 13 species of granivorous birds. I only trapped one Tristram´s jird (*Meriones tristrami* Thomas) and one house mouse (*Mus musculus* L.) in the almond orchards.

The abundance of all birds and of granivorous birds in the study sites was not correlated to an increasing percentage of natural habitats. I did find though that the bird species richness increased with increasing percentage of semi-natural habitat. Furthermore, I observed that the number of bird species was significantly higher at the edge compared to the interior of the study sites (edge effect). This was not true for just granivorous birds or for the abundance of birds. The percentage of natural and semi-natural habitat had no influence on seed predation. But I found that also, seed predation was significantly higher in the edge than in the interior of the study sites (edge effect). The percentage of seed predation increased with increasing abundance and species richness of birds. I performed an exclusion experiment in the almond orchards where I excluded birds, rodents, both or none from almond access. Compared to the exclusion of both, the percentage of seed predation increased significantly when just birds had access to the almonds, when just rodents had access to almonds and when both had access to almonds.

In Chapter II, I focused on the question how natural and semi-natural habitats surrounding almond fields influence almond pest infestation and predation by the almond wasp (dis-service), the abundance of its parasitoids (service) and how these habitats influence granivorous birds.

Almond wasps caused between 0 % and 77 % of almond predation and I observed higher almond wasp predation at the edge of orchards than in the interior (edge effect), with semi-natural habitat having a positive effect on almond wasp predation. I recorded 611 parasitoid individuals with 43 individuals (7%) from the genus *Adontomerus*, but in general parasitoid rates were low. Parasitoid abundance was not influenced by the percentage of semi-natural or natural habitats surrounding the orchards and I did not detect an edge effect. I observed a total of 220 granivorous birds from 20 species in all orchards. I did not find that the surrounding habitat had an effect on granivorous bird abundance, but the percentage of semi-natural habitat negatively influenced the abundance of granivorous birds. I found that parasitoid abundance was positively related to the percentage of almond wasp predation and that the percentage of almond wasp predation of the current year was positively influenced by almond wasp predation of the previous year (almond wasp predation in mummy nuts). On average, 56% of the almond shells found on the ground in orchards had bird feeding marks, rodents accounted for 3% of the damage and 41% of the almond shells did not show any feeding marks. I did not find a correlation between granivorous bird abundance and the number of mummy nuts. Granivorous bird abundance was also not related to the bird feeding marks on almond shells under the trees.

Different to the first two chapters, chapter III concentrated directly on birds as seed predators and the drivers for bird seed predation. Here, seed predation on sunflower seeds (Fig. F) at the field scale, decreased with increasing distance to the closest high tree within 50 m. At the landscape scale, seed predation at the field margins was higher than in the interiors of the fields. Similar to the findings at the field scale, seed predation at the margin sampling point of sunflower fields decreased with increasing distance to the closest high tree with a threshold of 50 m. When testing the effect of the 50 m threshold at the landscape scale, seed predation at the margin sampling point of sunflower fields was higher in fields surrounded by high trees within 50 m than in fields without high trees in this radius. At the margins, I found an average seed predation rate of 37%, with a maximum of up to 92% if high trees were present within 50 m. Less than 5% seed predation was observed at field margins if the closest high tree was further than 50 m away. While seed predation at the margins decreased with increasing distance to the closest high tree, it was not related to the overall percentage of tree cover in the surrounding landscape. Seed predation by birds at both sampling points was not related to the percentage of natural habitat surrounding the fields.

Figure F: Sunflower heads with ripe seeds on the left. On the right, after feeding activity by Rose-ringed parakeet (*Psittacula krameri* Scopoli).

General Discussion

Species of pests (dis-service) and natural bio-control agents (service)

My results show that birds and rodents occur in almond fields and birds also occur in sunflower fields, acting as seed predators (Fig. G). Even though I did not catch many rodents in almond fields, I found them acting as seed predators in the almond exclusion experiment. Additionally, I found rodent as well as bird feeding marks on nuts under the trees. Therefore, vertebrates foraging in almond and sunflower fields are birds and rodents of different species.

Figure G: Almonds on tree with vertebrate feeding marks. Considering the appearance of the feeding marks, they most likely resulted from rodents.

Other studies also report birds in agricultural crops like the Canada goose (*Branta canadensis* L.), the Chukar partridge (*Alectoris chukar* Gray), the Rose-ringed parakeet (*Psittacula krameri* Scopoli), the Ring-necked phesant (*Phasianus colchicus* L.) and Blackbirds (Icteridae), some of them are severe pests to agriculture (Moran, 2003; Linz *et al.*, 2011; Radtke & Dieter, 2011). The main bird species I observed damaging the sunflower harvest by predating sunflower seeds was the Rose-ringed parakeet (*Psittacula krameri* Scopoli). This bird has been described as one of the main bird pests to agriculture in Israel (Nemtzov, 2003). To a lesser extent I also observed Hooded crows (*Corvus cornix* L.) and Eurasian jays (*Garrulus glandarius* L.) in the sunflower study sites, while collecting seed predation data. The exclusion experiment and the feeding mark collection in almond fields showed that birds are the main drivers for seed predation in almond fields. Rodents were found to do less but still significant damage due to seed predation. In the exclusion experiment, I furthermore observed that also invertebrates caused some seed predation in almonds; I especially observed ants to feed on almond seeds. Invertebrates are known seed predators (Andersen, 1988; Cummings *et al.*, 1999) and could access almonds, which were protected from birds and rodents. The other main invertebrate I found infesting and destroying almonds was the almond wasp (Fig. H). I recorded predation rates between 0% and 77%. I furthermore found invertebrate parasitoids in the collected almonds from the genus *Adontomerus*, but in very low rates. Little is known about parasitoids of almond wasps and to the best of my knowledge; no research exists for the parasitoid species of the almond wasp in Israel. The difficult identification of these parasitoids that requires expert identification skills might play a role in this. With low parasitoid rates effective bio pest control is not possible. Further studies are necessary to find the limiting factors for parasitoids like suitable habitats (Lewis *et al.*, 1998; Shaw, 2006; Holzschuh *et al.*, 2009) which can provide food, nesting sites and refuges for natural pest enemies (Thies & Tscharntke, 1999; Bianchi *et al.*, 2006). Research is needed to create fitting habitats according to the needs of specific natural enemies, which is a key issue for the successful application of functional agrobiodiversity (Pfiffner, 2014).

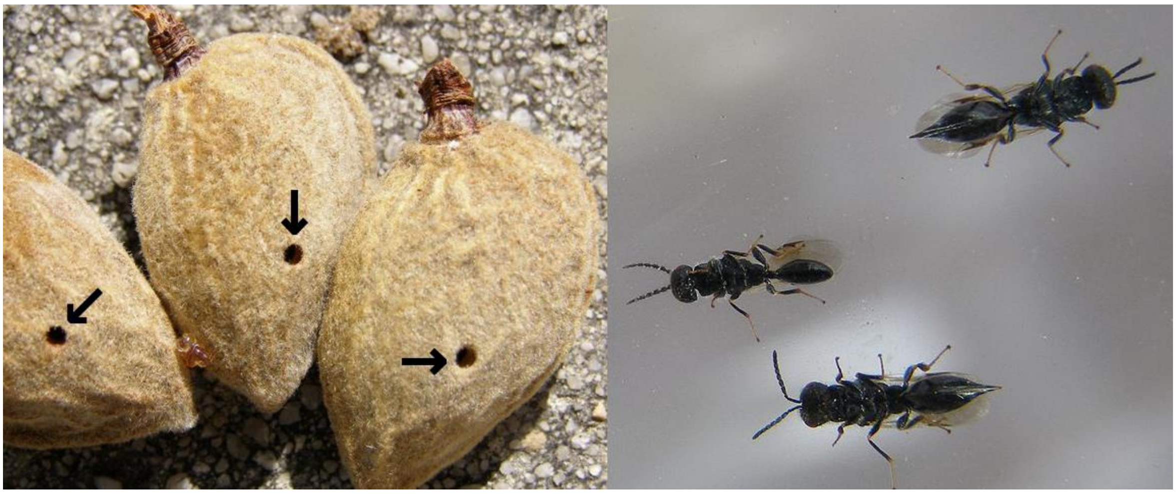

Figure H: On the left: The almond wasp emergence holes marked with black arrows. On the right: adult almond wasps. Left picture modified after
http://cultivodelalmendro.blogspot.co.il/2013/03/avispilla-del-almendro-eurytoma.html,
right picture modified after H. Dumas.

The influence of natural and semi-natural habitat on pests and service agents and their interactions

The concerns of farmers, that natural habitat might be a driver for pests in almond and sunflower fields; were miscalculated. I did not find bird abundance or bird species richness, for all and for granivorous birds, to be related to the percentage of natural habitat in the surrounding. Also almond wasp infestation and parasitoid abundance in almond and bird seed predation in sunflower fields was not related to natural habitat. In total, I did not find any negative impact of natural habitat on agriculture, not by enhancing pests or by reducing services. Therefore, farmers do not need to fear any dis-service or disadvantage from natural habitat with regards to bird seed predation and almond pests. Future landscape planning can consider promoting natural habitats in agricultural areas adjacent to crops for nature conservation reasons (Batáry *et al.*, 2010; Fischer *et al.*, 2010b; Tscharntke *et al.*, 2012) and for enhancing services to agriculture like pollination by wild pollinators or pest control services by vertebrates and invertebrates (Bianchi *et al.*, 2006; Mandelik *et al.*, 2012). Similar studies should be conducted in other study regions to understand to which landscapes and regional conditions these recommendations concerning natural habitat can be transferred.

For semi-natural habitat I found a more diverse set of results. The bird species richness was higher with a higher percentage of semi-natural habitat in the surrounding of almond and sunflower fields. Semi-natural habitat in my research area is interspersed with trees that might act as perches for birds. This can result in higher species richness in adjacent fields, because of a more diverse habitat compared to natural habitat which is lacking trees (Miller & Cale, 2000). Therefore, the positive relationship of bird species richness with semi-natural habitat but not with natural habitat may be explained by absent perches in the natural habitat. When I investigated the abundance of granivorous birds in almond fields I found a negative influence of percentage semi-natural habitat on the bird abundance. The availability of high trees, which are often used by raptors for perching (Hall *et al.*, 1981; Preston, 1990), can attract a higher number of raptors and their presence might scare off granivorous birds, since they may be prey for the raptors (Darawshi *et al.*, 2006). Even if semi-natural habitat did improve the species richness of birds, I did not find a higher abundance of granivorous birds, which could act as seed predators and thus would be classified as pests.

Semi-natural habitat did have a positive effect on almond wasp predation rates, but their parasitoids were not influenced by semi-natural habitat. Hence the dis-service was enhanced by semi-natural habitats but not the service. The link between semi-natural habitat and almond wasp seed predation might be through wild seeded almond trees in the semi-natural habitat, providing habitat for almond wasps (Plaut, 1971; Kouloussis & Katsoyannos, 1994) but also an indirect link through predation pressure might be possible. Granivorous birds that act as seed predators were less abundant in sites with higher semi-natural habitat in their surroundings. Granivorous birds possibly act as cleaning agents after harvest by feeding on leftover (mummy) nuts that are breeding habitats for the next generation of almond wasps and the birds would therefore provide a valuable service to farmers by controlling the pest abundance of the next season. If these birds appear in lower numbers in the sites, the cleaning effect might be less effective leading to higher pest abundances. This would also mean that the dis-service of bird seed predation before harvest could turn into a service after harvest by destroying the habitat for invertebrate pests. To investigate this theory, exact relations between granivorous birds, semi-natural habitat and almond wasp abundances need to be surveyed in more detail as well as the exact influence of bird seed predation after harvest. Hence data collection of bird feeding behaviour after almond harvest and almond wasp abundances of several years would be needed. With in-depth knowledge of these links it would be possible to develop management strategies for agricultural areas that support beneficial organisms without increasing pest pressures (Isaacs *et al.*, 2009; Martin *et al.*, 2013), and to give more precise management recommendations to farmers. Hence detailed knowledge about specific pests and bio-control agents for different services and dis-services is needed to plan the location, distribution, and size of agricultural fields in an advanced matter.

Predicting Services and Dis-services

In the field and landscape scale study I conducted in sunflower fields, I found that the dis-service of seed predation increased strongly with decreasing distance to the closest high tree or tree group within 50 m. Birds were the main sunflower seed predators and therefore pests in my study area. Our results agree with the findings of Hanspach et al. (2011) who found that scattered trees were key habitat structures for birds in semi-natural open areas. In areas with higher bird abundance, the pressure to locate food might be stronger and the foraging distance of 50 m might be exceeded. In the field scale study I found the highest dis-service of bird seed predation at the margin of the field adjacent to a high tree or small group of trees. The dependence of granivorous birds on trees might explain the high spatial variance in seed predation between different fields but a higher percentage of tree cover did not result in higher seed predation. Hence, this dis-service seems to be related to bird perches like high trees. Also Fischer *et al.*, (2010a) found that the number of trees is not important but the general presence of a single tree drives the bird richness. Therefore, individual trees and other perches should be taken into account in land-management planning and growing sunflowers distanced from high trees as well as removing non-native trees in agricultural areas might decrease this dis-service.

If granivorous birds, which are pests of almond before harvest (dis-service), would destroy almond wasp habitats after harvest, they could provide an important service of “bird cleaning”. Especially during bird migration, high numbers of birds pass through Israel in spring and autumn, thus before almonds are attractive to birds and after harvest. Migratory and overwintering granivorous birds can therefore not damage the crop but might act as service agents after harvest. The timing of pest predator arrival to agricultural fields was found to be an important issue for mediating pest control in agro ecosystems (Costamagna *et al., in press*) the same might apply for bird seed predation. In my study, I did not find that bird abundance was related to almond losses before harvest (dis-service) or destruction of mummy nuts (service). However, bird abundance data was collected after harvest but a change in bird abundance before and after harvest is likely due to migration. To examine the “bird cleaning” impact, bird feeding rates on almonds need to be investigated after harvest for a couple of months and to be compared with almond wasp predation rates of several years. Furthermore, the exact species providing the potential “bird cleaning” should be identified. Bird species which are known to be service agents could be supported by improving their habitats for example with feeding stations (Robb *et al.*, 2008) or water sources (Johnson, 2007). Also land sharing (e.g. agri-environment schemes, organic agriculture, environmental certification (Law & Wilson, 2015)) was found to benefit bird populations and crop production, due to the service of pest control provided by beneficial birds (Railsback & Johnson, 2014).

Agricultural management recommendations

Because I did not find a negative effect of natural habitat considering crop seed predation I recommend the consideration of conserving or restoring natural habitats adjacent to crop fields, to increase possible services to agriculture like pollination and pest control. Semi-natural habitat did have different positive and negative influences on agriculture and thus should be considered carefully in agricultural planning. Converting semi-natural habitat to a more “natural” state by reducing the abundance of non-native trees might mitigate this dis-service. But trees in Israel are protected by law, hence I think this might be a difficult and time consuming task and to convince pro forest activists like the Keren Kayemeth LeIsrael (www.kkl.org.il) whose goal is a “green Israel” will be tough. Regardless future landscape planning should take the impact of non-native trees into account when creating recreational sites in agricultural areas. In my opinion landscape planning should work in partnership with the farmers and scientists of the area to mitigate negative effects created by human hand before they exist. My findings highlight the importance to manage natural and semi-natural habitats in agricultural landscapes proactively to mitigate yield gaps (Bommarco *et al.*, 2013). This requires information of potential benefits (ecosystem services) and costs (ecosystem dis-services) for different habitats and ecosystems. Considering trade-offs and interactions of multiple ecosystem services and dis-services as well as different interspecific interactions between pests, their parasitoids, vertebrates and the influence of adjacent habitats as well as the time of seed predation before or after harvest are crucial for land managers and policy makers to enable sustainable management and maximize yields without compromising biodiversity.

Birds which were counted after harvest were not found to be related to bird seed predation on almonds before harvest. These birds could potentially provide an ecosystem services to agriculture by removing over-wintering and infested nuts after harvest, reducing the impact of almond wasps in following seasons. Birds and other vertebrates are known for controlling pest populations (Dix *et al.*, 1995; Mols & Visser, 2007; Railsback & Johnson, 2014), and the conservation and management of natural habitats in agricultural landscapes to enhance beneficials habitats should be further considered and studied. Gilroy *et al.* (2014) for example recently concluded that agri-environmental schemes on farmland (land sharing) are most effective for bird conservation when large blocks of natural habitats are available in these landscapes (land sparing).

According to my findings farmers should avoid growing crops, which are susceptible to seed predation by birds, adjacent to high trees that act as perches. The location and shape of fields should therefore be planned according to surrounding conditions. By growing bird seed predation sensitive crops at least 50 m away from bird perches and reducing the abundance of non-native trees bird suppression methods like culling or poisoning, could possibly be replaced by these advanced crop planning methods. These results show that for the planning of agricultural landscapes information on the habits of target pest species are valuable. Hence, future research should aim to understand the habitat requirements of pests and their foraging behavior.

General conclusions and future directions

My study highlights that connections between ecosystem dis-services and specific habitats or habitat structures exist. Interestingly, I did not observe that natural habitat increase ecosystem dis-service, which would allow combined conservation and agricultural management efforts in maintaining natural habitats in agricultural settings. Semi-natural habitat should be considered carefully in agricultural planning, due to its possible different influence on different services and dis-services. Single landscape structures like high trees can be predictors for dis-services, here seed predation by birds, and should be therefore taken into account in agricultural planning.

My study could address and answer some important questions concerning services and dis-services in agricultural areas but like any other research project I also opened up new research questions. In future research I would deepen the investigation about the effect of different habitat types and structures on multiple ecosystem dis-services. In my study I could show that semi-natural habitat has an effect on almond wasps, in future studies I would investigate which structures in semi-natural habitat are influencing almond wasp abundance. I would continue my research on parasitoids of the almond wasp, their limiting factors and if improved surrounding habitat conditions can improve their abundance. Maalouly *et al.* (2013) for example found, that the parasitoid community of codling moth in apple orchards is dependent on the presence of local hedgerows. Similar studies would also be sensible for the parasitoids of the almond wasp. I would find it highly interesting to investigate the tradeoffs between multiple ecosystem services and dis-services, since they can have different effects on each other. Would, for example a high abundance of granivorous birds, doing a leftover almond clean up in in almond fields after harvest, influence parasitoid abundances in the following year by destroying their habitats? If so, which of these two services has the higher value for farmers and should be supported?

I would continue my research on birds, but would go more into detail concerning bird seed predation in almond fields after harvest, mainly in winter for overwintering birds. Seed eaters like Chaffinch (*Fringilla coelebs* L.) or Greenfinch (*Carduelis chloris* L.) would be species of interest because the bird cleaning they could conduct might be fairly high since these birds are moving in flocks. In addition, I would continue to collect data about almond wasp predation rates over several seasons to compare this dis-service with the overwintering bird data to see if bird cleaning is an effective ecosystem service to agriculture.

I personally understood in the years of the preparation of my PhD the importance of scientists working hand in hand with the people of the research area, in my case farmers. In my mind applied science and research should try to address real world problems, find better solutions and help people and nature to live friendlier, more sustainable and healthily together. This is just possible if scientists really understand the needs and problems of people and nature, then try to find the reasons for the problems and provide possible solutions. There is no point in investigating a problem and offering a solution which cannot be applied in “real life”. Hence scientists also need to know the limitations of applying their findings and should be in close exchange with farmers or other locals. In my case it was very helpful to talk to farmers and hear their side of the problem and also what they think could be a solution. Much knowledge is gathered and passed from one generation to the next without any involvement of science. Therefore it seems sensitive to approach farmers right at the beginning, before data collection starts and keep them updated all the way. Like this they will also feel as part of the research and more likely agree to implement the findings in the end. I discussed my findings with Yoav Motro from the Ministry of Agriculture, who presented them in a conference especially for farmers in Israel. Following my presentation some farmers phoned me to ask further questions. Furthermore some of my findings were presented in the National Geographic Journal of Israel.

Another life experience I gained through my PhD was that problems bring people together even in conflict areas. The communication between Palestine and Israel is not always easy and many people from each side never met anyone from the other side.

The coordinator of a cross border project about biological pest control in agriculture heard about my research and invited me as a lecturer for an exchange visit between Palestinians, Israelis and Jordanians. At the beginning of the exchange people kept sitting together in groups connected to their country of origin. Then they started to talk about their challenges in crop management practices. On the second day new groups had come together. The sunflower farmers, the almond farmers, the olive farmers and so on of each country were sitting together discussing their problems and possible solutions. At that point none of them cared about any political conflict anymore as they all aimed to find solutions working for all of them. I was amazed by the fact that simple life problems, like how to keep wild boar away from your crop, can bring people together that would have never talked to each other otherwise. One quote of one farmer at the end of the exchange visit was “I was surprised that we are all the same, they are so much more like us than I thought”. If solving problems in farming can help bring people together in crisis areas then we as scientists can be part of a peace process.

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Tagungsbeiträge

2013

Schäckermann, J., Mandelik, Y., von Wehrden, H., Klein A.M., 2013. השפעות אופי שטחים פתוחים על חברת העופות והמכרסמים ושיעור טריפת זרעים בשטחים חקלאיים. "The impact of habitats on bird and rodent communities and seed predation in agricultural fields." Conference lecture at the 41st Annual Conference of the Israel Society for Ecology and Environmental Sciences.

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Schäckermann, J., Mandelik, Y., von Wehrden, H., Klein A.M., 2012. Landscape effects on bird and rodent communities and seed predation to agriculture in Israel. Conference lecture at the 42nd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, p.147.

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Eigenständigkeitserklärung

Ich versichere, dass ich die eingereichte Dissertation mit dem Titel *„Vertebrates and insects as pest and bio-control agents in agricultural landscapes of the Judean Foothills in Israel“* selbstständig und ohne unerlaubte Hilfe verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

Appendix Chapter I

Supplementary online material Chapter I

Fig. S1: The bird was observed feeding on the same sunflower for several minutes. Missing seeds were removed by the shown individual.

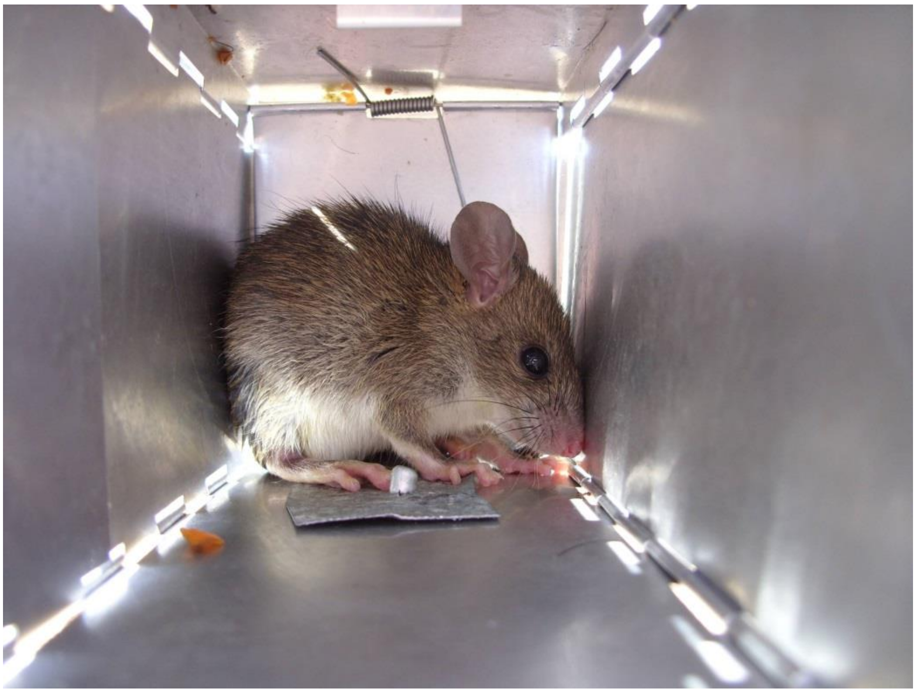

Fig. S2: The picture shows the mouse before removal from the trap, marking with colour codes in the neck and release.

Table S1: Correlation matrix of the explanatory landscape variables used to analyse wildlife and seed predation. Correlation coefficients are given on white background, p-values on grey background

	Natural habitat (%)	Semi-natural habitat (%)	Field size (ha)	Field age (years)
Almond				
Natural habitat (%)	-	0.6747	0.0591	0.4495
Semi-natural habitat (%)	-0.0759	-	0.5375	0.8152
Field size (ha)	-0.3320	-0.1113	-	-
Field age (years)	0.1363	-0.0423	-0.0260	-
Sunflower				
Natural habitat (%)	-	0.5573	0.2733	-
Semi-natural habitat (%)	-0.1096	-	0.0076	-
Field size (ha)	-0.2030	0.4702	-	-
Field age (years)	-	-	-	-
Almond and sunflower				
Natural habitat (%)	-	0.5051	0.0520	0.5523
Semi-natural habitat (%)	-0.0848	-	0.7514	0.7506
Field size (ha)	-0.2441	0.0404	-	0.0513
Field age (years)	0.0757	0.0405	0.2450	-

Table S2: Wildlife abundance and species richness in relation to the crop systems (almond or sunflower). Tested with generalized linear mixed model, fit by maximum likelihood. Significant relationships are highlighted in bold.

Response variable	Estimates	Std. Error	DF	t - Value	p - Value
Abundance of all birds	-0.1303	0.1204	6	-1.0818	0.3209
Species richness of all birds	-0.2026	0.0868	6	-2.3333	0.0584
Abundance of granivorous birds	0.1792	0.1475	6	1.2147	0.2701
Species richness of granivorous birds	-0.1553	0.0904	6	-1.7179	0.1366
Abundance of rodents	3.2280	0.0850	4	37.9400	0.0000
Species richness of rodents	2.2640	0.6840	4	3.3100	0.0297

Table S3: Correlation matrix of the response vertebrate variables. Correlation coefficients are given on white background, p-values on grey background

	Abundance of all birds	Species richness of all birds	Abundance of graniv. birds	Species richness of graniv. birds	Abundance of rodents	Species richness of rodents
Abundance of all birds	-	<0.0001	<0.0001	<0.0001	0.0985	0.4933
Species richness of all birds	0.7158	-	0.0018	<0.0001	0.8804	0.8569
Abundance of graniv. birds	0.8167	0.4844	-	<0.0001	0.0050	0.1215
Species richness of graniv. birds	0.6940	0.7674	0.6677	-	0.3339	0.7911
Abundance of rodents	0.2684	-0.0249	0.4401	0.1589	-	<0.0001
Species richness of rodents	0.1130	-0.0298	0.2521	0.0438	0.7462	-

Table S4: Bird and rodent species in the almond sunflower study sites. Numbers present the total abundance per species

Species	**Almond**	**Sunflower**
Birds		
Acrocephalus scirpaceus	0	20
Alectoris chukar	1	1
Bubulcus ibis	14	0
Burhinus oedicnemus	21	0
Carduelis cannabina	0	2
Carduelis carduelis	26	52
Carduelis chloris	15	5
Circus aeruginosus	0	1
Circaetus gallicus	1	0
Columba livia	4	0
Corvus corvus	32	7
Corvus monedula	1	6
Dendrocopos syriacus	2	1
Falco tinnunculus	3	4
Galerida cristata	93	215
Garrulus glandarius	45	2
Halcyon smyrnensis	0	1
Hippolais pallid	1	0
Hirundo daurica	0	11
Hirundo rustica	2	3
Locustella fluviatilis	0	1
Merops apiaster	0	10
Milaria calandra	0	4
Nectarina osea	4	7
Parus major	39	6
Passer domesticus	79	43
Passer hispaniolensis	5	0
Phylloscopus collybita	9	0
Prinia gracilis	63	73
Psittacula krameri	23	34
Pycnonotus xanthophygos	11	44
Serinus serinus	1	1
Streptopelia decaocto	228	13
Streptopelia turtur	7	25
Sylvia atricapilla	2	6
Sylvia communis	0	1
Sylvia crasirostris	1	0
Sylvia curruca	10	1
Sylvia melanocephala	13	16
Turdus merula	30	1
Vanellus spinosus	9	3
Rodents		
Mus musculus	1	46
Meriones tristrami	1	2

Appendix Chapter III

Supplementary online material Chapter III

Table S1:

Summary of recent studies focusing on seed predation by birds in sunflowers published between 2002 and 2014 and their main findings in the specific countries. For a full list of vertebrate species feeding on crops in Israel see: Moran, S. (2003). Checklist of vertebrate damage to agriculture in Israel, updated for 1993–2001. Phytoparasitica 31, 109–117. doi:10.1007/BF02980779.

Study title	Species	Country	Main findings	Journal and Year	Authors
Chronology and spatial distribution of cockatoo damage to two sunflower hybrids in south-eastern Australia, and the influence of plant morphology on damage	Cockatoos (Cacatua spp.)	Australia	Taller or lager sunflower heads were more, down-facing heads were less susceptible to seed predation. Early seed predation occurred near margins; later the whole crop was predated.	Agriculture, Ecosystems and Environment 91 (2002) 127–137	Peter J.S. Fleming, Arthur Gilmour, Jim A. Thompson
Optimizing the use of decoy plots for blackbird control in commercial sunflower	Blackbirds (Icterinae) (Agelaius phoeniceus, Quiscalus quiscula, Xanthocephalus xanthocephalus)	USA (northern Great Plains)	Lower blackbird seed predation was found in commercial sunflower fields that were closer than 2.4 km to decoy sunflower plots, than commercial sunflower fields >10 km away from decoy plots. In reference sunflower fields, birds removed 3.2 times more sunflower seed than in commercial sunflower fields near decoy plots.	Crop Protection 27 (2008) 1442–1447	Heath M. Hagy, George M. Linz, William J. Bleier
Effect of morphological traits of plant, head and seed of sunflower hybrids on house sparrow damage rate	House Sparrow (Passer domesticus)	Iran (Karaj)	Sunflower heads suffering lower seed predation by birds showed flower head traits such as greater diameter, flat and convex shape, fewer angles to the horizon, more down-faced heads, open and longer bracts, longer distances between adjacent stems or heads, longer distance of petiole from head, and lower seed density.	Crop Protection 30 (2011) 360-367	Abolghasem Khaleghizadeh
Comparisons between blackbird damage to corn and sunflower in North Dakota	Blackbirds (Icterinae)	USA (North America, Prairie Pothole Region)	Annual seed predation was on average 5.0 x 10^3 t (12 kg/ha, US $1.3 million) for corn, 7.2 x 10^3 t (45 kg/ha, US $3.5 million) for sunflower. Percent seed predation was significantly higher in sunflower than in corn fields.	Crop Protection 53 (2013) 1-5	Megan E. Klosterman, George M. Linz, Anthony A. Slowik, H. Jeffrey Homan
Application	Red-	USA	A positive concentration -	Crop	Scott J. Werner

strategies for an anthraquinone-based repellent to protect oilseed sunflower crops from pest blackbirds	Winged Blackbird (Agelaius phoeniceus)		response relationship among Blackbirds exposed to anthraquinone and an insecticide (a.i. 8.4 % esfenvalerate), or anthraquinone and a fungicide (a.i. 23.6 % pyraclostrobin) was observed. Blackbirds avoided fields treated with 1810 ppm anthraquinone and 0.1 % of the insecticide or 1700 ppm anthraquinone and 0.14 % of the fungicide in preference experiments.	Protection 59 (2014) 63-70	Shelagh K. Tupper, Susan E. Pettit, Jeremy W. Ellis , James C. Carlson, David A. Goldade, Nicholas M. Hofmann, H. Jeffrey Homan, George M. Linz
Non-Blackbird Avian occurrence and abundance in North Dakota sunflower fields	61 bird species (for full list see article, granivores see in findings)	USA (northern Great Plains)	Birds of the family Emberizidae (Sparrows) accounted for 33 % of the species and 38 % of the individuals. The families Fringillidae (Finches) and Columbidae (Doves) made up 17 % and 8 %, of the birds counted. Other granivores included Gallina-Ceous birds (Family Phasianidae), Crows and Jays (Family Corvidae), and Black-Capped Chickadee (Poecillus articapillus) (Family Paridae).	The Prairie Naturalist 40 (2008) 73-86	Dionn A. Schaaf, Georg M. Linz, Curt Doetkott, Mark W. Lutman, William J. Bleier
Bird damage to sunflower harvest.	Oriental Turtle Dove (Streptopelia orientalis), Oriental Greenfinch (Carduelis sinica), Eurasian Tree Sparrow (Passer montanus)	Japan (National Agricultural Research Center in Tsukuba city)	The total number and the appearance ratio in the fields were highest for the Greenfinch. The ratio of predated sunflower heads was 72.1 % in earlier sown fields and 30.8 % in later sown fields.	Japanese Journal of Ornithology 61 (2012) 124–129	Yasuhiro Yamaguchi, Hoshiko Yoshida, Masayuki Saito, Midori Saeki
Impact of blackbird damage to sunflower: Bioenergetic and economic models	Red-Winged Blackbird (Agelaius phoeniceus), Common Grackle (Quiscalus quiscula), Yellow-Headed Blackbird (Xanthocephalus xanthocephalus)	USA (northern Great Plains)	The annual loss was $ 5.4 ± 1.3 x 10′6 for all three species (Red-Winged Blackbirds did 52 % of the loss). Seed predation by Blackbirds represented 1.7 % of the dollar value of the 1999 sunflower harvest in the northern Great Plains.	Ecological Applications 13 (2003) 248–256	Brian D. Peer, H. Jeffrey Homan, Georg M. Linz, William J. Bleier
Assessment of bird-management strategies to protect	Blackbirds (Icteridae)	USA	Population suppression was intuitively appealing, but it typically fails beyond local scales because of avian mobility,	BioScience 61 (2011) 960-970	George M. Linz, H. Jeffrey Homan, Scott J. Werner, Heath

sunflowers			population dynamics, and public antipathy. Scare devices, repellents, habitat management, and decoy crops were found more likely to meet the test of predictable efficacy and practicality.		M. Hagy, William J. Bleier
Roost composition and Damage Assessment of Rose-Ringed Parakeet (Psittacula krameri) on maize and sunflower in Agro- Ecosystem of Central Punjab, Pakistan	Rose-Ringed Parakeet (Psittacula krmaeri)	Pakistan (Punjab)	The highest damage to sunflower seeds, (37.8 ± 4.58) was found on the mature sunflower stage. The minimum damage, (20.7 ± 2.3) occurred on the milky stage. For three crop sections, high damage (41.7 ± 9.9) was reported on the mature stage.	International Journal of Agriculture and Biology 13 (2011) 731–736	Shazad Ahmad, Hammad A. Khan, Muhammad D. Javed, Khalil Ur-Rehman
Anthraquinone-based bird repellent for sunflower crops	Red-Winged Black-Bird (Agelaius phoeniceus), Common Grackle (Quiscalus quiscula), Yellow-Headed Blackbird (Xanthocephalus xanthocephalus)	USA	A threshold concentration (i.e., 80 % repellency) of 9200 ppm anthraquinone for common grackles was predicted, when they were offered offered Avipel® -treated confectionery sunflower seed. During a field efficacy study for ripening confectionery sunflower, 18 % damage among anthraquinone-treated enclosures and 64 % damage among untreated enclosures populated with common grackles ($P < 0.001$) was observed.	Applied Animal Behaviour Science 129 (2011) 162–169	Scott J. Werner, George M. Linz, James C. Carlson, Susan E. Pettit, Shelagh K. Tupper, Michele M. Santer
Loss of sunflower seeds to columbids in South Africa: economic implications and control measures	Doves and Pigeons, (Columbidae)	South Africa	Most seed predation occurred in the center of the sunflower fields with a mean loss of 10.09 %, on the edges the mean loss was 4.76 %	Ostrich 80 (2009) 47–52	Johann van Niekerk
Evaluation of registered pesticides as repellents for reducing blackbird (Icteridae) damage to sunflower	Red-Winged Blackbird (Agelaius phoeniceus)	USA (north Dakota)	The feeding repellency of 8 pesticides was evaluated. Compared to untreated reference groups, feeding rates were reduced for 4 of the 5 pyrethroid insecticides. Only the organophosphorus (chlorpyrifos), however, significantly decreased feeding rates.	Crop Protection 25 (2006) 842-847	Georg M. Linz, H. Jeffrey. Homan, Anthony A. Slowik, Linda B. Penry
Evaluation of Bird Shield^TM as a blackbird repellent in ripening rice and sunflower fields	Blackbirds (Icteridae)	USA (north Dakota)	Daily bird counts from the first day of application until 5-7 days after the second application showed similar numbers of blackbirds within treated and control fields. No difference in bird seed predation on sunflower	Wildlife Society Bulletin 33 (2005) 251-257	Scott J. Werner, H. Jeffrey Homan, Michael L. Avery, George M. Linz, Eric A.

			before and after application was observed. Bird Shield was not effectively repelling blackbirds from sunflower fields.		
Lethal control of Red-Winged Blackbirds to manage damage to sunflower: an economic evaluation	Red-Winged Blackbird (Agelaius phoeniceus)	USA (northern Great Plains)	Potential population effects of the removal of up to 2 million Red-Winged Blackbirds annually under a 5-year program of baiting during spring with DRC-1339 (3-choloro-4methalalanine) treated rice were studied. Mean annual removals of 1,240,560 birds with density compensation and 1,231,620 birds without density compensation, with cost-benefit ratios of 1:2.3 and 1:3.6, respectively were reported. Annual intrinsic rates for the model population ranged from -1.4 to -4.8 %. Therefore only a marginal economic justification exists for spring baiting of Red-Winged Blackbirds, considering current nonlethal management efforts.	The Journal of Wildlife Management 67 (2003) 818-828	Bradley F. Blackwell, Eric Huszar, George M. Linz, Richard A. Dolbeer

Script S2:

#Statistical analyses script to be used in R software, to test our four hypotheses about the influence of the presence, distance and percentage of high trees on seed predation. We used generalized linear mixed models (glmm) with penalized quasi likelihood (PQL) and poisson or quasipoisson error distribution.

#correlation matrix correlating explanatory variables field size, presence of high trees, distance to high trees, percentage natural habitat, percentage high trees (Table 1)

```
suncor<- cbind(sizeha,PresenceHighTree,DistanceHighTree,percentnathab,percenttree)

colnames(suncor) <- c("sizeha","PresenceHighTree","DistanceHighTree","percentnathab","percenttree")

suncor<- as.data.frame(suncor)

cor.prob <- function(X, dfr=nrow(X) -2) { R <- cor(X) above <- row(R) < col (R) r2 <- R[above]^2 Fstat <- r2 * dfr / (1-r2)R[above] <- 1-pf(Fstat,1,dfr) R }

suncor<- na.omit(suncor)

X <- suncor

cor.prob(X)
```

#Field scale

#seed predation in relation to high tree distance within the entire field sampled in 2010 (Fig. 4)

```
model<-glmmPQL(seed_predation~DistanceHighTree,random=~1|location,family=quasipoisson)
```

#Landscape scale

#seed predation in relation to location (margin or interior) within the fields (Table 2)

```
model<-glmmPQL(seed_predation~location,random=~1|field,family=poisson)
```

#seed predation in relation to the presence of high trees within 50 m (Table 2)

```
model<-glmmPQL(seed_predation~PresenceHighTree,random=~1|field,family=poisson)
```

#seed predation in relation to the distance to the closest high tree for field margins (Table 2) (Fig.4)

```
model<-glmmPQL(seed_predation~DistanceHighTree,random=~1|field,family=poisson)
```

```
#seed predation in relation to the distance to the closest high tree for field interiors (Table 2)

model<-glmmPQL(seed_predation~DistanceHighTree,random=~1|field,family=poisson)


#seed predation in relation to the distance to the closest high tree for field margins and interiors (Table 2)

model<-glmmPQL(seed_predation~DistanceHighTree,random=~1|field/location,family=poisson)


#seed predation in relation to percentage of natural habitat (percentnathab), percentage of high trees (percenttree) in a 1 km radius surrounding the fields and field size (ha) (sizeha) (Table 2)

model<-glmmPQL(seed_predation~percentnathab,random=~1|field,family=quasipoisson)

model<-glmmPQL(seed_predation~percenttree,random=~1|field,family=quasipoisson)

model<-glmmPQL(seed_predation~sizeha,random=~1|field,family=quasipoisson)
```