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Landscape dynamics of tachinid parasitoids

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Padova, 30 January 2015

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Table of contents

Summary.....	7
Riassunto.....	9
Chapter I – Introduction.....	11
Chapter II – Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes.....	23
Chapter III – Organic farming enhances parasitoid diversity at the local and landscape scale.....	49
Chapter IV – Landscape effect on parasitoid spillover between crop and non-crop habitats.....	69
Chapter V – Spillover of natural enemies between contrasting field margins and crops.....	89
Chapter VI – Testing scale-dependent effects of semi-natural habitats on farmland biodiversity.....	107
Conclusions.....	129
References.....	135
Current affiliations of co-authors.....	159
Publications.....	161

Summary

Habitat fragmentation and the intensification of agricultural landscapes are among the main drivers affecting parasitoid diversity. Although many empirical and theoretical studies have elucidated the effects of these processes on populations and communities of parasitoids, the majority of the research has been focused on specialized groups of hymenopterans. In this study the highly-diverse group of tachinid parasitoids (Diptera: Tachinidae) was considered as an alternative model system to test the effects of landscape fragmentation and agricultural intensification on the third trophic level.

The effects of habitat fragmentation are evaluated in Chapter II. This chapter evaluates the relative importance of habitat loss, decrease of connectivity and their potential interaction on tachinid diversity. This chapter shows that the reduction of habitat area and the loss of connectivity significantly interacted, suggesting that management practices aimed to mitigate the negative effect of habitat fragmentation need to consider the connectivity in the surrounding landscape.

In the following chapters, diverse components of the intensification of agricultural landscapes were evaluated. In Chapter III, the diversity of tachinids was examined in relation to farm management (organic vs. conventional) at different spatial scales. This study shows that organic management improved the diversity of tachinids at both the local and landscape scales but only in arable crops while the effect in grasslands was neutral. Thus, any attempt to enhance parasitoid diversity needs to consider the local farming system in relation to the agricultural management in the surrounding landscape.

In Chapters IV and V the spatial dynamics and movement of parasitoids between crop and non-crop habitats were evaluated. These chapters show that the spillover of tachinid parasitoids was favored by the low contrast in habitat structure between the crop and non-crop habitats. The highest spillover of parasitoids to arable land was found from herbaceous semi-natural habitats, while woody structure reduced the exchange of individuals between arable crop and non-crop habitats. Finally, in Chapters V and VI the effects of different field margins to enhance farmland biodiversity were examined. The results from these chapters demonstrate that the positive effect of field margins to enhance the diversity of tachinids was related to the type and complexity of these semi-natural habitats. This research provides new insights into the consequences of landscape changes on the diversity of a key functional group that has been long overlooked in

ecological and conservation studies. The results will provide guidelines to implement conservation measures to halt or reduce biodiversity loss of this important group of parasitoids.

Riassunto

La frammentazione degli habitat e l'intensificazione dell'agricoltura sono riconosciuti tra i principali fattori che incidono negativamente sulla diversità dei parassitoidi. Nonostante numerosi studi hanno confermato questa tendenza, la gran parte di essi si è concentrata sugli imenotteri parassitoidi. Questa tesi si concentra invece sui tachinidi (Diptera: Tachinidae), considerati come sistema modello alternativo per testare gli effetti della frammentazione del paesaggio e dell'agricoltura intensiva sul terzo livello trofico.

In particolare, gli effetti della frammentazione degli habitat sono descritti nel Capitolo II, dove viene valutata l'importanza relativa della perdita dell'habitat, la diminuzione della connettività e la loro potenziale interazione nell'influenzare la diversità dei tachinidi. I risultati dimostrano che la riduzione dell'area e la perdita di connettività dell'habitat interagiscono significativamente, evidenziando che le pratiche di gestione finalizzate a mitigare gli effetti negativi della frammentazione dell'habitat non possono prescindere dal prendere in considerazione la connettività con il paesaggio circostante.

Nei capitoli successivi sono stati invece valutati vari impatti connessi all'intensificazione dell'agricoltura. Nel Capitolo III è stato esaminato come la gestione delle aziende agricole (biologica vs. convenzionale) possa influenzare la diversità dei tachinidi a diverse scale spaziali. I risultati dimostrano che la gestione biologica ha un effetto positivo sulla diversità di tachinidi sia a scala locale sia a livello di paesaggio, ma solamente nel caso dei seminativi mentre le praterie non ricevono nessun beneficio dall'agricoltura biologica. Quindi qualsiasi tipo di intervento per migliorare la diversità dei parassitoidi deve considerare il sistema di gestione agricolo locale in relazione al paesaggio circostante.

Nei Capitoli IV e V sono state trattate le dinamiche spaziali di spostamento dei parassitoidi tra ambienti coltivati e ambienti naturali. Questi capitoli dimostrano che il movimento dei tachinidi è stato favorito dalla bassa differenziazione strutturale dei due ambienti. Lo scambio di individui più elevato si è avuto dal margine erbaceo mentre il margine caratterizzato dalla presenza delle siepi riduce lo scambio di individui tra i due ambienti. Infine, nei Capitoli V and VI è stato valutato l'effetto di diverse tipologie di margine dei terreni agricoli sulla biodiversità. I risultati ottenuti da questi capitoli dimostrano che gli effetti positivi della presenza di margini semi-naturali sulla diversità dei tachinidi siano correlati alla tipologia e alla complessità degli habitat.

Questa tesi fornisce nuove informazioni su come i cambiamenti a livello di paesaggio influenzano la diversità di un gruppo funzionale chiave che è stato per lungo tempo poco considerato negli studi di ecologia e conservazione. I risultati potranno essere utilizzati per definire e implementare innovative misure di conservazione e mitigazione degli impatti considerati.

A large puzzle made of green leaf-shaped pieces is centered on a white background. The puzzle is mostly assembled, with a few pieces missing. On the assembled part of the puzzle, there is a detailed illustration of a fly with transparent wings and red eyes, and a fuzzy caterpillar with a yellow and black striped body and long black hairs. The text 'Chapter I' is printed in a bold, black, serif font on the right side of the puzzle.

Chapter I

Introduction

Threats to biodiversity: an overview

Biodiversity throughout the world continue to be threatened by multiple drivers. Species are facing a continuous decline due to reduced quality and extent of terrestrial natural ecosystems (Rosen 2000; Tilman et al. 2001). According to the Millennium Ecosystem Assessment (MEA 2005), one of the main drivers affecting biodiversity is the conversion of natural habitats into agricultural land. In the face of increasing food demand for a growing human population, agricultural land continues to spread at the detriment of natural habitats (Tilman et al. 2001; Foley et al. 2005; Godfray et al. 2010). It is estimated that more than one third of the world land surface is now being used by agriculture (Foley et al. 2005; Alexandratos & Bruinsma 2012; FAOSTAT 2014). This trend in land use is leading to the formation of simple landscapes with only few and scattered semi-natural habitats (Stoate et al. 2001; Robinson & Sutherland 2002). The biodiversity in agricultural landscapes is further affected by the homogeneous matrix that is dominated only by a few crops. Indeed, about 60% of food production is comprised only of three cereals: wheat, corn and rice (Tilman et al. 2001; Alexandratos & Bruinsma 2012). In this homogeneous landscapes, the disturbance and fragmentation of natural habitats disrupts important biophysical processes from local to regional scales (Lambin & Geist 2006; Karp et al. 2012), which is leading to an overall impoverishment of biological diversity.

In agricultural landscapes, remnant habitats play an important role in maintaining biodiversity and in providing important ecosystem services such as natural control of pests and pollination (Díaz et al. 2006; Bommarco et al. 2013). As the diversity of species is tightly related to natural ecosystems is clear that the intensification of agriculture and the resulting fragmentation of natural habitats are among the main drivers of biodiversity decline (MEA 2005). Although, a large body of research has accumulated over the past decades showing that biodiversity is directly affected by habitat fragmentation and agricultural intensification, the detailed understanding of how these factors are threatening biodiversity and ecosystem functioning is far to be completed. In fact, during the last decades we have experienced high rates of biodiversity loss, with future scenarios predicting that such losses are likely to increase (Ferraz et al. 2003; MEA 2005; Pereira et al. 2010; Barnosky et al. 2011). Even with these negative scenarios, there is still a large debate about how the loss of biodiversity is affecting the functioning of ecosystems and their ability to provide goods and services to our society (Díaz et al. 2006; Cardinale et al.

2012). There is a clear need to devise consensual approaches to enhance biodiversity in agricultural landscapes, but first we have the challenge to understand the dynamics and processes affecting the species response. For this reason, my research has focused on understanding how biodiversity is affected by (1) landscape fragmentation and (2) agricultural intensification.

Landscape fragmentation

Habitat fragmentation is considered one of the major threats to biodiversity worldwide (Sala et al. 2000). Fragmentation involves not only a reduction in the overall amount of original habitat, but also in the connectivity of the remnant patches. A decrease of both habitat area and connectivity are expected to reduce population viability and eventually species diversity (Hanski 1999). One of the most evident effects of landscape fragmentation is the reduction of the area of natural and semi-natural habitats. As the remnant patches become smaller, higher extinction rates due to environmental stochasticity in combination with a lower probability of receiving immigrants through dispersal may cause the often observed declines in abundance and species richness (Hanski 1999). The decline in diversity due to habitat fragmentation is not only the result of the reduction of habitat area, but also an increase in the isolation of the fragments. The conversion of continuous habitat into smaller and smaller fragments increases the distance between fragments. Landscape connectivity is therefore the degree to which the landscape facilitates or impedes movement among habitat fragments (Taylor et al. 1993; Hanski 1999; Fischer & Lindenmayer 2007).

A common approach for predicting patterns of diversity within fragmented habitats relies on the theory of island biogeography. Island biogeographic theory predicts that species occurrences within fragments will be regulated by extinction and colonization dynamics (MacArthur & Wilson 1967). However, this theory does not explicitly take into account the surrounding matrix and its influence on dispersal probabilities and new species contributions (Mendenhall et al. 2014). Therefore, the interactions among habitat area, connectivity and the surrounding matrix should be considered in the attempt to counteract negative impacts of habitat fragmentation. Species are predicted to be highly sensitive to the reduction of habitat area and connectivity as organisms are likely to

depend on a variety of resources across fragmented landscapes (Kruess & Tscharntke 1994; Valladares et al. 2006; Cagnolo et al. 2009). As habitats become smaller and less connected, the multi-trophic interactions of species can be easily disrupted or altered (Steffan-Dewenter & Tscharntke 2002; Nouhuys van 2005; Elzinga et al. 2007). Thus, the available habitat must exceed a certain threshold value for the species to persist. Landscapes with little and sparse habitats are likely to be below the extinction threshold, while landscapes with large habitat cover and connectivity are expected to be above this threshold (Pardini et al. 2010; Hanski 2011). After passing a species specific-habitat threshold, the negative fragmentation consequences on biodiversity accelerate non-linearly (e.g., Radford 2005; Pardini et al. 2010). However, it must be considered that the effects of habitat fragmentation for individual organisms are many and varied, as species with differing life histories are differently affected by habitat fragmentation. Thus, to counteract the negative effects of landscape fragmentation on biodiversity, further empirical evidence about the specific consequences of the reduction of habitat area and connectivity on taxa with differing life histories is urgently needed. Only then we may arrive to a global consensus about the threshold levels needed to guide the policy and efforts towards habitat conservation.

Agricultural intensification

While many crop species were traditionally cultivated together within patches of native vegetation, the specialization of agricultural systems into large agricultural fields of single or few species is becoming increasingly common. Modern agricultural farming is often occurring at large spatial scales, with extensive commercial fields replacing native habitats and smallholder farms (Robinson & Sutherland 2002; Tilman et al. 2001). Continuing this trend, the arable area in the world by 2050 is expected to expand by more than 60 million of hectares, with the greatest expansion coming from the developing world, where for example, agricultural expansion is expected to eradicate more than one third of the Amazon forest (Soares-Filho et al. 2006; Alexandratos & Bruinsma 2012). The intensification of agriculture results in the reproduction of similar crop environments over large distances, causing a local modification of habitats and a broader fragmentation of the landscape (Matson et al. 1997; Tscharntke et al. 2005). Agricultural intensification is not only the result of change in land use, it is a combination of different processes

acting at different spatial scales. At the local scale, farming systems are characterized by an intensive management due to the heavy use of external inputs like fertilizers and pesticides, the improvement of crop varieties, and mechanization. At the landscape scale, the intensification of agriculture is leading to an overall reduction of natural and semi-natural habitats and the homogenization of the crop matrix (Tscharntke et al. 2005; Wright et al. 2012). These practices are enhancing crop yields, but at the cost of reducing the quality and extent of natural habitats, thus compromising the diversity of species inhabiting these habitats (Matson et al. 1997; Tscharntke et al. 2005).

The broad scale transformation by agricultural intensification has been linked to local and regional declines in native biodiversity (e.g., Sotherton 1998; Donald et al. 2001; Deguines et al. 2014). Furthermore, as this transformation affect the composition and diversity of species in these landscapes, important ecosystem services such as biological control and pollination are being compromised (e.g., Thies & Tscharntke 1999; Klein et al. 2003; Hooper et al. 2005). As intensive agriculture replaces habitats that previously supported diverse communities of organisms, only a set of agriculture-associated species with a distinct set of physical, life-history, and functional traits will dominate these hostile landscapes. For instance, generalist species are likely to persist in these landscapes, while specialist species do not (Tscharntke et al. 2008; Pardini et al. 2010). To counteract the negative effects of agricultural intensification, the conservation of pristine natural habitats have traditionally pursued as the main goal. However, considering the importance of species migration between fragments, this conservation strategy has a limited value as their success depend not only on the natural habitats but also on the surrounding matrix (Tscharntke et al. 2008, 2012). In fact, Perfecto and Vandermeer (2010) stress the need to incorporate the agricultural matrix as an integral component of conservation programs. This also represent an opportunity to integrate the conservation of the biodiversity of natural ecosystems with the enhancement of ecosystems services in agricultural landscapes. However, to design efficient strategies we still need empirical evidence on how different local and landscape processes affect the diversity of species. For example, several local practices such as organic management, enhancement of field boundaries and the conservation of semi-natural habitats have been proposed as an alternative to increase farmland heterogeneity and enhance biodiversity (e.g., Bengtsson et al. 2005; Letourneau & Bothwell 2008; Crowder et al. 2010; Merckx et al. 2012; Haenke et al. 2014). However, the magnitude of the benefits derived from

these systems within contrasting managed landscapes remains unclear and, in particular, the potential scale-dependent response of biodiversity is relatively unexplored. Identifying sustainable alternatives to the intensification of agricultural landscapes and the scale at which biodiversity is affected by these alternatives is an important step to maximize the ecosystem services and the conservation of biodiversity.

Study system

Although many empirical and theoretical studies have elucidated the effects of habitat fragmentation and agricultural intensification on populations and communities of primary producers and consumers (Hanski 1999; Ewers & Didham 2006), less attention has been paid to the impacts of these drivers on the third trophic level. Furthermore, the majority of the research done has been focused on specialized groups of hymenopteran parasitoids (e.g., Cronin 2007; Elzinga et al. 2007; Rand & Tschardtke 2007; Holzschuh et al. 2010; Fenoglio et al. 2012; Coudrain et al. 2013). Therefore, predictions derived from studies on highly specialized taxa that parasitoids are highly susceptible to habitat fragmentation (e.g., the ‘specialist–consumer hypothesis’ Kruess & Tschardtke 1994; ‘trophic rank hypothesis’ Holt et al. 1999) and to the intensification of agricultural systems (e.g., Thies et al. 2008), cannot necessarily be extended to more generalist groups (Nouhuys van 2005; Fenoglio et al. 2010). Therefore, for this study the highly-diverse group of tachinid flies was used as an alternative model to test the effects of landscape fragmentation and agricultural intensification on insect parasitoids. In particular, the research on landscape fragmentation was focused on the effects of habitat area, connectivity and habitat quality, while the research on agricultural intensification was focus on the effects of local management and specific practices such as the management of field margins to enhance parasitoid diversity. Furthermore, the different experiments in this thesis were designed to contrast different spatial scales.

Among natural enemies, tachinid flies represent an optimal model group to examine effects of habitat fragmentation and agricultural intensification on the third trophic level. With almost 8,500 species, the Tachinidae family ranks second in diversity within Diptera and is the most diverse group of non-hymenopteran parasitoids (Stireman et al. 2006; O’Hara 2013). Species of this family are currently classified into four

subfamilies (Dexiinae, Exoristinae, Phasiinae, Tachininae), but in general the phylogenetic relationships of this family remains poorly known (although see Cerretti et al. 2014). Tachinids exhibit an impressive diversity of morphologies, ranging from small (e.g., <2 mm, *Catharosia minuta* (Townsend)) to large (e.g., 20 mm, *Tachina grossa* (L.)) body size, from brightly and metallic to dull colored. Tachinids are well represented in all biogeographical regions, but the Neotropical Region is by far the most species rich, accounting for more than one-third of the diversity of these flies (O'Hara 2014). However, only the Tachinidae of the Palearctic and Nearctic Regions are well known, with perhaps 90% of their species documented (Stireman et al. 2006).

Unlike hymenopteran parasitoids, tachinids do not have a piercing ovipositor and they do not inject any secretion derived from their reproductive system (i.e., paralyzing venoms). Additionally, all species in the Tachinidae develop inside their host, as endoparasitoids, and allow their host to continue to feed and grow while they develop, as koinobiont parasitoids (Askew & Shaw 1986). Another characteristic of tachinids is the high diversity of the reproductive strategies that they have evolved. The majority of tachinids are ovolarviparous, depositing eggs that contain fully developed first instar larvae. In some species, a special type of ovolarvipary has evolved in which eggs are laid on foliage and these eggs hatch only after being ingested by a host. Other groups of tachinids are oviparous, injecting eggs directly into a host using a modified piercing oviscap. The evolution of different reproductive strategies has allowed tachinids to attack a wide range of hosts, encompassing larvae as well as adult stages. As far as we know immobile stages like egg and pupa are not suited by tachinids.



Figure 1. *Meigenia simplex* Tschorsnig & Herting depositing eggs on the larvae of *Chrysomela populi* (L.). Photo credit: Inclán D. J.

The high diversity of tachinids is likely related to the diversity of their hosts. In contrast to the host range of hymenopteran parasitoids, tachinid species tend to attack a wider range of hosts (Eggleton & Belshaw 1993). Hosts of tachinids are all arthropods, mainly insects with only a few records of species attacking non-insect arthropods like centipedes and scorpions (Williams et al. 1990; Haraldseide & Tschorsnig 2014). The most commonly used hosts are phytophagous insects, primarily Lepidoptera, Coleoptera (e.g., Fig. 1), Symphyta, Hemiptera, and Orthoptera. However, tachinids have been also reported to attack hosts in at least six additional insect orders: Blattodea, Dermaptera, Diptera, Embioptera, Mantodea, and Phasmida. In general, tachinids have lower host specificity than other parasitoids such as hymenopterans (Stireman et al. 2006; Stireman 2005) and several species often attack large groups of host species across entire families or orders (Eggleton & Gaston 1993; Stireman 2005; Cerretti et al. 2014). While some species are known to be highly specialized in their host use, other species are highly polyphagous. In fact, the tachinid *Compsilura concinnata* (Meigen) (Fig. 2) is known to attack about 200 species of hosts belonging to more than ten families across Lepidoptera, Hymenoptera, and Coleoptera (Arnaud 1978). This high variation in host use and host specificity in this group makes the Tachinidae an ideal group for ecological research.



Figure 2. The highly polyphagous tachinid, *Compsilura concinnata* (Meigen), with one of their known hosts, *Orgyia antiqua* (L.). Photo credit: Inclán D. J.

Tachinids have an important role as natural enemies of agricultural pests. Several species play significant roles in regulating herbivore populations due to their predominance in attacking the larval stage of major groups of insect pests (Stireman et al. 2006; Cerretti et al. 2014). In general, about 100 species have been employed in biological control programs of crop and forest pests (Grenier 1988; Stireman et al. 2006). Some successful examples of tachinids used in biological control programs include the

release of *Cyzenis albicans* (Fallén) from Europe against the winter moth (*Operophtera brumata* L.) in Canada, and the release of *Lixophaga diatraeae* (Townsend) from Cuba and *Lydella minense* (Townsend) from Brazil against sugarcane borers (*Diatraea* spp.) in the Caribbean and South America (Grenier 1988; Lenteren & Bueno 2003). Beside the importance of this group as natural enemies, tachinids could play a role also as pollinators. Adult tachinids are flower-visiting insects and use nectar as an energy source (e.g., Tooker et al. 2006; Al-Dobai et al. 2012). Although the importance of tachinids in this respect has been largely unexplored (Stireman et al. 2006), few species are specialized pollinators of Asclepiadoideae (Ollerton & Liede 2014; Nihei & Schwarz 2011) and Orchidaceae (Dodson 1962) flowers.

Despite the great diversity and crucial role of tachinids as parasitoids, relatively little is known about their ecology and behavior. Their complex life styles are far to be understood, as even basic biological information on hosts, mating systems, and habitat requirements is known only for a few species. In fact, an enormous challenge still remain at the taxonomic level as the truly diversity of this group still remains to be described. However, giving the alarming rates of biodiversity loss, more research is needed to elucidate the effects of landscape fragmentation and agricultural intensification on this key functional group that has been long overlooked in ecological and conservation studies.

Research objectives and thesis structure

The overall aim of this dissertation is to examine the landscape dynamics of one of the most diverse and abundant group of non-hymenopteran natural enemies, the Tachinidae. To achieve this goal the research has focused specifically on habitat fragmentation and agricultural intensification as the main drivers of the diversity of tachinids. I aimed to understand the diversity patterns of tachinid parasitoids under the influence of habitat fragmentation and agricultural intensification by analyzing the spatial effects of these processes on abundance, species richness and species composition.

The effects of habitat fragmentation are discussed in Chapter II. Specifically, the main aim of this chapter was to evaluate the relative importance of habitat loss, decrease of connectivity and their potential interactions on tachinid diversity. In the following

chapters, diverse components of the intensification of agricultural landscapes were evaluated. Specifically, in Chapter III the diversity of tachinids was examined in relation to farm management (organic vs. conventional) at the local and landscape scales. In Chapters IV, the potential spillover of tachinids in commercial apple orchards localized in landscapes characterized by different proportions of crop and non-crop habitats was evaluated. Finally, in the following two chapters the effects of different field margins to enhance farmland biodiversity were examined. Specifically, Chapter V aimed to evaluate the spillover of natural enemies from two contrasting field margins (grass margins and hedgerows) into their adjacent crop, while Chapter VI aimed to test the effects of field margin quality and semi-natural habitats at multiple scales across three taxonomic groups.

Chapter II

Interactive effects of area & connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes



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Abstract

Although many empirical and theoretical studies have elucidated the effects of habitat fragmentation on the third trophic level, little attention has been paid to the impacts of this driver on more generalist groups of non-hymenopteran parasitoids. Here, we used the highly-diverse group of tachinid flies as an alternative model to test the effects of landscape fragmentation on insect parasitoids. Our aims were: (i) to evaluate the relative importance of habitat area and connectivity losses and their potential interaction on tachinid diversity, (ii) to test whether the effects of habitat fragmentation changes seasonally, and (iii) to further assess the effect of habitat diversity on tachinid diversity and whether different parasitoid-host associations modify the species richness response to fragmentation. In 2012 a pan-trap sampling was conducted in 18 semi-natural grasslands embedded in intensive agricultural landscapes along statistically orthogonal gradients of habitat area, connectivity and habitat diversity. We found an interaction between habitat area and connectivity indicating that tachinid abundance and species richness were more negatively affected by habitat loss in landscapes with low rather than with relatively large habitat connectivity. Although tachinid communities exhibited large within-year species turnover, we found that the effects of landscape fragmentation did not change seasonally. We found that habitat diversity and host association did not affect tachinid species diversity. Our results have important implications for biodiversity conservation as any attempts to mitigate the negative effects of habitat loss need to take the general level of habitat connectivity in the landscape into account.

Introduction

Habitat fragmentation is considered one of the major threats to biodiversity worldwide (Sala et al. 2000). Although many empirical and theoretical studies have shed light on the effects of habitat fragmentation on populations and communities of primary producers and consumers (Hanski 1999; Ewers & Didham 2006), less attention has been paid to the impacts of this driver on the third trophic level. Furthermore, the majority of the research done has been focused on specialized groups of hymenopteran parasitoids (e.g., Cronin 2007; Elzinga et al. 2007; Rand & Tscharrntke 2007; Holzschuh et al. 2010; Fenoglio et al. 2012; Coudrain et al. 2013). Therefore, the prediction derived from studies on highly

specialized taxa that parasitoids are highly susceptible to fragmentation (the ‘specialist–consumer hypothesis’ Kruess & Tscharntke 1994; ‘trophic rank hypothesis’ Holt et al. 1999) cannot necessarily be extended to more generalist groups (Nouhuys van 2005; Fenoglio et al. 2010). Among natural enemies, tachinid flies represent an optimal model group to examine effects of habitat fragmentation on the third trophic level. With almost 10,000 described species, the Tachinidae is one of the most diverse families of Diptera and represent the most diverse group of non-hymenopteran parasitoids (Brown 2001; O’Hara 2012). In general, tachinids have lower host specificity than other parasitoids such as hymenopterans (Stireman & Singer 2003; Stireman 2005) and several species often attack large groups of host species across entire families or orders (Stireman 2005; Cerretti et al. 2014). Our study provides one of the first empirical tests of the impact of fragmentation on one of the most diverse and abundant groups of non-hymenopteran natural enemies.

Fragmentation involves not only a reduction in the overall amount of original habitat, but also in the connectivity of the remaining habitat patches. A decrease of both habitat area and connectivity are expected to reduce population viability and eventually species diversity (Hanski 1999). Insect natural enemies such as predators and parasitoids are predicted to be highly sensitive to both processes as these organisms depend on complex interactions between habitat and host dynamics (Kruess & Tscharntke 1994; Valladares et al. 2006; Cagnolo et al. 2009). Given that parasitoids are typically associated with particular hosts, they can only utilize the parts of the landscapes where these resources occur. As habitats become smaller and less connected, the multi-trophic interactions among plants, herbivores and their natural enemies can be easily disrupted or altered (Steffan-Dewenter & Tscharntke 2002; Nouhuys van 2005; Elzinga et al. 2007). Responses of parasitoids to habitat fragmentation can therefore be more difficult to predict for primary producers or consumers.

Research on the impact of landscape fragmentation on species diversity has mostly considered the landscape from a static temporal perspective, especially in temperate regions. For parasitoids in particular, the persistence and success of the species depend on their synchronization with important resources like hosts and nectar for the adults that become available at different times depending on seasonality and environmental conditions (Tylianakis et al. 2005; Stireman et al. 2012; Letourneau et al. 2012). The agricultural matrix in which fragmented habitats are embedded can be also

highly dynamic over time due to crop phenology and agronomic interventions (Baudry et al. 2003; Vinatier et al. 2013). Given large fluctuations of resources between seasons, it is important to consider if effects of habitat fragmentation vary seasonally. For instance, as resources can be lower in certain time of the year the spatial requirements for a population to persist could considerably increase (Olson et al. 2005). Therefore, the relationship between habitat area, connectivity and parasitoids are expected to change with season.

In fragmented landscapes habitat diversity within the remnant patches is another key factor expected to influence natural enemies both directly and indirectly (Fenoglio et al. 2010). Direct effects are mainly related to the availability of food for the adults such as nectar or pollen resources (e.g., Géneau et al. 2012) and the provision of overwinter resources (Shaw 2006), while indirect effects are related to the influence of the habitat fragment quality on host availability (e.g., Segoli & Rosenheim 2013). While parasitoids with a high degree of specialization should primarily respond to host density, more generalist parasitoids are expected to respond to the richness and abundance of host species (Heisswolf et al. 2009). Parasitoids with low host specificity should benefit from patches with large habitat diversity, as these support greater abundance and diversity of herbivore species (Rosenzweig 1995; Marini et al. 2010). However, empirical studies (although see, Kruess 2003; Cronin & Reeve 2005; Holzschuh 2010) testing the relative importance of habitat diversity on natural enemies compared to habitat configuration are still lacking.

Considering the diversity and crucial role of non-hymenopteran parasitoids in managed and natural ecosystems, more research is needed to elucidate the response of this key functional group to habitat fragmentation. The main aims of this study were: (i) to evaluate the relative importance of habitat loss, decrease of connectivity and their potential interactions on tachinid diversity; (ii) to evaluate whether the effects of habitat fragmentation changes seasonally; and (iii) to further assess the effect of habitat diversity on tachinid diversity and whether different parasitoid-host associations modify the species richness response to fragmentation. Specifically, we addressed three primary hypotheses. First, according to the fragmentation threshold hypothesis (Andr n 1994; Pardini et al. 2010) we expect that the effect of habitat loss may depend on the level of habitat connectivity in the landscape (Hanski 2011). Due to the high mobility and relatively low specialization of tachinids, we expect that species diversity will respond to area only at

very low connectivity levels while in landscapes with relatively large connectivity the effect of habitat area should be less important (Rösch et al. 2013). Second, due to seasonal fluctuations in food resources and host density both in the patches and in the matrix, we expect that the effects of habitat fragmentation should vary between spring, summer and fall. Third, we hypothesized that fragments with high habitat diversity will support higher parasitoid diversity than patches dominated by a single habitat by providing larger resources for adults and more diverse host communities. In particular, species attacking host groups common in several habitats should respond more strongly to habitat diversity than species feeding on host groups that are mostly restricted to single habitats. We tested this hypothesis in isolated abandoned grasslands in intensive arable landscapes in a Mediterranean region, where shrub and tree encroachment in grasslands is expected to increase habitat diversity at the beginning of the succession, but declines as the cover of shrubs and trees gradually becomes continuous.

Methods

Study area and sampling design

The research was conducted within an area of c. 650 km² in the province of Siena (central Italy). The study region was characterized by a network of fragments of semi-natural grasslands, shrublands and forests within an intensively managed agricultural landscape. The grasslands patches are derived from eroded claystones (“biancane” badlands and “calanchi” claystones) which results in a mosaic of habitats that range from bare ground with scarce or no vegetation to grassland communities, with or without shrubs or trees. The prevailing land use in the landscape is highly homogenous being cultivated almost entirely with durum wheat. The agricultural matrix remains bare ground during summer and the beginning of fall due to the harvest (c. July) and ploughing (c. September). The cover of semi-natural grasslands in the surrounding landscape (2 km radius) varied between c. 1 and 10%.

Eighteen patches were selected along three statistically uncorrelated gradients of (1) area ranging from 0.2 to 11.5 ha, (2) habitat connectivity ranging from isolated to well-connected patches and (3) within-patch habitat diversity varying from open grasslands or shrublands to complex mosaics of grasslands with shrubs and trees (Table

S1). The selection of the focal patches was designed to minimize the correlation between these three factors: log(area) vs. connectivity ($r_s = 0.009$, $P = 0.97$), log(area) vs. habitat diversity ($r_s = 0.003$, $P = 0.99$), and connectivity vs. habitat diversity ($r_s = 0.039$, $P = 0.87$). An initial prescreening of the patches was made by using high resolution satellite images from Google Earth 6.2 (Google Inc., Silicon Valley, California, USA) and the final selection of the focal patches was adjusted by direct field observations. Focal patches were selected to be separated by at least 2 km (mean minimum distance = 2.8 km) (Fig. 1) and only two patches presented a shorter distance (0.8 km).

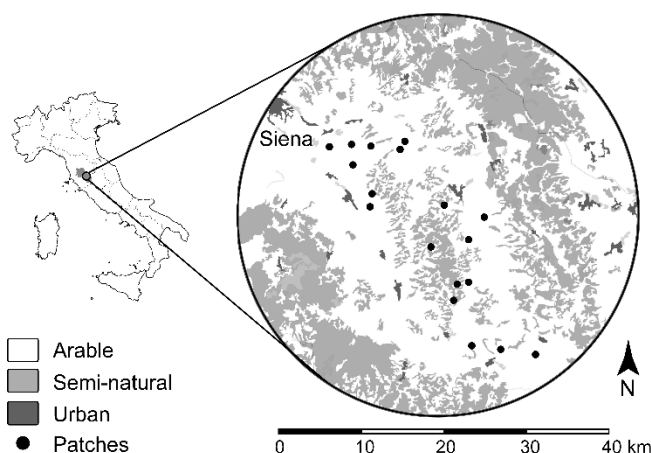


Figure 1. Study area showing the location of the 18 patches and the cover of semi-natural and arable land in the landscape. The land-use map is from the CORINE land cover (<http://www.eea.europa.eu>).

Explanatory variables

(i) *Area and connectivity*

Habitat area was quantified by digitizing the patches using aerial photographs. Habitat connectivity was obtained by mapping all the patches of semi-natural habitats within a 2 km radius from the edge of the 18 focal patches. Data on the average dispersal range of tachinids are not available. We therefore selected the radius for quantifying the connectivity using information derived from other parasitoid species (e.g., Roland & Taylor 1997; Thies et al. 2003). To assess connectivity, habitat patches were first identified as independent polygons for grasslands and forest using high resolution satellite images from Google Earth. Once the patches were identified, the area and the centroid of

each polygon within 2 km from the focal patch were calculated using ArcGIS 10.0 (ESRI, Redlands, California, USA). Initially the connectivity was calculated separately for grassland and forest, but in preliminary analyses connectivity computed using forest patches was never associated with our response variables. Thus, in the present study we presented only the grassland connectivity (see Table S1).

Habitat connectivity (SI) for each of the 18 focal patches (i) was measured using the Hanski's connectivity index (Hanski 1999):

$$SI_i = \sum_{i \neq j} e^{-\alpha d_{ij}} A_j^b \text{ for all } d_{ij} < 2.0 \text{ km}$$

$$i \neq j$$

Where A_j is the size of neighboring habitat patches and d_{ij} is the distance from the center of the neighboring patch j to the center of the focal patch i . The parameter α is a proxy for dispersal distance and b is a parameter that scales the size of the surrounding habitat patches. Although information about specific dispersal abilities of tachinids is still lacking (Letourneau et al. 2012), we used a value of $\alpha = 0.5$. Nonetheless, assigning other dispersal abilities with α between 1 and 2.0 did not substantially change the connectivity index. For the scaling parameter b we chose $b = 0.5$ according to the assumptions that the ratio of patch edge to patch area decreases with $A^{0.5}$ when patch area increases (Moilanen & Nieminen 2002). In preliminary analyses we also tested the connectivity index based on a 1 km radius and found that the results were qualitatively similar with those found for the 2 km radius. The model fit and the significance of the connectivity effect were, however, slightly better for the 2 km than for the 1 km radius. We therefore presented the results based on the former.

(ii) *Within-patch habitat diversity*

Three main habitat types can be identified within the patches: (i) bare ground with little or sparse vegetation, (ii) shrublands and (iii) open grasslands. All patches were formerly grazed and/or burnt, but due to the suspension of these traditional managements the semi-natural grasslands have experienced shrubland encroachment (Maccherini et al. 2000). All the patches were unmanaged at the time of the sampling but the time since the abandonment differed. The dominant vegetation cover depended on the time since

suspension of management occurred; more recently burnt and grazed areas were dominated by open grasslands while areas abandoned decades ago were increasingly covered by shrubs and trees (Marini et al. 2010). Within the patch, the area covered by bare ground, grasslands and shrublands was independently calculated using aerial photographs (1:1500) with the software ImageJ (NIH, Bethesda, Maryland, USA). We estimated habitat diversity using the Shannon index. Due to the low number of habitats present, habitat diversity showed a tight hump-shaped relationship with the cover of both grasslands and shrublands ($y = -0.0002x^2 + 0.0127x + 0.5713$, $R^2 = 0.59$, $P < 0.01$ for shrublands; $y = -0.0003x^2 + 0.0249x + 0.2284$, $R^2 = 0.79$, $P < 0.01$ for grasslands). Due to the broad resolution of host associations, it was not possible to measure any meaningful variable related to host density or diversity. However, habitat diversity can be considered a good proxy of host availability as insect herbivore diversity is often positively correlated with habitat or resource heterogeneity (Tews et al. 2004).

Insect sampling

A Pan-trap sampling was conducted in the 18 semi-natural patches using a sampling effort proportional to patch area. Two clusters of five pan-traps were used for each patch with an area equal or smaller than 1.5 ha. In larger patches, one cluster of traps was added for each additional ha. Each cluster of traps consisted of three standard yellow (500 ml, 16 cm diameter) and two UV-yellow plastic bowls (300 ml, 10 cm diameter) filled with a solution of water and 3% dishwashing detergent (SoleTM). Yellow pan-traps have been used as a reliable method for sampling tachinid flies (e.g., Stireman 2008). One UV-yellow and one standard yellow pan-traps were held approximately 1 m above the ground using a wood support and one UV-yellow and two standard yellow pan-traps were placed on the ground within a two meter radius of the wood support. The cluster position was kept fixed within the grassland patch, leaving a distance of at least 20 meters from the borders and avoiding areas completely covered by shrubs. The sampling was conducted every two to three weeks between March and November 2012. A total of 16 samplings were performed covering the whole season during which the insects were active. During each sampling, traps were set for a period of 48 hours. Samples were stored in alcohol (70%) for sorting and identification. The specimens were identified to species level using Cerretti (2010) and Cerretti et al. (2012). All the specimens are currently housed in the insect collection of P. Cerretti at the MZUR (Museo di Zoologia, Università di Roma La Sapienza, Rome, Italy).

Host association

Host association of the tachinid species was derived from Cerretti and Tschorsnig (2010) and Cerretti (2010). Unlike most parasitoids that are highly specialized at the host-species level, tachinids frequently attack a broad spectrum of hosts (Stireman & Singer 2003; Stireman 2005; Cerretti et al. 2014). Therefore, host association was defined at the insect order level. In cases where hosts were uncertain or unknown, the classification was inferred from the genus except for the few genera that are known to attack different orders (e.g., *Exorista* Meigen). We identified seven orders of potential hosts: Lepidoptera (n = 65), Coleoptera (n = 19), Hemiptera (n = 25), Hymenoptera (n = 3), Dermaptera (n = 2), Orthoptera (n = 1), Diptera (n = 1) and Chilopoda-Lithobiomorpha (n = 1). For 12 species, it was not possible to assign host association due to the lack of data. For the host association analysis, only the species attacking lepidopterans, coleopterans and hemipterans were included (n = 109).

Statistical analyses

To test the effects of habitat loss, connectivity and season, we used a general linear model (GLM) for tachinid abundance and a generalized linear mixed model (GLMM) with a Poisson distribution and a log-link function for species richness. The response variable was the cumulative number of individuals/species per patch obtained per each sampling event. Season was included in both models as a categorical factor with three levels, where spring included the first five samplings (16th March - 12th May), summer the following six (26th May - 8th August) and fall the last five samplings (26th August - 24th November). Both models included the focal patch as random factor to account for the repeated sampling in the same patch. Area and abundance were log-transformed in each model to improve linearity. The model tested the effect of area, connectivity, season and the interactions between area, connectivity and season. We first build a full model and then we simplified the model by removing one-by-one, starting from the interaction, the least significant terms with $P > 0.05$. The GLM and GLMM analyses were performed using the “nlme” (Pinheiro et al. 2013) and “lme4” (Bates et al. 2014) packages, respectively, implemented in R (R Development Core Team, 2013).

To test whether tachinid abundance and species richness respond differently to habitat diversity according to host association, we used a GLM for abundance and a GLMM with a Poisson distribution and a log-link function for species richness. Similar to

the models described above, abundance and area were log-transformed to improve linearity in both models. The response variable was the cumulative number of individuals/species per each host group and patch obtained per each season. The low occurrence of tachinids did not allow to work with the data from the single sampling event. Both models included the focal patch as random factor to account for the repeated sampling in the same patch of different host groups. Both models included host as a categorical fixed effect with three levels (species attacking Lepidoptera, Coleoptera or Hemiptera). The other fixed effects, in both models, were area, connectivity, habitat diversity and the interaction between habitat diversity and host. We did not test interactions between host, area and connectivity as we did not have any specific ecological hypotheses to support these tests. However, in preliminary analyses we explored all these interactions and found no clear effects for any of them. To simplify the model we applied a backwards deletion procedure as explained above.

To explore the effect of the proportional sampling on the fragmentation effects we used a widespread species richness estimator and species rarefaction curves (Magurran et al. 2010). The congruence between the results using the raw data and the asymptotic estimators would indicate that the effects detected are not a sampling artifact. First, we calculated the Jack1 species richness estimator using the function “specpool” from the statistical package “vegan” (Oksanen et al. 2007), implemented in the software R (R Development Core Team, 2013). Then, we run a similar model as explained above, where our response variable was the species richness estimator by patch, as the estimator takes in account the species accumulated after the sixteen samplings. Additionally, we constructed the species rarefaction curves to describe the species accumulation in relation to our sampling effort. For each focal patch, the rarefaction curve and its 95% intervals of confidence was calculated and plotted using 1,000 permutations with the function “accumcomp” from the “BiodiversityR” package (Kindt & Coe 2005) based on functions of the “vegan” package (Oksanen et al. 2007), implemented in R (R Development Core Team, 2013). To explore the species community changes between seasons, we calculated the number of shared species and the Jaccard similarity index (Magurran et al. 2010) using the software EstimateS 9.0 (Colwell 2013). Values close to 1 of this index indicate low beta-diversity between seasons.

A potential problem with data obtained for many ecological observational studies is that the variables sampled may have a spatial component. For instance, our species

richness or abundance measures in neighbouring patches are likely to be similar. This can result in spatial autocorrelation which causes problems for statistical methods that make assumptions about the independence of residuals (Legendre & Legendre 1998). We therefore tested for spatial autocorrelation using Mantel correlograms (Borcard & Legendre 2012). Specifically, we tested whether model residuals obtained for both abundance and species richness were spatially auto-correlated. Spatial correlograms were constructed using 12 lag intervals. Each interval was 2.61 km wide, ranging from 0.93 to 33.25 km. The first lag distance allowed to include the mean distance between focal patches. Mantel correlation coefficients were calculated for each lag interval and tested for significance with a permutation test, using 1999 permutations. Each correlogram was tested for significance using a Bonferroni-corrected α of 0.01 (Legendre & Legendre 1998). The spatial autocorrelation analysis was performed using the “mpmcorrelogram” (Pinheiro et al. 2013) implemented in R (R Development Core Team, 2013).

Results

General results

From March to November 2012, a total of 1528 individuals were observed (see Table S2). One-hundred-twenty-nine species belonging to 78 genera were identified. Three species appeared to be dominant accounting for almost 50% of the total specimens: *Zeuxia aberrans* (Loew), *Gastrolepta anthracina* (Meigen), and *Besseria reflexa* Robineau-Desvoidy, representing 18, 17 and 12.4% of the specimens collected, respectively. In general, the most abundant species were associated with Hemiptera (e.g., *B. reflexa*) and Coleoptera hosts (e.g., *Z. aberrans* and *G. anthracina*). However, more than half of the species collected were associated to lepidopteran hosts (see host association section below). Additionally, the species *Chetogena micronychia* (Masson) and *Pseudomintho diversipes* (Strobl) were recorded for the first time in Italy. The estimated rarefaction curves for each focal patch ended with a fairly similar slope, suggesting that the observed species richness was comparable between patches (Fig. S1).

Table 1. Results from the mixed models testing the effects of patch area, connectivity, and season on tachinid (a) log-abundance and (b) species richness. Patch was included as a random factor and area was log-transformed to improve linearity in both models. For abundance we used general linear models with a normal distribution while for species richness we used a generalized linear mixed model with a Poisson distribution (log-link function). The interactions between season and area and between season and connectivity were removed from the model with a backwards deletion procedure ($P > 0.05$). For the full model refer to Table S3.

(a) Abundance	Estimate	SE	t value	P value
Intercept	-9.320	2.271	-4.104	<0.001
Log(Area)	2.549	0.514	4.960	<0.001
Connectivity	0.246	0.110	2.246	0.041
Season-spring	-0.869	0.106	-8.200	<0.001
Season-summer	-0.361	0.113	-3.181	0.001
Log(Area) x Connectivity	-0.057	0.024	-2.291	0.037
(b) Species richness			z value	
Intercept	-10.845	2.374	-4.567	<0.001
Log(Area)	2.675	0.525	5.095	<0.001
Connectivity	0.277	0.115	2.413	0.016
Season-spring	-0.967	0.096	-10.067	<0.001
Season-summer	-0.219	0.086	-2.558	0.011
Log(Area) x Connectivity	-0.060	0.025	-2.376	0.018

Species composition and abundance varied strongly over time. Of the 1528 specimens sampled, 53% were collected in fall and 31% and 16% were collected in summer and spring, respectively. The most species-rich season was summer with 82 species followed by fall and spring with 79 and 34 species, respectively. Additionally, we found that more than half of the species collected were restricted to only one particular season. Specifically, 26, 25 and 9% of the species were found exclusively in summer, fall and spring, respectively. The communities from summer and autumn are the most similar, sharing more than half of the species, while spring was more dissimilar from summer and fall (Table 2).

Effect of area, connectivity and season

We found a significant effect on tachinid abundance and species richness of both habitat area and connectivity (Table 1). We also found in both models an interaction between

area and connectivity, *i.e.* when connectivity was low the area effect was stronger, while when connectivity was large the area effect became less apparent (Fig. 2). The model using the species estimator as our response variable led to similar results as those obtained using observed species richness (Table S4). We found no support for any interaction between seasons and either area or connectivity indicating that the effects of both factors were consistent among seasons (Table S3), even if the species assemblages changed substantially over time (Table 2). We did not find significant spatial autocorrelation in the residuals of both abundance and species richness models. At all the distances, the Mantel correlations were close to zero.

Table 2. Tachinid community similarity between the different seasons. Jaccard similarity index varies between 0 (completely different communities) and 1 (completely similar communities) (Magurran et al. 2010).

Season	Shared species	Jaccard similarity
Spring vs. Summer	18	0.19
Spring vs. Autumn	14	0.14
Autumn vs. Summer	44	0.38

Host association and habitat diversity

Although tachinids exhibit a wide range of hosts, three insect orders were identified as their main hosts. Species attacking lepidopterans represented half of the species collected, while hemipterans and coleopterans grouped 19 and 15% of the species, respectively. However, the most abundant species were related mainly to coleopterans and hemipterans. The interaction between habitat diversity and host association was not significant for both tachinid abundance and species richness. Similarly, we did not find any support that connectivity or area interacted with host association (Table S5).

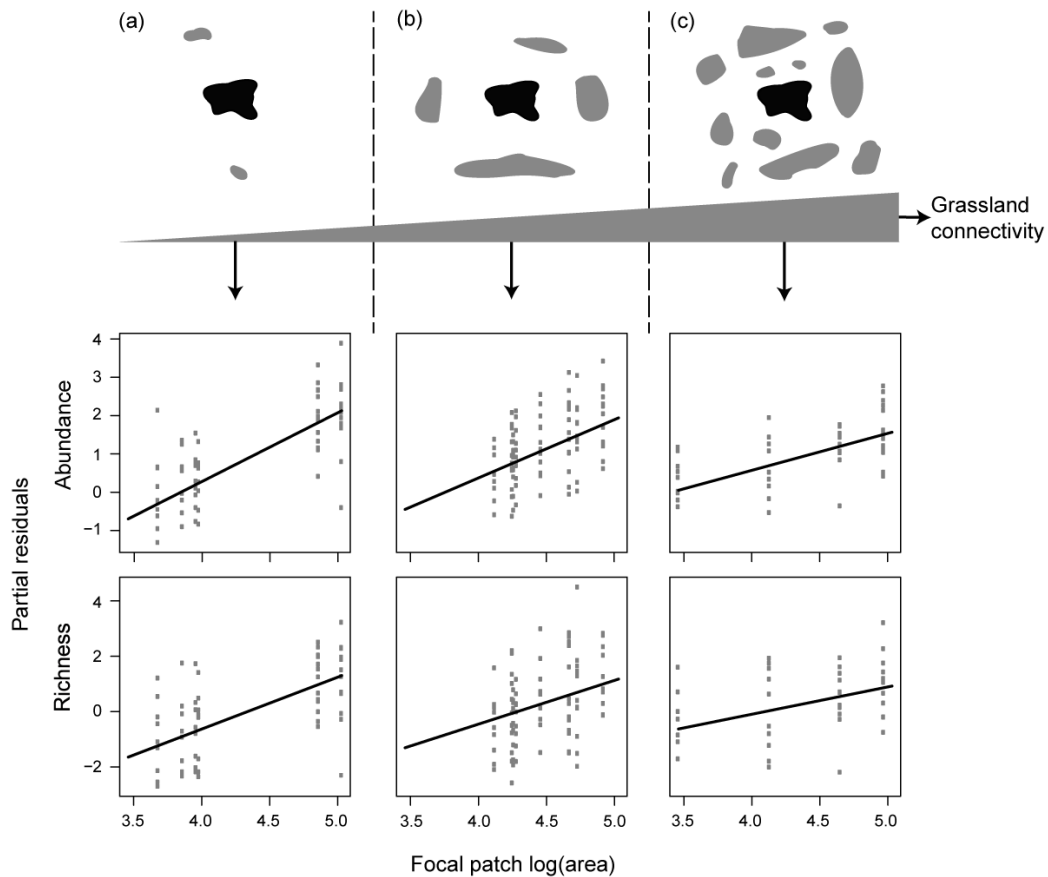


Figure 2. Plots showing the interaction between area and connectivity on tachinid log-abundance and species richness. Panels are ranked from left (a) to right (c) according to increasing habitat connectivity. The fitted line is a general linear model estimate for log-abundance and a generalized linear mixed model estimate for species richness. The points represent the partial residuals from the respective models described in Table 1. Panels were drawn using the “visreg” function from the library “visreg” in R.

Discussion

Our study is one of the few testing simultaneously the effect of habitat area, connectivity and habitat diversity on species diversity on non-hymenopteran parasitoids. Tachinid parasitoids showed a clear species–area relationship with a linear increase in abundance and species richness as the area of the patches increases. However, the strength of the habitat loss effect depended on the degree of habitat connectivity. Abundance and species richness were negatively affected by habitat loss in highly fragmented landscapes, but the effect was less evident in landscapes with relatively high habitat connectivity. This result has important implications for biodiversity conservation as any attempts to mitigate the negative effects of habitat loss need to take the general level of habitat connectivity in the landscape into account (see also Rösch et al. 2013).

Habitat fragmentation often consists of a combination of area reduction with a decrease in connectivity among remnant fragments. As the habitat patches become smaller, higher extinction rates due to environmental stochasticity in combination with a lower probability of receiving immigrants through dispersal may cause the often observed declines in abundance and species richness (Hanski 1999). A growing body of research further suggests that low connectivity can significantly affect the dispersal and species persistence in fragmented landscapes (Roland & Taylor 1997; Cronin 2007). In accordance with these predictions, we found that tachinid species diversity was positively related to habitat connectivity, but this effect also interacted with habitat loss. As the habitat patches became highly isolated, the abundance and richness of tachinids were more dependent on habitat area. Contrastingly, as the patches became relatively well connected the effect of habitat area was less evident. These contrasting effects of habitat loss at different levels of habitat connectivity, has been already shown for leafhopper communities (Rösch et al. 2013). The observed interaction between area and connectivity is consistent with the concept of extinction threshold applied at the community level (Andrén 1994; Pardini et al. 2010), i.e. for a given species, the total quantity of habitat available must exceed a certain threshold value for the species to persist. Landscapes with little and fragmented habitat are likely to be below the extinction threshold, while landscapes with large habitat cover and connectivity are expected to be above this threshold (Hanski 2011). The persistence of diverse tachinid parasitoid communities in our study area despite the high levels of fragmentation and low connectivity support the view that more generalist parasitoids can cope better with fragmentation pressure than more specialist groups (e.g., Pardini et al. 2010). This also suggests that tachinids may be good dispersers and/or they can use alternative hosts in the adjacent agricultural matrix, although this remains to be tested.

Although tachinids exhibited large within-year species turnover, we found that this large temporal replacement did not modify the overall effects of landscape fragmentation. While most of the studies regarding habitat fragmentation have ignored changes in species through time, the few studies considering this effect have reported that species interact differently with habitat type in the different seasons (Letourneau et al. 2012). Differently to our initial hypothesis that the effects of habitat fragmentation varies between seasons, our results indicated that the parasitoid community that we examined had a relatively constant response to both area and connectivity.

Contrary to our predictions, we did not find a relationship between habitat diversity and overall parasitoid abundance and species richness. The low host specificity of tachinids may have led to the lack of habitat diversity effect. Tachinids are expected to further depend on host density rather than just host diversity. Increasing habitat diversity has been proved to support a greater variety of species (e.g., Landis et al. 2005; Scherber et al. 2006), but not necessarily an increase in species abundances (e.g., Johnson et al. 2006; Bennett & Gratton 2013). In fact, host density is often more associated to landscape variables such as area and connectivity (e.g., Ekroos et al. 2013; Veres et al. 2013). Similarly, we did not find an interaction between habitat diversity and host association indicating that the parasitoid species did not respond to this variable irrespective of their host association.

Contrary to the hypothesis that parasitoids are highly susceptible to habitat fragmentation (Kruess & Tschardtke 1994; Holt et al. 1999), we showed that relatively polyphagous parasitoids may not be as severely affected by habitat loss. However, we found that for tachinid parasitoids their diversity still depends on minimum levels of remnant habitats in the landscape (c. 10%). The processes of habitat area reduction and loss of connectivity significantly interacted indicating that management practices to mitigate the negative effect of habitat loss at the local scale need to consider the surrounding landscape. In particular, the conservation of habitat connectivity needs to be specially considered on landscapes with small remnant habitats. Maintaining large habitat diversity within the habitat remnants appeared to be neutral to more generalist parasitoids. Our study provides new insights into the consequences of landscape changes on the diversity of a key functional group that has been long overlooked in ecological and conservation studies. The next step will be to understand the consequences of the loss of parasitoid diversity on ecosystem functioning (e.g., Fenoglio et al. 2012) to fully understand how fragmentation affects the complex multi-trophic interactions in highly fragmented landscapes.

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Supplementary Material

Table S1. Description of the sampled patches with the indication of area, connectivity (% of semi-natural coverage), and within patch habitat composition.

Locality	ID	No traps	Area (ha)	Coordinates (decimal degrees)		Semi-natural (%) (2 km buffer)			Within patch habitat composition (%)		
				Long	Lat	Grass	Forest	Total	Bare	Shrub	Grass
Asciano	ID47	2	0.28	11.602	43.204	7	12.6	19.6	4.5	50.9	44.6
Arbia	N01	2	0.48	11.452	43.278	5.9	2.8	8.7	16.5	1.9	81.6
San Quirico d'Orcia	DI17	2	0.72	11.618	43.070	3.1	7.6	10.7	1.3	45.3	53.4
Pienza	N05	2	0.92	11.665	43.064	4.9	1.2	6.1	3	56.6	40.4
San Giovanni d'Asso	N08	2	0.95	11.577	43.139	4.9	20.1	25	2.4	73.3	24.2
Chiusure	DI44	2	1.3	11.580	43.181	3.5	13.3	16.9	3	58.5	38.6
Asciano	DI50	2	1.36	11.548	43.216	4.2	26.6	30.8	35.9	17.7	46.5
Torrenieri	N06	3	1.76	11.557	43.122	7.5	25.5	33	4	54.4	41.6
Vescona Chiesa	DI52	3	1.81	11.498	43.281	4.1	1.3	5.4	17.6	9.3	73.1
Monteroni d'Arbia	DI10	3	1.92	11.451	43.229	3.1	21.7	24.9	2.9	19.7	77.4
San Giovanni d'Asso	N04	4	2.91	11.563	43.136	2	34.2	36.1	4.8	84.5	10.7
Bollano	N03	5	4.43	11.529	43.175	10.1	46	56.1	1.5	88.7	9.8
Arbia	ID22	6	4.66	11.397	43.278	2.3	6.3	8.6	5.1	13.2	81.7
Vescona Chiesa	DI34	6	5.36	11.492	43.274	2.5	10.3	12.8	7.5	33.7	58.8
Monteroni d'Arbia	DI09	8	7.2	11.449	43.218	1.5	0.7	2.2	0.9	42.3	56.8
Arbia	DI38	9	8.34	11.427	43.281	5.3	1	6.3	4.6	30.6	64.8
San Quirico d'Orcia	N07	10	9.36	11.579	43.075	4.5	13.9	18.4	1.1	44.2	54.8
Arbia	ID12	12	10.82	11.428	43.260	2.8	4.4	7.2	6.6	31.2	62.3

Table S2. Tachinid species and their abundance in the study area.

Species	Total of specimens
<i>Acemya acuticornis</i> (Meigen, 1824)	1
<i>Aplomya confinis</i> (Fallén, 1820)	17
<i>Atylomyia loewii</i> Brauer, 1898	3
<i>Besseria reflexa</i> Robineau-Desvoidy, 1830	199
<i>Bithia immaculata</i> (Herting, 1971)	1
<i>Bithia modesta</i> (Meigen, 1824)	7
<i>Blepharipa pratensis</i> (Meigen, 1824)	1
<i>Bothria frontosa</i> (Meigen, 1824)	2
<i>Campylocheta latigena</i> Mesnil, 1974	1
<i>Carcelia falenaria</i> (Rondani, 1859)	53
<i>Catharosia albisquama</i> (Villeneuve, 1932)	2
<i>Catharosia pygmaea</i> (Fallén, 1815)	2
<i>Cestonia cineraria</i> Rondani, 1861	2
<i>Chetina setigena</i> Rondani, 1856	14
<i>Chetogena filipalpis</i> Rondani, 1859	5
<i>Chetogena micronychia</i> (Masson, 1969)***	1
<i>Chetogena rondaniana</i> (Villeneuve, 1931)	2
<i>Clairvillia pniinae</i> Kugler, 1971	1
<i>Clausicella suturata</i> Rondani, 1859	4
<i>Clemelis massilia</i> Herting, 1977	9
<i>Clemelis pullata</i> (Meigen, 1824)	1
<i>Clytiomya sola</i> (Rondani, 1861)	1
<i>Cylindromyia auriceps</i> (Meigen, 1838)	8
<i>Cylindromyia bicolor</i> (Olivier, 1812)	1
<i>Cylindromyia brassicaria</i> (Fabricius, 1775)	3
<i>Cylindromyia brevicornis</i> (Loew, 1844)	1
<i>Cylindromyia intermedia</i> (Meigen, 1824)	6
<i>Cylindromyia pilipes</i> (Loew, 1844)	7
<i>Cylindromyia pusilla</i> (Meigen, 1824)	1
<i>Cylindromyia rufifrons</i> (Loew, 1844)	1
<i>Cylindromyia rufipes</i> (Meigen, 1824)	2
<i>Cyrtophleba ruricola</i> (Meigen, 1824)	2
<i>Dolichocolon paradoxum</i> Brauer & Bergenstamm, 1889	17
<i>Drino atropivora</i> (Robineau-Desvoidy, 1830)	3
<i>Dufouria nigrata</i> (Fallén, 1810)	2
<i>Ectophasia crassipennis</i> (Fabricius, 1794)	2
<i>Eriothrix rufomaculata</i> (DeGeer, 1776)	2
<i>Erycia festinans</i> (Meigen, 1824)	10
<i>Erynniopsis antennata</i> (Rondani, 1861)	1
<i>Eurysthaea scutellaris</i> (Robineau-Desvoidy, 1848)	1
<i>Exorista civilis</i> (Rondani, 1859)	1
<i>Exorista larvarum</i> (Linnaeus, 1758)	1
<i>Exorista mimula</i> (Meigen, 1824)	1
<i>Exorista nympharum</i> (Rondani, 1859)	3
<i>Exorista rustica</i> (Fallén, 1810)	4
<i>Gaedia connexa</i> (Meigen, 1824)	4

Table S2. continued

<i>Gaedia distincta</i> Egger, 1861	4
<i>Gastrolepta anthracina</i> (Meigen, 1826)	276
<i>Gonia picea</i> (Robineau-Desvoidy, 1830)	1
<i>Hebia flavipes</i> Robineau-Desvoidy, 1830	1
<i>Kirbya moerens</i> (Meigen, 1830)	2
<i>Lecanipa leucomelas</i> (Meigen, 1824)	1
<i>Leucostoma anthracinum</i> (Meigen, 1824)	4
<i>Leucostoma nudifacies</i> Tschorsnig, 1991	5
<i>Leucostoma simplex</i> (Fallén, 1815)	6
<i>Leucostoma tetraptera</i> (Meigen, 1824)	21
<i>Linnaemya frater</i> (Rondani, 1859)	2
<i>Linnaemya soror</i> Zimin, 1954	2
<i>Linnaemya vulpina</i> (Fallén, 1810)	6
<i>Litophasia hyalipennis</i> (Fallén, 1815)	1
<i>Loewia setibarba</i> Egger, 1856	12
<i>Lomachantha parra</i> Rondani, 1859	3
<i>Macquartia dispar</i> (Fallén, 1820)	1
<i>Macquartia tessellum</i> (Meigen, 1824)	1
<i>Macquartia viridana</i> Robineau-Desvoidy, 1863	2
<i>Medina collaris</i> (Fallén, 1820)	1
<i>Medina separata</i> (Meigen, 1824)	6
<i>Meigenia dorsalis</i> (Meigen, 1824)	3
<i>Meigenia majuscula</i> (Rondani, 1859)	15
<i>Meigenia mutabilis</i> (Fallén, 1810)	5
<i>Meigenia uncinata</i> Mesnil, 1967	1
<i>Microphthalma europaea</i> Egger, 1860	4
<i>Microsoma exiguum</i> (Meigen, 1824)	1
<i>Mintho rufiventris</i> (Fallén, 1817)	26
<i>Nemorilla maculosa</i> (Meigen, 1824)	48
<i>Ocytata pallipes</i> (Fallén, 1820)	2
<i>Opesia cana</i> (Meigen, 1824)	1
<i>Opesia grandis</i> (Egger, 1860)	17
<i>Oswaldia muscaria</i> (Fallén, 1810)	4
<i>Pales pavidata</i> (Meigen, 1824)	21
<i>Panzeria puparum</i> (Fabricius, 1794)	1
<i>Paratryphera barbatula</i> (Rondani, 1859)	18
<i>Paratryphera bisetosa</i> (Brauer & Bergenstamm, 1891)	8
<i>Paratryphera mesnili</i> Herting, 1977	1
<i>Paratryphera palpalis</i> (Rondani, 1859)	7
<i>Peleteria iavana</i> (Wiedemann, 1819)	8
<i>Peleteria meridionalis</i> (Robineau-Desvoidy, 1830)	4
<i>Peleteria rubescens</i> (Robineau-Desvoidy, 1830)	9
<i>Peleteria ruficornis</i> (Macquart, 1835)	6
<i>Peribaea apicalis</i> Robineau-Desvoidy, 1863	2
<i>Peribaea tibialis</i> (Robineau-Desvoidy, 1851)	5
<i>Periscepsia carbonaria</i> (Panzer, 1798)	11
<i>Periscepsia latifrons</i> (Zetterstedt, 1844)	1
<i>Periscepsia spathulata</i> (Fallén, 1820)	1

Table S2. continued

<i>Phania funesta</i> (Meigen, 1824)	21
<i>Phasia mesnili</i> (Draber-Monko, 1965)	3
<i>Phasia obesa</i> (Fabricius, 1798)	1
<i>Phasia pandellei</i> (Dupuis, 1957)	5
<i>Phorinia aurifrons</i> Robineau-Desvoidy, 1830	2
<i>Platymya antennata</i> (Brauer & Bergenstamm, 1891)	1
<i>Platymya fimbriata</i> (Meigen, 1824)	1
<i>Prosopaea nigricans</i> (Egger, 1861)	5
<i>Pseudogonia parisiaca</i> (Robineau-Desvoidy, 1851)	12
<i>Pseudogonia rufifrons</i> (Wiedemann, 1830)	4
<i>Pseudomintho diversipes</i> (Strobl, 1899)***	24
<i>Pseudoperichaeta palesioidea</i> (Robineau-Desvoidy, 1830)	1
<i>Siphona geniculata</i> (DeGeer, 1776)	3
<i>Siphona pauciseta</i> Rondani, 1865	3
<i>Smidtia laticauda</i> (Mesnil, 1963)	1
<i>Spallanzania rectistylum</i> (Macquart, 1847)	1
<i>Staurochaeta albocingulata</i> (Fallén, 1820)	1
<i>Stomina caliendrata</i> (Rondani, 1862)	4
<i>Stomina calvescens</i> Herting, 1977	19
<i>Stomina tachinoides</i> (Fallén, 1817)	3
<i>Tachina magnicornis</i> (Zetterstedt, 1844)	6
<i>Thecocarcelia trichops</i> Herting, 1967	1
<i>Thelaira nigripes</i> (Fabricius, 1794)	1
<i>Thelaira solivaga</i> (Harris, 1780)	2
<i>Thelyconychia solivaga</i> (Rondani, 1861)	1
<i>Triarthria setipennis</i> (Fallén, 1810)	5
<i>Voria ruralis</i> (Fallén, 1810)	88
<i>Wagneria cunctans</i> (Meigen, 1824)	1
<i>Wagneria gagatea</i> Robineau-Desvoidy, 1830	1
<i>Zaira cinerea</i> (Fallén, 1810)	2
<i>Zeuxia aberrans</i> (Loew, 1847)	289
<i>Zeuxia cinerea</i> Meigen, 1826	8
<i>Zeuxia erythraea</i> (Egger, 1856)	4
<i>Zeuxia zejana</i> Kolomiets, 1971	1
<i>Ziminia masiceraeformis</i> (Portshinsky, 1881)	2
Total of species	129
Total specimens	1528

***Indicates new species recorded for Italy

Table S3. Results from the mixed models testing the effects of patch area, connectivity, and season on tachinid (a) log-abundance and (b) species richness. Patch was included as a random factor and area was log-transformed to improve linearity in both models. For abundance we used a general linear model while for species richness we used a generalized linear mixed model with a Poisson distribution (log-link function).

(a) Abundance	Estimate	SE	t value	P value
Intercept	-10.910	2.382	-4.581	<0.001
Log(Area)	2.875	0.539	5.335	<0.001
Connectivity	0.255	0.110	2.317	0.036
Season-spring	1.051	1.046	1.005	0.316
Season-summer	2.037	1.120	1.820	0.070
Log(Area) x Connectivity	-0.057	0.025	-2.292	0.038
Connectivity x spring	-0.009	0.015	-0.578	0.564
Connectivity x summer	-0.016	0.016	-1.013	0.312
Log(Area) x spring	-0.403	0.235	-1.717	0.087
Log(Area) x summer	-0.479	0.251	-1.906	0.060
(b) Species richness			z value	
Intercept	-11.114	2.461	-4.516	<0.001
Log(Area)	2.715	0.542	5.013	<0.001
Connectivity	0.287	0.115	2.487	0.0129
Season-spring	-2.091	1.258	-1.663	0.0964
Season-summer	0.924	1.072	0.863	0.3884
Log(Area) x Connectivity	-0.061	0.025	-2.418	0.0156
Connectivity x spring	0.005	0.013	0.403	0.6868
Connectivity x summer	-0.016	0.012	-1.277	0.2017
Log(Area) x spring	0.220	0.260	0.848	0.3963
Log(Area) x summer	-0.182	0.221	-0.824	0.4102

The categorical factor season included three levels (spring, summer, and fall). All the other variables were continuous.

Table S4. Results from the generalized linear model using the Jack1 species richness estimators as response variable. The generalized linear model tested the effects of patch area, connectivity and their interaction on the estimated species richness. GLM was performed using a Poisson distribution (log-link function). The model did not include season as the estimator used the 16 sampling events to estimate species richness.

	Estimate	SE	z value	P value
Intercept	-4.645	1.483	-3.132	0.002
Log(Area)	1.813	0.321	5.650	<0.001
Connectivity	0.150	0.074	2.030	0.042
Log(Area) x Connectivity	-0.032	0.016	-1.991	0.046

Table S5. Results from the mixed models testing the effects of patch area, connectivity, host type and habitat diversity on tachinid (a) log-abundance and (b) species richness. Patch was included as a random factor and area was log-transformed to improve linearity in both models. For abundance we used general linear models while for species richness we used a generalized linear mixed model with a Poisson distribution (log-link function).

(a) Abundance	Estimate	SE	<i>t</i> value	<i>P</i> value
Intercept	-13.237	2.605	-5.081	<0.001
Log(Area)	3.446	0.620	5.558	<0.001
Connectivity	0.414	0.133	3.109	0.008
Hemiptera host	0.418	0.943	0.443	0.658
Lepidoptera host	1.839	0.943	1.950	0.053
Habitat diversity	0.112	0.990	0.113	0.912
Log(Area) x Connectivity	-0.096	0.030	-3.174	0.007
Habitat diversity x Hemiptera host	-1.473	1.272	-1.158	0.249
Habitat diversity x Lepidoptera host	-2.536	1.272	-1.993	0.048
(b) Species richness			<i>z</i> value	
Intercept	-11.150	3.096	-3.601	<0.001
Log(Area)	2.438	0.720	3.385	0.001
Connectivity	0.263	0.158	1.664	0.096
Hemiptera host	1.125	0.774	1.454	0.146
Lepidoptera host	2.051	0.658	3.119	0.002
Habitat diversity	0.687	0.977	0.703	0.482
Log(Area) x Connectivity	-0.057	0.035	-1.616	0.106
Habitat diversity x Hemiptera host	-1.533	1.034	-1.483	0.138
Habitat diversity x Lepidoptera host	-1.441	0.871	-1.655	0.098

The categorical factor host included three levels (Coleoptera, Hemiptera and Lepidoptera hosts). All the other variables were continuous.

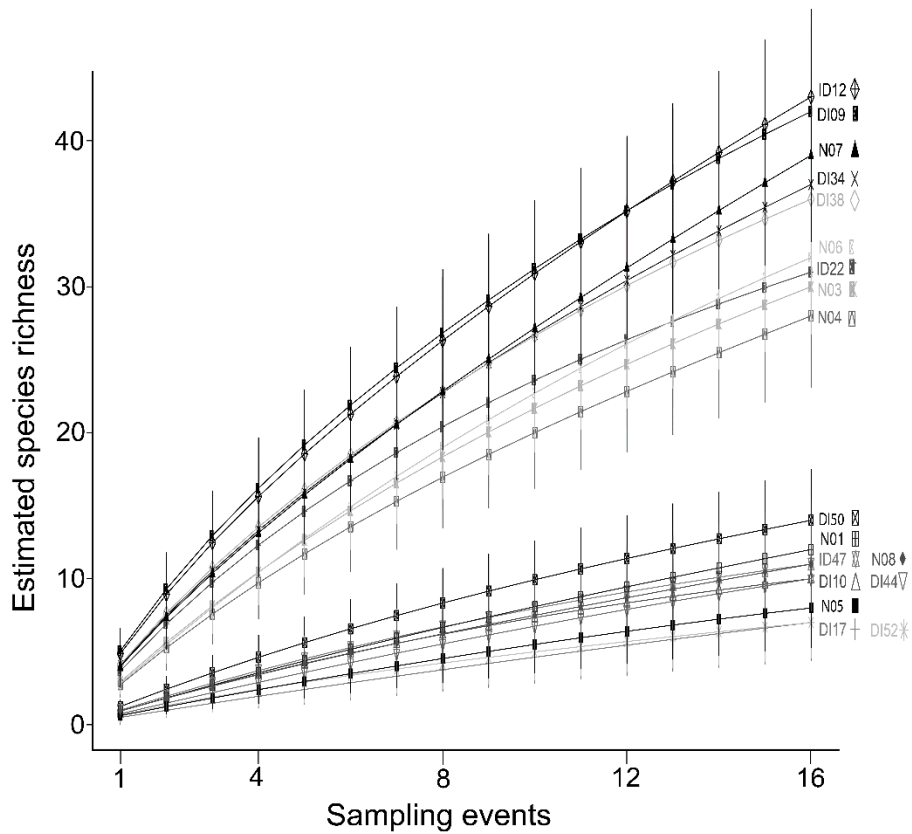


Figure S1. Accumulation curves of tachinid species richness against the number of sampling events for each focal patch. The vertical lines in the accumulation curves represent the 95% CI. Rarefaction curves are based on 1000 randomizations. Curves were drawn using the “accumcomp” function from the library “BiodiversityR” in R. For specific patch information refer to TableS1 using the ID code.



Chapter III

Organic farming enhances parasitoid diversity at the local & landscape scale

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Abstract

The magnitude of the benefits derived from organic farming within contrasting managed landscapes remains unclear and, in particular, the potential scale-dependent response of insect parasitoids is relatively unexplored. Identifying the scale at which parasitoids are affected by organic farming will be an important step to enhance their conservation. We sampled tachinid parasitoids at the centre and margin of arable and grassland fields on paired organic and conventional farms located in landscapes with different proportions of organic land. A total of 192 fields were sampled in two biogeographical regions of the UK. We found that the positive effect of organic farming on tachinid parasitoid diversity can be observed at multiple spatial scales. At the local scale, we found higher abundance and species richness of tachinid parasitoids on organic than on conventional farms and on field margins than on field centres. At the landscape scale, the diversity of tachinids was higher in landscapes with higher proportions of organic land. At both scales, the positive effect of organic farming was clear for arable fields, while it was almost neutral for grasslands. Any attempt to enhance parasitoid diversity in agricultural landscapes needs to consider the local management in relation to habitat type, location within the field and agricultural management in the surrounding landscape. Organic management in arable fields is clearly enhancing tachinid diversity, while the management of organic grasslands needs to be reconsidered. To increase the biodiversity of grasslands, organic management should aim to enhance habitat heterogeneity and to reduce mowing frequency and grazing intensity. To restore parasitoid diversity, the promotion of organic agriculture should aim to increase both the total extent of organic farming and the connectivity of individual organic farms. As the benefits of organic farming clearly spread beyond individual farm boundaries, any economic assessment of organic farming should consider these positive externalities.

Introduction

In the last few decades, agricultural intensification has strongly increased crop productivity through mechanization and the use of improved crop varieties, chemical fertilizers and pesticides leading to severe ecological simplification of European agroecosystems (Swift et al. 1996; Tilman et al. 2001; Wilby & Thomas 2002; Bengtsson et

al. 2005; Fuller et al. 2005; Holzschuh et al. 2010; Geiger et al. 2010). This simplification has resulted in a marked reduction in the diversity of insect natural enemies with possible negative effects on pest control services (Wilby & Thomas 2002; Bianchi et al. 2006; MacFayden et al. 2009; Thies et al. 2011; Jonsson et al. 2012). Although it is relatively well known that intensive agricultural systems are responsible for the decline of species diversity and the abundance of natural enemies in general (e.g., Fuller et al. 2005; Letourneau & Bothwell 2008; Macfadyen et al. 2009, 2011; Lohaus et al. 2013), the understanding of the effects of agricultural management at different spatial scales on important natural enemies such as parasitoids is still incomplete.

In Europe, to counteract the decline in farmland biodiversity, several agri-environment schemes (AES) have been implemented, including subsidies to support organic farming. In contrast to conventional agriculture, organic farming is a production system considered to be more sustainable because the use of synthetic fertilizers and pesticides are excluded. These practices increase farmland heterogeneity and often enhance parasitoid diversity and possibly natural pest control (Bengtsson et al. 2005; Letourneau & Bothwell 2008; Macfadyen et al. 2009, 2011; Crowder et al. 2010), although the specific contribution of insect parasitoid diversity to pest control remains unclear (Finke & Denno 2004; Pérez-Lachaud et al. 2004; Batchelor et al. 2005). Research on parasitoids has only focused on organic management at the local scale, ignoring potential effects at the landscape scale. Although several studies have considered the effects of landscape composition on insect diversity, this research has mainly focused on the role of semi-natural habitats or habitat heterogeneity in the landscape (see review of Tuck et al. 2014), rather than effects of management type within the same land-use class (but see Holzschuh et al. 2008; Rundlöf et al. 2010; Gabriel et al. 2010). The magnitude of the benefits derived from organic farming within diverse agricultural managed landscapes remains unclear. Similarly, while recent research has highlighted that different taxa respond to organic management at different spatial scales (Gabriel et al. 2006; Clough et al. 2007; Gabriel et al. 2010), the potential scale-dependent response of insect parasitoids is relatively unexplored. Identifying the scale at which parasitoids are most strongly affected by organic farming will be an important step to maximize the benefits from AES and potentially to enhance the biocontrol of pests.

Most of the studies that have elucidated the effect of agricultural management and landscape on parasitoids have focused on single or a few species of hymenopteran

parasitoids (e.g., Thies et al. 2011; Jonsson et al. 2012; Lohaus et al. 2013). In this work, we used tachinids (Diptera: Tachinidae) as an alternative and non-hymenopteran parasitoid group. With almost 8,500 species, the Tachinidae family ranks second in diversity within the Diptera and is the most diverse group of non-hymenopteran parasitoids (Stireman et al. 2006; O'Hara 2013). Tachinids tend to have a wider range of hosts than hymenopteran parasitoids and can be very important natural enemies of agricultural pests. Tachinids often play significant roles in regulating herbivore populations due to their predominance in attacking the larval stage of lepidopterans, coleopterans, hemipterans and other major groups of insect herbivores (Stireman et al. 2006; Cerretti et al. 2014). In general, about 100 species have been employed in biological control programs of crop and forest pests (Grenier 1988; Stireman et al. 2006). Additionally, adult tachinids are flower visiting insects as they use nectar as an energy source and may even act as pollinators (Al-Dobai et al. 2012), although their importance in this respect has been largely unexplored (Stireman et al. 2006). Considering the diversity and crucial role of tachinids as parasitoids, more research is needed to elucidate the effects of management across different scales on this key functional group.

The main aim of our study was to examine how local farm management (organic vs. conventional) and the proportion of land under organic farming in the landscape affects species richness and the abundance of tachinid parasitoids. Specifically, we addressed four main questions. First, due to the marked differences in local management between organic and conventional farming, does organic farming enhance the local diversity of parasitoids? Second, if organic management has a positive effect on tachinid diversity, is this effect stronger for arable crops than for grasslands? Third, due to the greater difference in the local management of field centres between the two farming regimes, is there a more pronounced effect of organic farming in field centres than in field margins? Fourth, according to the source-sink hypothesis (Pulliam 1988), is organic farming acting as “source” of parasitoids from where conventional farms could benefit as “sink” habitats through the spill-over of individuals? If so, it is expected that parasitoid diversity in conventional farms located in landscapes with high coverage of organic farming will be greater than in landscapes dominated by conventional agriculture.

Methods

Study area and sampling design

The study design and the site selection are described in full detail in Gabriel et al. (2010). In summary, sixteen landscapes of 10 x 10 km were selected containing different proportions of land under organic farming (Fig. 1a). Landscapes were arranged in eight clusters of paired landscapes. Paired landscapes were chosen to have similar environmental conditions (i.e. very similar landscape composition), but contrasting amounts of organic farming, i.e. organic “hotspot” versus “coldspot” depending on the proportion of land under organic farming (hotspot mean 17.2%, range 8.9–36.8% vs. coldspot mean 1.4%, range 0.5–3.3%) (see Gabriel et al. 2009). The paired landscapes within each cluster were located within an average distance of 28.3 ± 14.4 km. Four clusters were located in the Central South West and four in the North Midlands of England (Fig 1a). Each landscape (both hotspot and coldspot) contained one focal organic and one conventional farm with similar enterprise structure (Fig 1b). The paired farms were located within an average distance of 2.9 ± 1.4 km. This study design ensured that the local farm management and the proportion of land under organic farming in the landscape were uncorrelated enabling us to test the interaction between the two scales. Within each farm, three cereal fields (mainly winter wheat) and three grassland fields (mainly grazed permanent pastures) were selected (Fig. 1b). A total of 192 fields were sampled, within 16 organic and 16 conventional farms located in eight clusters divided in two regions.

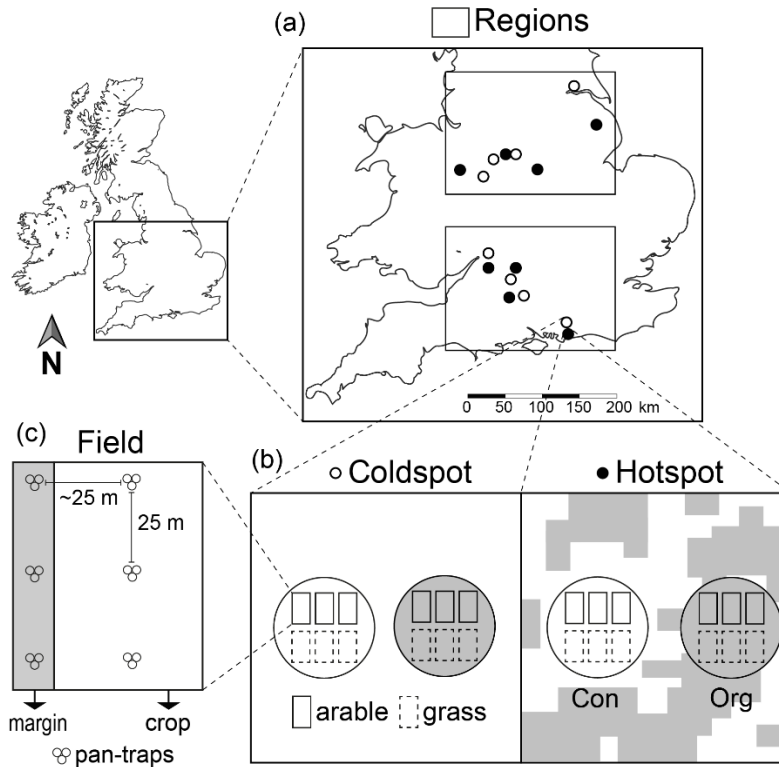


Figure 1. Scheme showing the hierarchical sampling design. (a) Distribution of the 16 paired landscapes across two regions in England. (b) Landscapes with grey shading representing low (coldspot) or high (hotspot) amount of organic land in the landscapes. Each landscape contains one conventional (white circle) and one organic farm (grey circle). Farms contain three arable (solid rectangles) and three grass (dashed rectangles) fields. (c) Within each field three groups of three pan-traps were placed in the field margin and in the field centre.

Insect sampling

Within each field, pan-trap sampling was conducted along two transects. The first transect was placed in the margin of the field (uncultivated area) and the second transect was placed in the field centre, about 25 m from the margin. On each transect, three groups of three pan-traps were placed separated by 25 m (Fig. 1c). Each group of pan-traps consisted of three UV-reflecting colored plastic bowls (yellow, white and blue) with an internal diameter of 11 cm. Pan-traps were held just above the top of the vegetation by a wooden stake and the bowls were half filled with water to which a drop of detergent was added to break the surface tension. The sampling was conducted twice in 2007 in June and July when the average temperature was above 15°C. During each sampling round, traps were set for a period of 48 hours after which insects were retrieved and stored in alcohol (70%) for sorting and identification. A total of 2,304 samples were processed and the specimens belonging to the family Tachinidae (Diptera) were identified to species

level using Cerretti (2010) and Cerretti et al. (2012). All the specimens were housed in the insect collection of P. Cerretti at the MZUR (Museo di Zoologia, Università di Roma La Sapienza, Rome, Italy).

Statistical analyses

To test the effects of cover of organic land in the landscape (hotspot and coldspot), farm management (organic and conventional), habitat (arable and grassland fields), and trap location (margin vs. centre) we used generalized linear mixed effect models. The response variable was the species richness per field and the total number of individuals per field. For abundance we used a generalized linear mixed model with a negative binomial distribution. For species richness we used a generalized linear mixed model with a Poisson distribution. The families and link functions used in the models were selected based on residual deviance and distribution of residuals. Both models included region (Central South and North Midlands), landscape (hotspot and coldspot), farm management (organic and conventional), habitat (arable and grassland fields), and location (margin and centre) as categorical fixed effects. Both models included landscape-cluster ($n = 8$), landscape ID ($n = 16$), farm ID ($n = 32$) and field ID ($n = 192$) as random factors to account for the nested design of the sampling. Although due to its nature region could be a random effect, we include it as a fixed factor because it only had two levels (Bolker et al. 2008). The analyses were performed using the package “glmmADMB” (Fournier et al. 2012), implemented in R 3.0.2 (R Development Core Team 2013).

To compare the fit of all the possible combinations of predictors in our models we used the second-order Akaike’s information criterion (AICc) corrected for small samples (Whittingham et al. 2006). We first built a global model containing the variable region and all the interactions among landscape, farm management, habitat, and location. Region was not included in any interactions, as we did not have any ecological hypothesis to support these analyses. We compared all the models using ΔAICc and Akaike weights ($\sum w_i$). A model is usually considered plausible if its ΔAICc is below two (Burnham & Anderson 2002). To evaluate the relative importance of each predictor, we summed the w_i across the models in the set in which the predictor occurred. The model inference analyses were performed using the “MuMIn” package (Barton 2013) implemented in R (R Development Core Team 2013).

To assess the variability explained by the fixed and random effects, we calculated the pseudo- R^2 . We did not perform this analysis on the abundance model, as currently it is not possible to calculate the pseudo- R^2 of a GLMM with a negative binomial distribution (Nakagawa & Schielzeth 2013; Johnson 2014). To calculate the pseudo- R^2 for the species richness model, we built a mixed model including all parameters that were included in models with a ΔAICc below two. Then, we calculated the marginal and conditional pseudo- R^2 using the function “r.squaredGLMM” implemented in the “MuMIn” package (Barton 2013). The marginal pseudo- R^2 describes the proportion of variance explained by the fixed factors alone, while the conditional pseudo- R^2 describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2013).

Results

A total of 12,954 individuals were collected belonging to 50 species (for species list see Table S1), 8,041 individuals belonging to 40 species were collected in organic farms, while 4,913 individuals belonging to 35 species were collected in conventional farms. Fifteen species were only found on organic farms, while 10 were only found on conventional farms. Two species were dominant accounting for more than 80% of the total abundance. *Siphona geniculata* (DeGeer) and *Eriothrix rufomaculata* (DeGeer) represented 68% and 19% of the individuals collected, respectively. *Siphona geniculata* is one of the few parasitoids known to attack crane fly larvae (Diptera: Tipulidae) which are important agricultural pests damaging grasslands and cereals, although they can also be a problem in other crops, particularly where they are grown after grass leys (Belshaw 1993; Blackshaw & Coll 1999). *Eriothrix rufomaculata* is a parasitoid of lepidopteran larvae, known to attack pyralid larvae (Lepidoptera: Pyralidae) in grasses (Paston & Rotheray 2009).

Table 1. Sum of Akaike weights (Σw_i) across all models for tachinid abundance and species richness. For each predictor, Σw_i is the sum of weights of the models that contain that variable. Σw_i can vary between 0 and 1 and represent the relative importance of the variables (Burnham & Anderson 2002).

	Abundance	Species richness
	Σw_i	Σw_i
Habitat	1.00	0.96
Landscape	1.00	1.00
Location	1.00	1.00
Management	1.00	0.96
Region	1.00	1.00
Habitat x Landscape	0.99	0.85
Habitat x Location	0.44	0.69
Habitat x Management	1.00	0.47
Landscape x Location	0.64	0.72
Landscape x Management	0.50	0.31
Location x Management	0.42	0.41
Habitat x Landscape x Location	0.12	0.19
Habitat x Landscape x Management	0.26	0.05
Habitat x Location x Management	0.14	0.08
Landscape x Location x Management	0.07	0.03
Habitat x Landscape x Location x Management	0	0

For tachinid abundance, six plausible models were selected ($\Delta AICc < 2$, Table S2). The sum of model weights for each predictor gave support for strong effects of region, landscape, farm management, habitat, and trap location on tachinid abundance (Table 1). This indicates that the tachinid abundance was higher in Central South (mean = 48.56 ± 5.72 SE) than North Midlands (21.38 ± 2.72 SE), higher in hotspots (42.63 ± 5.44 SE) than in coldspots (27.18 ± 3.43 SE) (Fig. 2b), higher in organic (43.47 ± 5.86 SE) than in conventional (26.27 ± 2.61 SE) farms (Fig. 2a), higher in grasslands (42.09 ± 5.54 SE) than in arable crops (27.86 ± 3.35 SE), and higher in the field margins (48.26 ± 5.60 SE) than in the field centres (21.24 ± 2.84 SE). We also found a good support for two interactions: management x habitat and landscape x habitat. The first interaction (management x habitat) indicated that organic management exhibited higher abundance than conventional management in arable fields but not in grassland fields (Fig. 3a). Similarly, hotspots had a higher abundance than coldspots in arable fields but not in

grasslands (Fig. 3b; landscape x habitat interaction). Although less strong, we found two additional interactions: landscape x location and landscape x management. The first interaction (landscape x location) indicated that the difference in abundance between field margins and centres was less evident in hotspots than in coldspots. The second interaction (landscape x management) indicated that in hotspots the abundance of tachinids on conventional farms was more similar to that of organic farms.

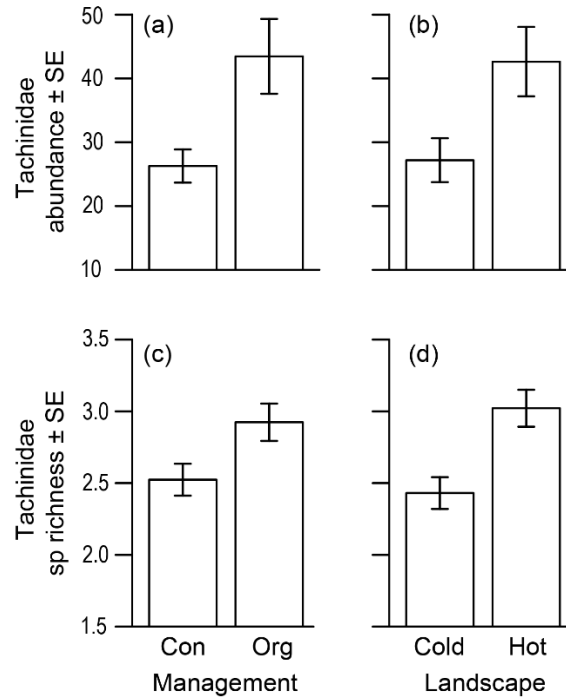


Figure 2. Mean values (\pm SE) of tachinid abundance (a, b) and species richness (c, d) per farm management (Con: conventional, Org: organic) and landscape composition (Cold: coldspot, Hot: hotspot).

For tachinid species richness, 10 plausible models were selected (Δ AICc < 2, Table S2). Similar to tachinid abundance, we found a strong effect of region, landscape, farm management, habitat, and trap location on tachinid species richness (Table 1). This indicates that the tachinid species richness was higher in Central South (3.28 ± 0.12 SE) than North Midlands (2.18 ± 0.11 SE), higher in hotspots (3.02 ± 0.13 SE) than in coldspots (2.43 ± 0.11 SE) (Fig. 2d), higher in organic (2.92 ± 0.13 SE) than in conventional (2.52 ± 0.11 SE) farms (Fig. 2c), higher in arable crops (2.80 ± 0.13 SE) than in grasslands (2.64 ± 0.12 SE), and higher in the field margins (3.36 ± 0.13 SE) than in the field centres (2.08 ± 0.10 SE). As above, we also found strong support for an interaction between landscape and habitat, where hotspots displayed higher species richness than coldspots in arable fields, but not in grasslands (Fig. 3d). Although less

supported, we found two additional interactions: habitat x location and landscape x location. These interactions indicate that the differences in species richness between field margins and centres were less evident in grasslands than in arable crops and in hotspots than in coldspots. We further found that fixed effects explained the majority of the variability of the mixed model containing all the parameters with a $\Delta AICc < 2$. Specifically, we found a pseudo- R^2 of 0.30 for the proportion of variance explained by the fixed factors alone, while for the proportion of variance explained by both the fixed and random factors we found a pseudo- R^2 of 0.32.

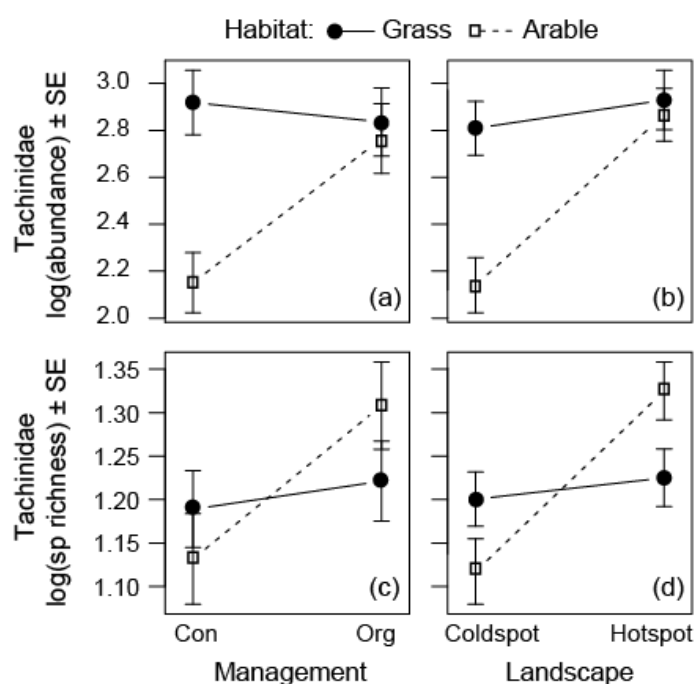


Figure 3. Interaction between management (Con: conventional, Org: organic) and habitat (a, c) and between landscape and habitat (b, d) on tachinid log-abundance and log-species richness. Dots represent mean values and bars represent the SE.

Discussion

Our study indicates a positive effect of organic farming on tachinid parasitoid diversity at multiple spatial scales. We found higher abundance and species richness both on organic farms and in hotspot landscapes. However, the tachinid parasitoid response was complex and various interactions between the organic farming and local habitat were found. In particular, the positive effect of organic management was clear for arable fields while it was almost neutral for grasslands, either at the local or at the landscape scale. These

results have important implications for management, as any attempt to enhance parasitoid diversity in agricultural landscapes needs to consider the local management in relation to habitat type, location within the field and agricultural management in the landscape.

At the local scale, we found that tachinid diversity was always higher in the field margins. Several studies have shown that field margins are important semi-natural habitats within agricultural landscapes hosting high insect diversity (Marshall & Moonen 2002; Benton et al. 2003; Carvell et al. 2007; Olson & Wäckers 2007; Vickery et al. 2009; Macfadyen & Muller 2013; Ó hUallacháin et al. 2014; Dainese et al. 2015), but how margins interact with their adjacent fields is less clear. For example, Olson and Wäckers (2007) showed that managing margins for beneficial insects along conventional fields of cotton increased the diversity of tachinid parasitoids, but there was no effect on the spill-over of individuals into the field. By contrast, Schröter and Irmeler (2013) found in a transitional experiment from conventional to organic farming that after 4 years under organic farming the community of carabid predators of the field centre resembled that of the field margins. In our study we found no effects of local management on the spill-over of tachinids. However, we found a marginal effect of the landscape on the local spill-over of parasitoids from the margin to the field center, suggesting that for highly mobile organisms the effect of management needs to be considered at larger scales.

At the local and landscape scale, we further found that tachinid diversity was differently affected by the organic farming depending on habitat type (grassland or arable land). Specifically, the positive effect of organic management was exhibited strongly in arable fields, but was almost absent for grasslands. Similar results have been found by other authors (Eyre & Leifert 2011; Batáry et al. 2012; Eyre, Luff & Leifert 2013; Kleijn et al. 2011; Scheper et al. 2013), suggesting that differences in the effectiveness of organic farming between these habitats may be explained by differences in disturbance together with their specific management. As arable crops are generally more disturbed by agricultural activities than grasslands, the benefit generated by organic management is expected to be more evident in the former (Kleijn et al. 2011; Scheper et al. 2013). Hence, we found that organic arable land yielded even higher species richness than grasslands. On the one hand, in arable crops under conventional agriculture insects are expected to be negatively affected by the use of chemical pesticides, compared to organic farms where such chemicals are not applied (Boatman et al. 2007; Geiger et al. 2010). For example,

pesticide applications in winter wheat are well known to have negative effects on non-target organisms such as parasitoids (e.g., Longley 1999; Holland et al. 2000). On the other hand, pesticides are not usually applied in grasslands in either organic or conventional farms, and often the intensity of management does not differ significantly between the two farming systems (Geiger et al. 2010; Batáry et al. 2012; Gaujour et al. 2012). In both conventional and organic grasslands, insect diversity is mainly affected by fertilization and mechanical disturbances such as mowing frequency and grazing intensity (van Elsen 2000; Humbert, Ghazoul & Walter 2009; Kruess & Tscharntke 2002; Marini et al. 2009; Gaujour et al. 2012). The main difference between organic and conventional grasslands is in their use of organic and mineral fertilizers respectively, which are actually thought to have very similar effects on flower-visiting insects such as tachinids (Al-Dobai et al. 2012).

Although the local factors explained above were important determinants of the diversity of tachinids, we also found that the proportion of organic land in the landscape played a major role. A greater cover of land under organic farming in the landscape enhanced the diversity of tachinids that can colonize both organic and conventional farms. Specifically, we found that the abundance and species richness of tachinid parasitoids was always higher within hotspot landscapes. The proportion of organic land in the landscape has been found to be important for other insect groups such as butterflies, epigeal arthropods, and solitary bees (Gabriel et al. 2010). These effects may arise because the distribution and persistence of species across landscapes depend on the species' dispersal ability and the proximity of suitable habitats that can support viable population sources (Pulliam 1988; Hanski & Ovaskainen 2002). As tachinid flies have been found to respond to habitat connectivity (Letourneau et al. 2012; Inclán et al. 2014), the amount of organic farming in agricultural landscapes appears to be a potential means of re-establishing heterogeneity of farmland habitats, and thereby enhancing farmland parasitoid diversity (Benton et al. 2003). Therefore, to restore biodiversity in agricultural landscapes, strategies promoting organic agriculture should aim to increase both the total extent of organic farming and the contiguity of individual organic farms.

Conclusions

Our results have important implications for parasitoid conservation in agricultural landscapes. In particular, any attempt to enhance parasitoid diversity, by means of organic management, needs to consider the local management in relation to habitat type and agricultural management in the landscape. At the local scale, organic management in arable fields is clearly enhancing tachinid diversity, while the management of organic grasslands needs to be reconsidered (Batary et al. 2012). As it has been shown by other authors, the effects of AES measures increase with the size of the ecological contrast created by the measure (Kleijn et al. 2011; Scheper et al. 2013). The contrast between conventional and organic wheat fields is much higher than that between conventional and organic grasslands. Therefore, to increase the biodiversity of grasslands, organic management should aim to enhance heterogeneity and to modify management practices such as mowing and grazing intensity (Humbert et al. 2009; Gaujour et al. 2012). At the landscape scale, our results exemplify how landscapes with higher proportion of organic land improved the overall diversity of tachinid parasitoids. Conventional farms had 42 and 18% higher tachinid abundance and species richness in organic landscapes than in landscapes with high cover of conventional agriculture. Thus, as the benefits of organic management spread beyond the borders of individual farms, any economic assessment of the costs and benefits of organic farming should incorporate these “positive externalities” that are not captured in the farms’ balance sheets. To restore parasitoid diversity in agricultural landscapes, the promotion of organic agriculture (i.e. as an AES strategy) should aim to increase both the total extent of organic farming and the connectivity of individual organic farms. Subsequently, the biodiversity restored by the implementation of organic management (either at the local or landscape scale) could support important ecosystem services. As organic management increased the abundance of tachinid parasitoids (by about 40%), the pest control in these systems is expected to be greater. Additionally, as tachinid parasitoids have a wide range of hosts, increasing their diversity would increase also the potential to control a wide spectrum of pests (i.e. the two most abundant species in our study attack two completely different host groups). Furthermore, we expect that the results found here on tachinid parasitoids, could be extended to other groups of insect parasitoids. However, to justify and facilitate the increase of organic farming, future research is still needed to demonstrate the specific contribution of parasitoids to key ecosystem services such as biological control.

Acknowledgements

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Supplementary Material

Table S1. Tachinid species and their abundance in the study sites.

Species	Total of individuals
<i>Actia infantula</i> (Zetterstedt, 1844)	1
<i>Actia lamia</i> (Meigen, 1838)	1
<i>Admontia maculisquama</i> (Zetterstedt, 1859)	2
<i>Bithia spreta</i> (Meigen, 1824)	2
<i>Catharosia pygmaea</i> (Fallén, 1815)	4
<i>Compsilura concinnata</i> (Meigen, 1824)	2
<i>Demoticus plebejus</i> (Fallén, 1810)	1
<i>Dexia rustica</i> (Fabricius, 1775)	1
<i>Dexiosoma caninum</i> (Fabricius, 1781)	1
<i>Dinera grisea</i> (Fallén, 1817)	94
<i>Drino lota</i> (Meigen, 1824)	1
<i>Dufouria chalybeata</i> (Meigen, 1824)	2
<i>Epicamocera succincta</i> (Meigen, 1824)	44
<i>Eriothrix rufomaculata</i> (DeGeer, 1776)	2524
<i>Exorista larvarum</i> (Linnaeus, 1758)	3
<i>Exorista rustica</i> (Fallén, 1810)	113
<i>Freraea gagatea</i> Robineau-Desvoidy, 1830	2
<i>Loewia foeda</i> (Meigen, 1824)	3
<i>Lydella grisea</i> Robineau-Desvoidy, 1830	40
<i>Lydella stabulans</i> (Meigen, 1824)	3
<i>Macquartia grisea</i> (Fallén, 1810)	1
<i>Macquartia praefica</i> (Meigen, 1824)	2
<i>Medina separata</i> (Meigen, 1824)	2
<i>Meigenia incana</i> (Fallén, 1810)	1
<i>Meigenia mutabilis</i> (Fallén, 1810)	322
<i>Nemorilla maculosa</i> (Meigen, 1824)	3
<i>Nowickia ferox</i> (Panzer, 1809)	17

Table S1. continued

<i>Ocytata pallipes</i> (Fallén, 1820)	21
<i>Pales pavidata</i> (Meigen, 1824)	5
<i>Panzeria anthophila</i> (Robineau-Desvoidy, 1830)	1
<i>Periscepsia spathulata</i> (Fallén, 1820)	3
<i>Phania funesta</i> (Meigen, 1824)	502
<i>Phasia obesa</i> (Fabricius, 1798)	4
<i>Phasia pusilla</i> Meigen, 1824	10
<i>Phryxe heraclei</i> (Meigen, 1824)	1
<i>Phryxe nemea</i> (Meigen, 1824)	3
<i>Phryxe vulgaris</i> (Fallén, 1810)	4
<i>Prosenia siberita</i> (Fabricius, 1775)	223
<i>Pseudoperichaeta nigrolineata</i> (Walker, 1853)	1
<i>Siphona geniculata</i> (DeGeer, 1776)	8914
<i>Solieria pacifica</i> (Meigen, 1824)	4
<i>Sturmia bella</i> (Meigen, 1824)	1
<i>Tachina fera</i> (Linnaeus, 1761)	2
<i>Tachina grossa</i> (Linnaeus, 1758)	1
<i>Thelaira nigripes</i> (Fabricius, 1794)	32
<i>Triarthria setipennis</i> (Fallén, 1810)	18
<i>Trixa conspersa</i> (Harris, 1776)	1
<i>Voria ruralis</i> (Fallén, 1810)	17
<i>Zaira cinerea</i> (Fallén, 1810)	6
<i>Zophomyia temula</i> (Scopoli, 1763)	1

Table S2. Plausible candidate models (within 2 $\Delta AICc$ of the top model) explaining species richness and abundance of tachinid parasitoids. Models are ranked according to their second-order Akaike's information criterion ($AICc$). For each tested variable $\sum w_i$ indicates the sum of model weights.

	Abundance							Species richness										
	Best	2nd	3rd	4th	5th	6th	$\sum w_i$	Best	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	$\sum w_i$
$\Delta AICc$	0	0.33	1.42	1.7	1.74	1.82	-	0	0.49	0.81	1.18	1.28	1.31	1.42	1.56	1.76	1.9	-
Model weight	0.11	0.09	0.05	0.05	0.05	0.04	-	0.06	0.05	0.04	0.03	0.03	0.03	0.03	0.03	0.03	0.02	-
Intercept	0.87	0.98	0.73	0.83	0.82	0.83	-	0.11	0.07	0.04	0.07	0.19	0	0.21	0.02	0.15	0.16	-
Habitat	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	0.96
Landscape	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
Location	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
Management	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	0.96
Region	*	*	*	*	*	*	1	*	*	*	*	*	*	*	*	*	*	1
Habitat x Landscape	*	*	*	*	*	*	0.99	*	*	*	*	*	*	*	*	*	*	0.85
Habitat x Location	-	-	-	-	*	-	0.44	*	*	*	*	-	*	*	*	-	*	0.69
Habitat x Management	*	*	*	*	*	*	1	-	*	-	-	-	*	-	*	*	*	0.47
Landscape x Location	*	-	*	*	*	*	0.64	*	*	*	*	*	*	-	*	*	-	0.72
Landscape x Management	-	-	*	*	-	-	0.5	-	-	-	-	-	-	-	-	-	-	0.31
Location x Management	-	-	-	-	-	*	0.42	-	-	-	*	-	-	-	*	-	-	0.41
Habitat x Landscape x Location	-	-	-	-	-	-	0.12	-	-	*	-	-	*	-	-	-	-	0.19
Habitat x Landscape x Management	-	-	*	-	-	-	0.26	-	-	-	-	-	-	-	-	-	-	0.05
Habitat x Location x Management	-	-	-	-	-	-	0.14	-	-	-	-	-	-	-	-	-	-	0.08
Landscape x Location x Management	-	-	-	-	-	-	0.07	-	-	-	-	-	-	-	-	-	-	0.03
Habitat x Landscape x Location x Management	-	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	0

* Indicates that the categorical variable was included in the models.



Chapter IV

**Landscape effect on
parasitoid spillover
between crop
& non-crop habitats**

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**Manuscript
submitted**

Abstract

The intensification of agriculture has led to a severe simplification of agricultural landscapes, resulting in a marked reduction in the diversity of insect natural enemies. However, how this simplification shapes the community composition of insect parasitoids is still unclear. We examined the potential spillover of tachinid parasitoids from semi-natural habitats into apple orchards across different landscapes. We sampled commercial apple orchards localized in landscapes characterized by different proportions of crop and non-crop habitats (forest and grasslands) to first evaluate if increasing the cover of semi-natural habitats will affect the local species richness of apple orchards. Second, we tested whether the contribution of forest and grassland habitats to the local tachinid community composition of apple orchards changes according to landscape composition. We found that increasing the cover of semi-natural habitats did not affect local tachinid species richness in apple orchards, while it strongly affected the species composition. Independently of the landscape, we found highly nested communities of tachinids between apple orchards and forest habitats suggesting a strong spillover of tachinids between these habitats. In contrast, tachinids in apple orchards were nested with grassland habitats when the proportion of semi-natural habitats was very low. Our results have important implications for the conservation of insect parasitoids in agricultural landscapes, as the spillover of species in agricultural land can be affected by the type and the proportion of semi-natural habitats in the surrounding landscape.

Introduction

In the last decades, the intensification of agriculture has led to a severe simplification of agricultural landscapes (Swift et al. 1996; Tilman et al. 2001). This simplification has been caused by an increase of the size of crop fields and a marked reduction of the remaining natural and semi-natural habitats, which has resulted in landscapes dominated by only a few crop types (Robinson & Sutherland 2002; Tscharntke et al. 2012). The simplification of agricultural landscapes has resulted in a marked reduction of the diversity of insect natural enemies with possible negative effects on pest control service (Wilby & Thomas 2002; Bianchi et al. 2006; Thies et al. 2011; Jonsson et al. 2012). Although the overall negative effects of landscape simplification on the species richness

of natural enemies are relatively well known (e.g., Macfadyen & Muller 2013; Inclán et al. 2014; Martinson & Fagan 2014), how this process shapes the community composition of important natural enemies such as parasitoids is still unclear.

The ecological contrast between habitats within intensive agricultural landscapes is an important factor determining the spillover of species between these habitats. Therefore, the contrast between agricultural and semi-natural habitats will determine species immigration and emigration (Polis et al. 1997; Schellhorn et al. 2014). Several authors have found species flow from natural habitats into adjacent agricultural fields (e.g., Landis et al. 2000; Geiger et al. 2008; Rusch et al. 2010; Blitzer et al. 2012), but dispersal in the opposite direction has also been found (e.g., Tschardt et al. 2005; Rand et al. 2006; Blitzer et al. 2012; Frost et al. 2014). This spillover of parasitoids has also been shown to affect important ecosystem services such as natural pest suppression (Landis et al. 2000; Macfadyen & Muller 2013; Gagic et al. 2014). Although it is clear that the spillover of organisms like parasitoids can affect trophic interactions in the recipient habitat (Tschardt et al. 2005; Rand & Louda 2006; Rand et al. 2006; Klapwijk & Lewis 2012; Macfadyen & Muller 2013; Martinson & Fagan 2014), how the spillover of parasitoids change in relation to specific habitats within different landscapes is still a little understood topic.

Studies about spillover of natural enemies from natural habitats into adjacent agricultural fields have focused on predators with limited dispersal range like most ground-dwelling predators (e.g., see review of Blitzer et al. 2012) and less attention has been paid on the spillover of more mobile organisms such as parasitoids (although see Olson & Wäckers 2007; Macfadyen & Muller 2013; Frost et al. 2014). Furthermore, the majority of these studies have focused on the effects on species richness, ignoring the effects on species composition (but see Gagic et al. 2014). In this work, we used tachinid flies (Diptera: Tachinidae) as a model group to investigate the spillover of a highly mobile and diverse group of parasitoids. The family Tachinidae, with almost 8,500 species, ranks second in diversity within the Diptera and is the most diverse group of non-hymenopteran parasitoids (Stireman et al. 2006; O'Hara 2013). Tachinids can be very important natural enemies because of their predominance in attacking major groups of insect herbivores as lepidopterans, coleopterans and hemipterans (Stireman et al. 2006; Cerretti et al. 2014). In this study, we examined the spillover of tachinid parasitoids from two semi-natural habitats into agricultural land in contrasting landscapes. Specifically, we

sampled commercial apple orchards localized in landscapes characterized by different proportions of crop and non-crop habitats (forest and grasslands). Specifically, we have addressed three main hypotheses. First, we expected that increasing the cover of semi-natural habitats will increase the local species richness of apple orchards. Higher species richness in apple orchards located in forest- or grassland-dominated landscapes will indicate a high spillover between these habitats. Therefore, a significant interaction between local habitat and landscape will be indicative of spillover between habitats. Second, as we expected that the spillover will vary across different habitats and landscapes, we tested the contribution of forest and grassland habitats to the local diversity of apple orchards located in landscapes with different proportions of semi-natural habitats. We used an index of nestedness to compare the species composition between crop and non-crop habitats. Third, due to the high mobility and relatively low specialization of tachinids, we expected that the spillover of tachinids will not be limited by distance. In particular, we tested the role of dispersal in shaping the spillover of species by testing the distance-decay of similarity within habitats across different landscapes.

Methods

Study area

The research was conducted within an area of c. 160 km² in the province of Trento, NE Italy. Specifically, the sites were located within an elevation of 450–600 m across the Valsugana Valley, in the southern European Alps. The study region is in one of the major apple production areas of Europe with ~12,000 ha of intensive orchards. In recent decades, there has been a dramatic landscape homogenization that has created large areas covered exclusively by apple orchards (Marini et al. 2012). Within these homogenous landscapes, it is still possible to find some scattered orchards located in a non-crop matrix composed mainly of grasslands and forests. Apple orchards, forests and grasslands represented the main land uses in the region. Apple orchards, mainly the variety ‘Golden Delicious’, are characterized by a highly specialized conventional management with only very few organic or traditionally managed orchards. Grassland habitats are usually heavily fertilized (>150 kg N ha⁻¹ yr⁻¹) and mown 2–4 times per year resulting in dense

swards dominated by grasses and with low forb abundances (see Marini et al. 2008). Forest habitats are mainly composed of Scots pine mixed with broad-leaf tree species (mainly *Fraxinus ornus* L. and *Ostrya carpinifolia* Scop.).

Table 1. Habitat composition by each type of landscape. The mean and SE were calculated from the percentage of coverage of each habitat within a 500 m radius.

Landscape type	Apple orchards		Forests		Grasslands	
	mean	SE	mean	SE	mean	SE
Apple-dominated	52.78	6.13	19.09	5.12	14.25	4.38
Forest-dominated	9.18	2.55	65.73	5.49	20.15	6.01
Grassland-dominated	11.93	3.28	10.92	3.42	67.75	2.87

Sampling design

Twenty-one commercial apple orchards were selected in landscapes characterized by different proportions of crop and non-crop habitats. We selected seven orchards in landscapes (0.5 km radius) dominated by apple plantations, seven in landscapes dominated by forests and seven in landscapes dominated by grasslands (Table 1). Landscapes were selected to be separated by at least 1 km (mean minimum distance = 2.2 km) and only three landscapes were separated by a shorter distance (0.8 km). Within each landscape three sites representing apple, forest and grassland habitats were selected (Fig. 1). The three sites were separated by no more than 60 m and were located in the centroid of each landscape (Fig. 1c). We identified the habitats embedded in the three landscape classes by quantifying the landscape composition within a 500 m radius around the centroid of the three selected habitats using detailed land-use maps (Servizio Urbanistica, Provincia di Trento) in ArcGIS 10 (ESRI®). For each selected landscape, we quantified the cover of apple, forests and grasslands. For each landscape, we selected the habitats with about the same local management and located at elevations between 450 and 600 m such that the management and elevation did not differ among the three landscape classes.

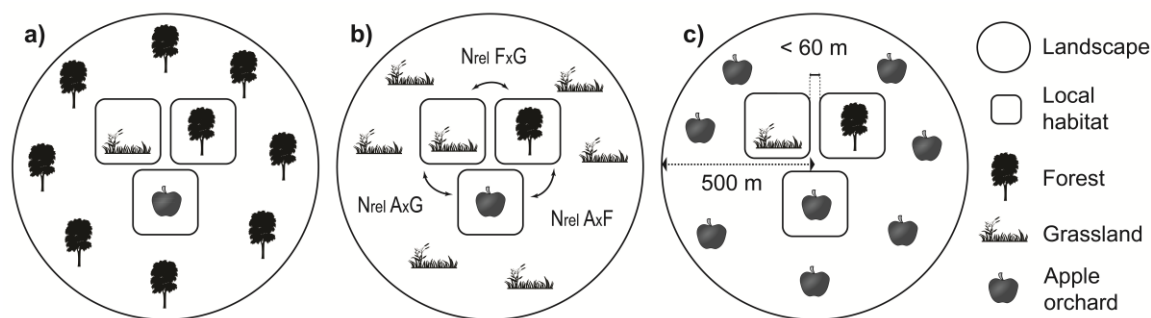


Figure 1. Experimental design showing the tree local habitats (forest, grassland and apple orchards; square blocks in the center of each landscape) sampled across (a) forest-dominated, (b) grassland-dominated and (c) apple-dominated landscapes (circles). As shown in (c), the landscapes were based on a radius of 500 m and each of the three habitats was located in its centroid, each one separated by no more of 60 m. As shown in (b), within each landscape the relativized nestedness (N_{rel}) was calculated for each pair of habitats: A-G (Apple - Grassland), A-F (Apple - Forest) and F-G (Forest - Grassland).

Insect sampling

Pan-trap sampling was conducted across the 21 landscapes. Within each landscape, the three habitats were sampled using three clusters of pan-traps. Within each habitat, each cluster of traps was separated by 25 m. Each cluster of traps consisted of one standard yellow and two UV-reflecting yellow plastic bowls (500 ml, 16 cm diameter) filled with a solution of water and 3% dishwashing detergent (Sole TM). Within each cluster, pan-traps were placed on the ground, each one separated about one meter from each other. The cluster position was kept fixed within each habitat, leaving a distance of at least 10 meters from the borders and avoiding areas completely covered by shrubs. The sampling was conducted between July and September 2013. A total of four samplings were performed covering the main season during which the insects were active. During each sampling round, traps were set for a period of 48 hours after which insects were retrieved and stored in alcohol (70%) for sorting and identification. The specimens belonging to the Tachinidae (Diptera) were identified to species level using Cerretti (2010) and Cerretti et al. (2012). All the specimens were housed in the insect collection of P. Cerretti at the Museo di Zoologia, Università di Roma La Sapienza, Rome, Italy (MZUR).

Statistical analyses

(i) *Species richness analysis*

To test whether tachinid species richness responded differently to local habitat and landscape composition, we used a generalized linear mixed model (GLMM) with a

Poisson distribution for species richness. The family and link function used in the model were selected based on residual deviance and distribution of residuals. The response variable was the cumulative number of species per habitat obtained across the four samplings. The model included landscape (apple-dominated, forest-dominated and grassland-dominated) and habitat (apple, forest and grassland) as categorical fixed effects. Landscape identity was included in the model as a random factor to account for the nested design of the sampling. The models tested all the main effects and their interactions. We first built a full model and then simplified the model by removing terms one-by-one, starting from the highest interactions, the least significant terms with $P > 0.05$. Further pairwise comparisons between landscapes and habitats were assessed by post hoc Tukey tests. The GLMM and the post hoc Tukey test analyses were performed using the packages “lme4” (Bates et al. 2014) and “lsmeans” (Lenth 2013), respectively, implemented in R (R Development Core Team 2013).

(ii) *Nestedness analysis*

To evaluate the variation in species compositions we calculated the nestedness between different landscapes and habitats (as in Fig. 1b). As our main aim was to evaluate if a community represented a subset of another community depending on the habitat or the landscape, we performed a pairwise comparison between habitats in the same landscape and calculated the “relativized nestedness” (N_{rel}) of Podani and Schmera (2011)

$$N_{rel} = (a + |b - c|) / n$$

where, a represents the number of species shared by both habitats, b and c the number of species present only in habitat 1 and 2, respectively, and n the total of species in the two habitats. Although Baselga (2010) proposed a different index of nestedness (β_{nes}), we found a monotonic relationship between β_{nes} and N_{rel} (Fig. S1), where this index was highly correlated with N_{rel} ($r_s = 0.98$, $P = <0.001$) and yielded to similar results; therefore, we presented here the results based on the N_{rel} index (see Podani & Schmera 2011, 2012; Carvalho et al. 2013; Legendre 2014). The N_{rel} matrix was computed using the function “beta.div.comp” (Legendre 2014) implemented in R (R Development Core Team 2013). This matrix contained the pairwise nestedness between apple-forest, apple-grassland and forest-grassland habitats across the different landscapes (Fig. 2). As the nestedness of a certain group can be defined as the mean of the pairwise nestedness within the group (Legendre et al. 2005), differences in nestedness among different groups were calculated

by comparing with ANOVA the mean of the within pairwise nestedness among groups (Bacaro et al. 2013). Since the pairwise nestedness are not independent from each other, the significance of the analysis of variation was based on 9,999 permutations. Therefore, the ANOVA P values was calculated by randomly permuting only the within group nestedness among our focal groups without replacement (Bacaro et al. 2013). As our aim was to evaluate the difference in nestedness between habitats, the analysis was performed only on the pairwise nestedness between apple-forest, apple-grassland and forest-grassland habitats, disregarding the within-habitat dissimilarities (apple-apple, forest-forest and grassland-grassland; see Fig. 2). The permutational analysis of variance was performed using the function “Beta Dispersion 2.0” implemented in R (R Development Core Team 2013).

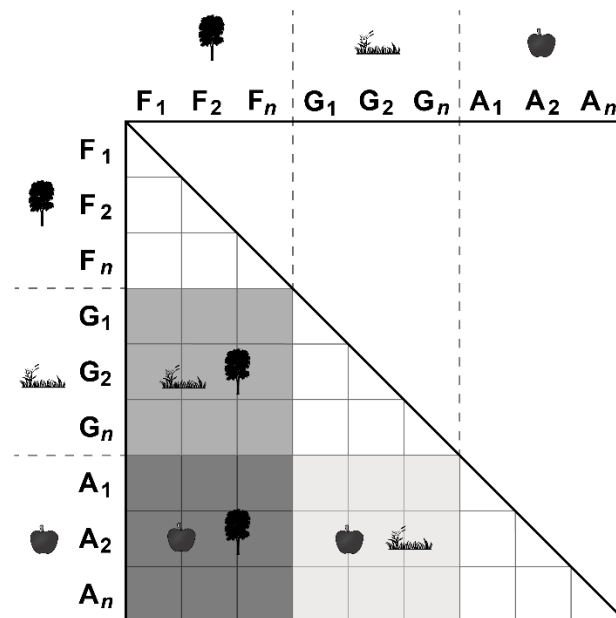


Figure 2. Schematic design of the pairwise analysis of the relativized nestedness (N_{rel}) between paired habitats: F-G (Forest - Grassland), A-F (Apple - Forest) and A-G (Apple - Grassland). First, a dissimilarity matrix was computed among all pairs of habitats. The mean values of the pairwise dissimilarities were calculated only for the between-habitat- N_{rel} (F-G, A-F and A-G; shadow blocks in the lower corner of the half-matrix) and p values were calculated by randomly permuting among these groups without replacement and disregarding the within-habitat dissimilarities (F-F, G-G and A-A; the sub-diagonal half-matrix).

(iii) *Distance decay analysis*

The pattern and significance of spatial autocorrelation across different geographical distances were examined using Mantel correlograms (Legendre & Legendre 1998; Borcard & Legendre 2012). The response variable was the dissimilarity matrix of the relativized nestedness (Podani & Schmera 2011; Legendre 2014). As explained above,

the N_{rel} matrix was computed using the function “beta.div.comp” (Legendre 2014). Following the N_{rel} matrix, the distance matrix was constructed based on the geographical distance between each pair of habitats. Spatial autocorrelation was evaluated using 11 lag intervals. Each interval was 2.4 km wide, ranging from 1.2 to 26.2 km. Mantel correlation coefficients were calculated for each lag interval and tested for significance with a permutation test, using 1,999 permutations. Each distance class was tested for significance using a Bonferroni-corrected α of 0.01 (Legendre & Legendre 1998). The spatial autocorrelation analysis was performed using the function “mantel.correlog” in the “vegan” package (Oksanen et al. 2013) implemented in R (R Development Core Team 2013).

Results

General results

A total of 2,617 individuals were collected belonging to 110 species of Tachinidae (Table S1). Forty specimens that were not possible to identify to species level (e.g., some females of *Exorista* Meigen and *Meigenia* Robineau-Desvoidy) were excluded from the analyses. Two species were dominant and accounted for more than 70% of the total abundance. *Voria ruralis* (Fallén) and *Phania funesta* (Meigen) represented 63% and 9% of the individuals collected, respectively. *Voria ruralis* is a parasitoid of lepidopteran larvae while *P. funesta* is a parasitoid of hemipterans (Cerretti 2010). Additionally, the species *Linnaemya zachvatkini* Zimin and *Oswaldia eggeri* (Brauer & Bergenstamm) were recorded for the first time in Italy.

Table 2. Results from the generalized linear mixed model testing the effects of habitat and landscape on tachinid species richness.

	df	Chi-Square	<i>P</i> value
Habitat	2	60.35	< 0.001
Landscape	2	9.57	< 0.001
Habitat x Landscape	4	11.3	0.02

Species richness

For tachinid species richness, we found that increasing the cover of semi-natural habitats did not increase the local species richness of apple orchards. Specifically, we found a

significant effect of habitat and landscape (Table 2), where forest habitats and forest landscapes had the highest species richness (Fig. 3). Pairwise comparisons between habitats showed that each habitat was different within each other (Tukey HSD; $P < 0.001$). Pairwise comparisons between landscapes showed that apple landscapes were significantly different from forest landscapes (Tukey HSD; $P = 0.002$), while grasslands were not different from apple (Tukey HSD; $P = 0.22$) and forest (Tukey HSD; $P = 0.18$) landscapes. We further found an interaction between landscape and habitat (Table 2), where the species richness on forest habitats was higher on forest landscapes (Fig. 3). Specifically, the species richness on apple and grassland habitats did not differ across different landscapes (Tukey HSD; $P > 0.1$). In contrast, the species richness on forest habitats was higher on forest landscapes, being similar to that of grassland landscapes (Tukey HSD; $P = 0.15$), but significantly different to that of apple landscapes (Tukey HSD; $P = 0.001$).

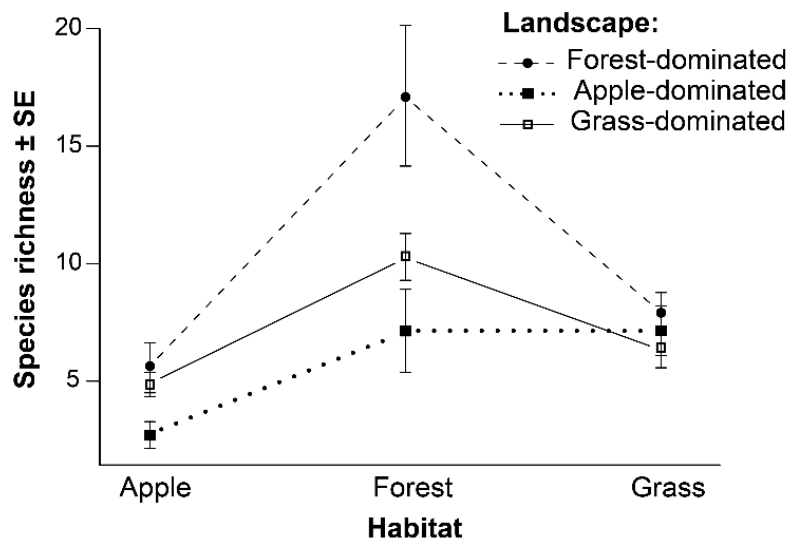


Figure 3. Interaction between habitat (Apple, Forest, and Grassland) and landscape composition (Apple-dominated, Forest-dominated, and Grassland-dominated) on tachinid species richness. Dots indicate mean values and bars the SE.

Nestedness

For the relativized nestedness, we found a significant effect of habitat ($P = 0.001$) and landscape ($P = 0.001$). At the local scale, apple orchards were highly nested with forest habitats ($N_{rel} = 0.66 \pm 0.02$), contrasting with the lower nestedness between apple and grassland ($N_{rel} = 0.52 \pm 0.02$) and grassland and forest ($N_{rel} = 0.49 \pm 0.02$) habitats. At the landscape scale, we found the highest nestedness within apple landscapes ($N_{rel} = 0.64 \pm 0.02$), contrasting with the lower nestedness within forest ($N_{rel} = 0.53 \pm 0.02$) and

grassland ($N_{rel} = 0.51 \pm 0.02$) landscapes. We further found an interaction between landscape and habitats (Fig. 4), where the N_{rel} on apple-forest ($P = 0.03$) and apple-grassland ($P = 0.001$) habitats was significantly different across different landscapes, contrasting with the N_{rel} of forest-grassland ($P = 0.67$) habitats that were similar across the different landscapes. Specifically, we found that apple habitats were highly nested with forest habitats mainly on apple landscapes ($N_{rel} = 0.73 \pm 0.04$), being lower on forest ($N_{rel} = 0.64 \pm 0.04$) and grassland ($N_{rel} = 0.62 \pm 0.03$) landscapes. Similarly, apple habitats were highly nested with grassland habitats only in apple landscapes ($N_{rel} = 0.71 \pm 0.04$), being lower on forest ($N_{rel} = 0.43 \pm 0.04$) and grassland ($N_{rel} = 0.43 \pm 0.03$) landscapes. Contrastingly, we found that the nestedness between grassland and forest did not change across different landscapes.

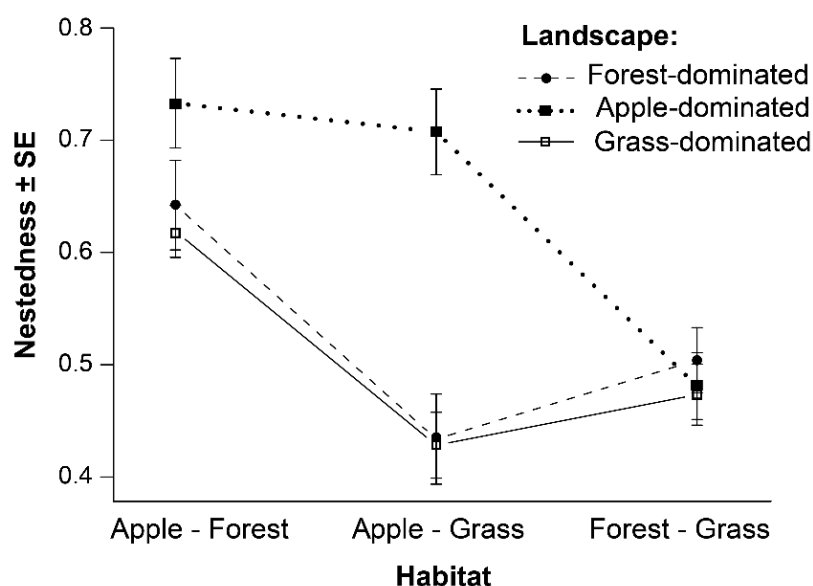


Figure 4. Interaction between pairs of habitat (Apple - Forest, Apple - Grass and Forest - Grassland) and landscape composition (Apple-dominated, Forest-dominated, and Grassland-dominated) on the tachinid relativized nestedness (N_{rel}). Dots indicate mean values and bars the SE.

Distance decay

We found no spatial structure with geographical distance indicating that the species were not dispersal limited in our study area. We did not find significant correlation between the relativized nestedness of different habitats and geographical distance. At all the distances, the Mantel correlations were not significant (Table S2).

Discussion

Our results show a potential high spillover of tachinid parasitoids from semi-natural habitats into apple orchards. Although increasing the cover of semi-natural habitats did not affect the local tachinid species richness in apple orchards, we found evidence of spillover at the community level. However, the tachinid parasitoid response was complex and various interactions between the habitat type and proportion of semi-natural habitats were found. Tachinid species inhabiting apple orchards were likely to be a subset of the forest or the grassland habitats, but this depended on the landscape type. Specifically, the highly nested community of tachinids between apple orchards and forest habitats suggest a strong spillover of tachinids between these habitats. In contrast, tachinids in apple orchards were nested with grassland habitats only when the proportion of semi-natural habitats was low. Our results have important implications for the conservation of insect parasitoids in agricultural landscapes, as the spillover of species in agricultural land can be affected by the type and the proportion of semi-natural habitats in the surrounding landscape.

As crop fields can be hostile environments for the persistence of natural enemies, the surrounding natural habitats represent a key element for their survival. Parasitoids are known to benefit from natural and semi-natural areas, as these habitats provide alternative host species, energy sources for adults, over-wintering sites and/or pesticide-free zones (Tscharntke et al. 2007; Schellhorn et al. 2014). Although several studies have shown that the proportion of natural habitats within agricultural fields can influence the abundance and species richness of insect parasitoids (e.g., Bianchi et al. 2006; Tscharntke et al. 2007; Klapwijk & Lewis 2012; Veres et al. 2013; Schellhorn et al. 2014), the contribution of local habitat and landscape to the composition of parasitoid communities remains less clear (but see Gagic et al. 2014). While in our study the coverage of semi-natural habitats did not affect the species richness of tachinid parasitoids in apple orchards, we found evidence for a spillover as the tachinid community inhabiting these habitats were highly nested depending on the type and the proportion of semi-natural habitats in the landscape. Independently of the proportion of forest in the landscape, the tachinid community composition of apple orchards was likely to be a subset of the forest habitats. In contrast, tachinids in apple orchards were nested with grassland habitats only on landscapes dominated by apple orchards. Thus, the diversification of agricultural landscapes have the

potential to enhance spillover of parasitoid communities, but further considerations related to the type and spatial configuration of semi-natural habitats need to be considered.

Landscapes with high proportions of semi-natural habitats have been hypothesized to promote a higher parasitoid diversity as these have a more favorable arrangement of crop and non-crop habitats in relation to simple landscapes with low extents of semi-natural habitats (Bianchi et al. 2006; Tscharntke et al. 2012). Although we found that semi-natural habitats can act as sources of parasitoid diversity in agricultural landscapes, increasing the proportion of semi-natural areas did not always enhance the spillover of parasitoids. The type, area and the spatial arrangement of semi-natural habitats are important features affecting the spatial distribution of species (Dunning et al. 1992; Polis et al. 1997; Tscharntke et al. 2012; Schellhorn et al. 2014). According to Dunning et al. (1992), these features can affect the movement of species between patches in the landscape depending on four ecological processes: (1) “*landscape complementation*” and (2) “*landscape supplementation*” occur when species depend on resources of different habitats that are non-substitutable or substitutable, respectively; (3) “*source-sink dynamics*” occurs when particular patches act as a source of species that disperse to less productive patches; and (4) “*the neighborhood effect*” appears when species are more affected by the characteristics of the surrounding patch than by more distant patches. In our study, the spillover of tachinids is likely to be affected by one or more of these processes depending on the configuration of the landscape. For instance, the spillover between forest and apple habitats could be the result of species searching for alternative resources (*landscape supplementation*) and/or species from forest habitats emigrating to apple orchards (*source-sink dynamics*). In contrast, different processes could act on grassland habitats (i.e. *the neighborhood effect*), as the spillover of tachinids between grasslands and apple orchards is likely to be affected by the large ecological contrast of the two habitats, as well as the size and distribution of these habitats (Dunning et al. 1992; Polis et al. 1997; Tscharntke et al. 2012). Therefore, as the proportion of semi-natural grasslands increases in the landscape the spillover of tachinids species from grasslands to apple orchards is less likely to occur when species may find all the resources to complete their life cycles within the semi-natural habitat and/or they are not dispersal limited (Klapwijk & Lewis 2012). However, in landscapes dominated by agricultural land species

cannot persist in the reduced semi-natural habitat and are more likely to explore for alternative resources in the crop landscape.

The dispersal of parasitoid species is linked to their movement and navigation capacity (Godfray 1994; Klapwijk & Lewis 2012; Schellhorn et al. 2014). Here, we found no spatial structure with geographical distance in the tachinid community, suggesting that the species were not dispersal limited in our study area. Tachinids, like many other parasitoids, are known to use diverse cues to forage for resources, starting with long-range cues (i.e. location of the habitat of their hosts using plant volatiles) and short-range cues (i.e., finding a suitable host by host kairomones and/or visual cues) (Godfray 1994; Stireman 2002; Ichiki et al. 2013). Thus, as the search for alternative hosts in the landscape could change in different species the spillover will also depend on how parasitoid species can perceive the environment. This could explain the low nestedness between forest and grassland habitats, as these habitats are structurally different and parasitoids are likely to avoid the movement between these habitats. Therefore, the spillover of parasitoids may be influenced by the specialization of species on different cues (e.g., Stireman 2002; Ichiki et al. 2013) that can be related to a specific set of habitats within the landscape. These results are also in line with the edge-permeability hypothesis (Stamps et al. 1987), where habitats with high degree of contrast are expected to be relatively impermeable to movement, while similar habitats are likely to be more permeable. Although we found that different compositions of semi-natural habitats in the landscape affect the species spillover to apple orchards, the spillover of species into crops with different structure and phenology may be affected in different ways. Further empirical studies considering how the community of parasitoids changes across different spatio-temporal scales within different arrangements of crop and non-crop habitats are needed.

Conclusions

The majority of studies testing the effects on spillover have focused on the effects on species richness of natural enemies, ignoring the changes of community composition. Here we found that increasing the cover of semi-natural habitats did not affect the local tachinid species richness in apple orchards, but it strongly affected the parasitoid species

composition. Although we found that semi-natural habitats can act as sources of parasitoid diversity in agricultural landscapes, increasing the proportion of semi-natural areas did not always enhance the spillover of parasitoids. The type, area and the spatial arrangement of semi-natural habitats are important features affecting the tachinid community composition. This is of particular importance in simplified landscapes (i.e. our apple-dominated landscape) where the spillover of parasitoids is likely to depend on the semi-natural areas present in these landscapes. Our results have important implications for the conservation of parasitoids and semi-natural habitats in agricultural landscapes, as the diversification of agricultural landscapes have the potential to enhance spillover of parasitoid communities depending on the type and the proportion of semi-natural habitats in the surrounding landscape.

Acknowledgements

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Supplementary Material

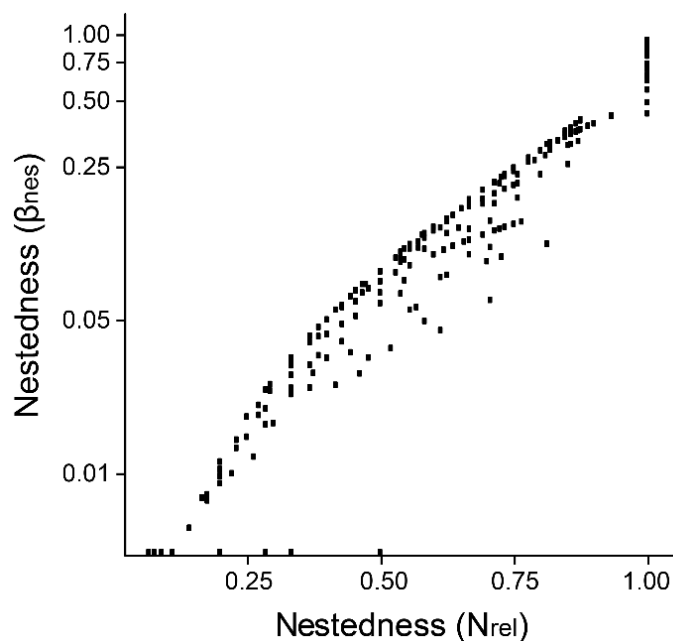


Figure S1. Relationship between β_{nes} (Baselga 2009) and N_{rel} (Podani and Schmera 2011) nestedness indices of pairs of habitats (Apple - Forest, Apple - Grass and Forest - Grassland) located in the three types of landscape (Apple-dominated, Forest-dominated, and Grassland-dominated). In these paired habitats we found a monotonic relationship between β_{nes} and N_{rel} ($r_s = 0.98$, $P = < 0.001$).

Table S1. Tachinid species and their abundance in the study area.

Species	Total of individuals
<i>Admontia blanda</i> (Fallen, 1820)	3
<i>Allophorocera ferruginea</i> (Meigen, 1824)	1
<i>Amelibaea tultschensis</i> (Brauer & Bergenstamm, 1891)	2
<i>Bessa parallela</i> (Meigen, 1824)	1
<i>Bessa selecta</i> (Meigen, 1824)	1
<i>Billaea pectinata</i> (Meigen, 1826)	4
<i>Billaea triangulifera</i> (Zetterstedt, 1844)	1
<i>Bithia spreta</i> (Meigen, 1824)	2
<i>Blondelia inclusa</i> (Hartig, 1838)	2
<i>Blondelia nigripes</i> (Fallen, 1810)	5
<i>Carcelia bombylans</i> Robineau-Desvoidy, 1830	4
<i>Carcelia falenaria</i> (Rondani, 1859)	8
<i>Carcelia gnava</i> (Meigen, 1824)	2
<i>Carcelia lucorum</i> (Meigen, 1824)	3
<i>Carcelia tibialis</i> (Robineau-Desvoidy, 1863)	3
<i>Catharosia pygmaea</i> (Fallen, 1815)	4
<i>Chetogena filipalpis</i> Rondani, 1859	9
<i>Clemelis massilia</i> Herting, 1977	1

Table S1. continued

<i>Clemelis pullata</i> (Meigen, 1824)	1
<i>Compsilura concinnata</i> (Meigen, 1824)	19
<i>Cylindromyia bicolor</i> (Olivier, 1812)	2
<i>Cylindromyia brassicaria</i> (Fabricius, 1775)	2
<i>Cyrtophleba ruricola</i> (Meigen, 1824)	3
<i>Dexia vacua</i> (Fallen, 1817)	40
<i>Dinera carinifrons</i> (Fallen, 1817)	1
<i>Dinera ferina</i> (Fallen, 1817)	5
<i>Dinera grisescens</i> (Fallen, 1817)	153
<i>Dionaea aurifrons</i> (Meigen, 1824)	1
<i>Drino lota</i> (Meigen, 1824)	1
<i>Drino atropivora</i> (Robineau-Desvoidy, 1830)	4
<i>Drino gilva</i> (Hartig, 1838)	5
<i>Epicampocera succincta</i> (Meigen, 1824)	3
<i>Eriothrix monticola</i> (Egger, 1856)	5
<i>Eriothrix rufomaculata</i> (DeGeer, 1776)	2
<i>Erythroceras nigripes</i> (Robineau-Desvoidy, 1830)	3
<i>Eumea linearicornis</i> (Zetterstedt, 1844)	4
<i>Eumea mitis</i> (Meigen, 1824)	1
<i>Eurysthaea scutellaris</i> (Robineau-Desvoidy, 1848)	2
<i>Exorista glossatorum</i> (Rondani, 1859)	1
<i>Exorista rustica</i> (Fallen, 1810)	15
<i>Freraea gagatea</i> Robineau-Desvoidy, 1830	1
<i>Gaedia connexa</i> (Meigen, 1824)	1
<i>Gymnosoma rotundatum</i> (Linnaeus, 1758)	1
<i>Hemyda obscuripennis</i> (Meigen, 1824)	1
<i>Hemyda vittata</i> (Meigen, 1824)	1
<i>Hubneria affinis</i> (Fallen, 1810)	1
<i>Labigastera forcipata</i> (Meigen, 1824)	1
<i>Leskia aurea</i> (Fallen, 1820)	1
<i>Linnaemya comta</i> (Fallen, 1810)	31
<i>Linnaemya frater</i> (Rondani, 1859)	1
<i>Linnaemya impudica</i> (Rondani, 1859)	2
<i>Linnaemya picta</i> (Meigen, 1824)	2
<i>Linnaemya soror</i> Zimin, 1954	2
<i>Linnaemya tessellans</i> (Robineau-Desvoidy, 1830)	27
<i>Linnaemya zachvatkini</i> Zimin, 1954**	1
<i>Litophasia hyalipennis</i> (Fallen, 1815)	1
<i>Loewia brevifrons</i> (Rondani, 1856)	2
<i>Loewia foeda</i> (Meigen, 1824)	1
<i>Loewia nudigena</i> Mesnil, 1973	1
<i>Lomachantha parra</i> Rondani, 1859	1
<i>Macquartia chalconota</i> (Meigen, 1824)	1
<i>Macquartia grisea</i> (Fallén, 1810)	1
<i>Macquartia pubiceps</i> (Zetterstedt, 1845)	1
<i>Macquartia tenebricosa</i> (Meigen, 1824)	1
<i>Medina luctuosa</i> (Meigen, 1824)	1

Table S1. continued

<i>Medina melania</i> (Meigen, 1824)	3
<i>Medina multispina</i> (Herting, 1966)	8
<i>Medina separata</i> (Meigen, 1824)	19
<i>Meigenia dorsalis</i> (Meigen, 1824)	22
<i>Meigenia majuscula</i> (Rondani, 1859)	1
<i>Meigenia mutabilis</i> (Fallen, 1810)	16
<i>Meigenia simplex</i> Tschorsnig & Herting, 1998	3
<i>Meigenia uncinata</i> Mesnil, 1967	3
<i>Microsoma exiguum</i> (Meigen, 1824)	5
<i>Nemoraea pellucida</i> (Meigen, 1824)	27
<i>Nilea hortulana</i> (Meigen, 1824)	3
<i>Oswaldia eggeri</i> (Brauer & Bergenstamm, 1889)**	3
<i>Pales pavidata</i> (Meigen, 1824)	11
<i>Pales processioneae</i> (Ratzeburg, 1840)	2
<i>Paratryphera barbatula</i> (Rondani, 1859)	11
<i>Paratryphera bisetosa</i> (Brauer & Bergenstamm, 1891)	1
<i>Peleteria prompta</i> (Meigen, 1824)	1
<i>Peribaea tibialis</i> (Robineau-Desvoidy, 1851)	13
<i>Periscepsia prunaria</i> (Rondani, 1861)	1
<i>Periscepsia spathulata</i> (Fallen, 1820)	6
<i>Phania funesta</i> (Meigen, 1824)	222
<i>Phryxe nemea</i> (Meigen, 1824)	27
<i>Phryxe vulgaris</i> (Fallen, 1810)	1
<i>Platymya fimbriata</i> (Meigen, 1824)	9
<i>Prooppia nigripalpis</i> (Robineau-Desvoidy, 1848)	4
<i>Pseudoperichaeta nigrolineata</i> (Walker, 1853)	1
<i>Rhacodinella apicata</i> (Pandelle, 1896)	10
<i>Senometopia lena</i> (Richter, 1980)	1
<i>Senometopia separata</i> (Rondani, 1859)	2
<i>Siphona flavifrons</i> Staeger, 1849	2
<i>Siphona geniculata</i> (De Geer, 1776)	1
<i>Siphona paludosa</i> Mesnil, 1960	6
<i>Solieria fenestrata</i> (Meigen, 1824)	35
<i>Strongygaster globula</i> (Meigen, 1824)	2
<i>Sturmia bella</i> (Meigen, 1824)	2
<i>Tachina fera</i> (Linnaeus, 1761)	16
<i>Tachina magnicornis</i> (Zetterstedt, 1844)	8
<i>Thelaira leucozona</i> (Panzer, 1809)	3
<i>Thelaira nigripes</i> (Fabricius, 1794)	3
<i>Thelaira solivaga</i> (Harris, 1780)	7
<i>Triarthria setipennis</i> (Fallen, 1810)	2
<i>Vibrissina turrita</i> (Meigen, 1824)	20
<i>Voria ruralis</i> (Fallen, 1810)	1615
<i>Winthemia quadripustulata</i> (Fabricius, 1794)	3
<i>Zophomyia temula</i> (Scopoli, 1763)	2

**Indicates new species recorded for Italy

Table S2. Spatial autocorrelation between the relativized nestedness (N_{rel}) and the geographical distance between pair of habitats (AxF, Apple x Forest; AxG, Apple x Grassland; GxF, Grassland x Forest). Mantel correlation coefficients were calculated for each lag interval and tested for significance with a permutation test, using 1,999 permutations. Each distance class was tested for significance using a Bonferroni-corrected α of 0.01.

N_{rel}	Distance class	Distance (m)	N	Mantel.cor	P (Mantel)	P (corrected)
AxF	1	1296	234	-0.02	0.27	0.27
	2	3788	170	0.01	0.44	0.88
	3	6280	148	0.05	0.13	0.40
	4	8772	316	0.00	0.48	1.00
	5	11264	180	0.03	0.25	1.00
	6	13755	176	-0.02	0.30	1.00
	7	16247	162	-0.01	0.39	1.00
	8	18739	110	0.05	0.08	0.68
	9	21231	92	-0.05	0.17	1.00
	10	23723	84	-0.01	0.46	1.00
	11	26215	48	-0.05	0.20	1.00
AxG	1	1295	232	-0.04	0.16	0.16
	2	3777	166	0.03	0.21	0.43
	3	6260	152	0.07	0.06	0.17
	4	8743	304	0.00	0.46	1.00
	5	11225	194	0.00	0.46	1.00
	6	13708	170	-0.03	0.22	1.00
	7	16191	160	0.04	0.21	1.00
	8	18673	116	0.02	0.30	1.00
	9	21156	88	-0.07	0.12	1.00
	10	23639	84	0.03	0.32	1.00
	11	26121	52	-0.06	0.16	1.00
GxF	1	1278	230	-0.02	0.24	0.24
	2	3771	174	-0.03	0.26	0.52
	3	6265	146	-0.01	0.38	1.00
	4	8759	312	0.04	0.12	0.47
	5	11252	190	0.00	0.46	1.00
	6	13746	168	0.01	0.48	1.00
	7	16239	168	0.00	0.49	1.00
	8	18733	108	0.03	0.24	1.00
	9	21227	92	-0.08	0.05	0.43
	10	23720	84	0.06	0.10	1.00
	11	26214	48	0.00	0.46	1.00



Chapter V

Spillover of natural enemies between contrasting field margins & crops

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**Manuscript
submitted**

Abstract

The intensification of agricultural systems has led to a rapid increase of arable land with a consequent fragmentation of natural habitats, causing a reduction in the diversity of insect natural enemies. The introduction of high-quality field margins has been proposed to counteract this decline in farmland biodiversity, but how these margins can affect the spillover of natural enemies between crop and non-crop habitats is still unclear. In this work we investigated the spillover of two contrasting groups of natural enemies: the Tachinidae and the Syrphidae. We examined the spillover from two types of field margin (grass margin and hedgerow) into adjacent maize fields located in landscapes with different proportion of arable land. The spillover of natural enemies can be affected by field margins, but the response varied significantly between the two groups. For hoverflies, abundance and richness was always higher toward the center of the crop fields compared to the margin. In contrast, the complexity of field margins appeared to have a positive effect on the diversity of tachinids, but this effect was not reflected in the spillover of these parasitoids. The spillover of tachinids was related to the degree of contrast between the margin and the crop as the spillover of this group was more evident on the grass margin. Our results have important implications for the conservation of natural enemies in fragmented landscapes. Measures focusing on the creation and management of field boundaries need to consider the local contrast between field margins and crops in relation to the dispersal ability of different taxa.

Introduction

The intensification of agricultural systems has led to a rapid increase of arable land with a consequent fragmentation of natural habitats (Tilman et al. 2001). Agricultural landscapes are often characterized by a mosaic of semi-natural habitats interspersed within a hostile matrix dominated by only a few crops. These simplified landscapes are responsible for the severe reduction in the diversity of insect natural enemies, which in turn is possibly negatively affecting important ecological services such as the biological control of pests (Wilby & Thomas 2002; Bianchi et al. 2006; MacFayden et al. 2009; Thies et al. 2011; Jonsson et al. 2012). In Europe, agri-environment schemes (AES) have been implemented to counteract this decline in farmland biodiversity. Within farms, the conservation and

implementation of semi-natural elements such as hedgerows, field margins and wildflower strips are among the most commonly interventions (Marshall & Moonen 2002; Haaland et al. 2011). Although there is growing empirical evidence suggesting that the presence of these semi-natural elements can help to mitigate the negative effects of agricultural intensification on insect diversity (e.g., Merckx et al. 2012; Haenke et al. 2014; Dainese et al. 2015), the understanding of how these farmland interventions affect the spillover of natural enemies is still unclear.

The spillover of natural enemies represents the movement of species from one habitat to another in search of specific resources (e.g., prey/hosts, nectar for adults, shelter). In agricultural landscapes, the spillover of natural enemies is known to be affected by the shape and the contrast of the different habitats within these landscapes (Polis et al. 1997; Schellhorn et al. 2014). Habitats with high degree of contrast are expected to be relatively impermeable to movement, while structurally similar habitats are likely to be more permeable (Stamps et al. 1987). Furthermore, there is growing evidence suggesting that the spillover of natural enemies is not only affected by local variables such as the shape and contrast of habitats, but also by landscape processes (i.e., the proportion of forests and mass-flowering crops in the landscape, Haenke et al. 2014). Several authors have found spillover of species from natural habitats into adjacent agricultural fields (e.g., Landis et al. 2000; Geiger et al. 2008; Rusch et al. 2010; Blitzer et al. 2012), but movement in the opposite direction has also been observed (e.g., Rand et al. 2006; Blitzer et al. 2012; Frost et al. 2014). Although there are several studies showing that the spillover of natural enemies can alter important ecosystem services such as pollination and natural pest suppression (Landis et al. 2000; Macfadyen & Muller 2013; Gagic et al. 2014; Haenke et al. 2014), most of these studies have focused on the interactions of semi-natural habitats like forest and grassland patches with agricultural fields, while little is known about the spillover of natural enemies from managed field margins.

Studies about the spillover of natural enemies have often focused on single taxa ignoring that dispersal dynamics can vary substantially across different groups of natural enemies. While some groups of natural enemies are tightly associated to semi-natural habitats and are highly sensitive to the fragmentation, other taxa are well adapted to fragmented landscapes and are capable to use ephemeral and spatially patchy resources (Tschardt et al. 2005). In this work we investigated the potential spillover of two

contrasting groups of natural enemies: tachinids (Diptera: Tachinidae) and hoverflies (Diptera: Syrphidae). On the one hand, the vast majority of tachinid parasitoids are known to depend on semi-natural habitats in the landscape (Letourneau et al. 2012; Inclán et al. 2014). On the other hand, several species of hoverflies are well-adapted to disturbed habitats, where they can be commonly found in high densities (Meyer et al. 2009). Besides these differences, both groups are important natural enemies as the predominance of tachinid parasitoids in attacking major groups of insect herbivores (Stireman et al. 2006; Cerretti et al. 2014) and the prevalence of hoverflies as aphidophagous predators (Alhmedi et al. 2008; Almohamad et al. 2009). Additionally, adults of both groups can provide pollination service: tachinids are flower visiting insects given that they commonly use nectar as an energy source (Stireman et al. 2006; Al-Dobai et al. 2012), while hoverflies are well known pollinators of wild flowers and flowering-crops (e.g., Jauker & Wolters 2008; Haenke et al. 2014).

In this study, we examined the spillover of tachinids and hoverflies from two contrasting field margins (grass margins and hedgerows) into the adjacent crop (maize fields) located in landscapes with different proportion of arable land. Specifically, we have addressed three main hypotheses. First, we expected that increasing the complexity of field margin (grass margins vs. hedgerows) will enhance the diversity of natural enemies. Here, we hypothesized that the diversity of tachinids and hoverflies would be higher in hedgerows as these boundaries provide more diverse resources (i.e., diverse hosts/preys) than grass margins. Second, we investigated if an increase of species diversity in a given field margin is translated into an increased spillover to the adjacent crop fields. According to the “edge-permeability hypothesis” (Stamps et al. 1987), it is expected a greater spillover of natural enemies when the field margin is more structurally similar to their adjacent crop. Therefore, we expected that natural enemies inhabiting grass margins would be more likely to move into the adjacent maize field, while species from hedgerows would be more likely to stay at the margin. Third, we expected that the spillover of tachinids and hoverflies could be also affected by the landscape and that the spillover of both groups of natural enemies would be more pronounced in landscapes with low proportion of arable land (e.g., Haenke et al. 2014).

Methods

Study area

The investigated area extended for about 10,000 km² in the Venetian-Friulian Plain (north-eastern Italy). The climate was humid sub-Mediterranean with annual rainfall ranging between 1200 – 1500 mm year⁻¹ and a mean annual temperature of 13°C. The majority of the study area (~ 65 %) was dominated by intensive agriculture where maize, wheat, and soybean were the dominant crops. These intensive landscapes were intermixed with scattered fragments of semi-natural habitats such as forests, grasslands and hedgerows.

Sampling design

To identify the effect of agricultural intensification on the spill-over of natural enemies, we first selected 12 landscapes to span a gradient in the proportion of arable land (19 – 99 %). The landscape composition was assessed using a buffer with a 500 m radius. For each buffer, arable fields were manually digitized from a visual inspection of high-resolution satellite images (Google Earth). In GIS (Quantum GIS 1.7, Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>), we quantified the area of each patch and then we calculated the proportion of arable land within each buffer.

To test the effect of different field margins on the spillover of natural enemies we kept constant the crop type and we selected two contrasting field margins. In each landscape, we selected two maize fields with two different field margins: (i) a grass margin and (ii) a hedgerow. The grass margins were characterized by a perennial grass strip without any nearby tree (average width 2.3 m), while the hedgerows consisted of a grass strip adjacent to a hedge formed by a combination of different shrubs and tree species (average width 2.5 m). To evaluate the spillover of species from the field margin into the crop, we set up one transect of pan-traps in the middle of each field margin. Within each transect, we sampled at six different distances, starting within the field margin and at 0, 2, 6, 15 and 40 m into their adjacent maize field.

Insect sampling

We sampled hoverflies and tachinid flies using pan-traps. At the different distances (field margin, 0, 2, 6, 15 and 40 m into the crop), one cluster of pan-traps was used. The cluster of traps consisted of one standard yellow and one UV-reflecting yellow plastic bowls (500 ml, 16 cm diameter) filled with a solution of water and 2% dishwashing detergent. Within each cluster, pan-traps were placed directly on the ground between two crop rows, each one separated one meter from the other. The sampling was done from the end of May until the beginning of July 2013, allowing us to sample the maize fields when the plants were less than 0.6 m tall. A total of four samplings were performed covering the season during which the crop is more susceptible to insect pest attack (e.g., Showers 1993, Hance 1997). During each sampling round, traps were set for a period of 72 hours after which insects were collected and stored in alcohol (70%) for sorting and identification. Hoverflies were identified to species level using Bartsch (2009) and Speight (2010), while tachinids were identified to species level using Cerretti (2010) and Cerretti et al. (2012). All the specimens are housed at the MZUR (Museo di Zoologia, Università di Roma La Sapienza, Rome, Italy) insect collection.

Data analysis

To test the effect of landscape composition, field margin and trap distance we used general and generalized linear mixed models (GLMMs). The response variable was the species richness and the total abundance calculated by pooling together the samples for each taxon within each cluster of traps during the four samplings. For the abundance of both taxa we used generalized linear mixed models with a negative binomial distribution and for the species richness of both taxa we used general linear mixed models with a normal distribution. The families and link functions used in the models were selected based on residual deviance and distribution of residuals. In each model, field margin type was entered as categorical fixed factor, while the proportion of arable land and the trap distance were set as continuous fixed factors. Trap distance was further log-transformed to account for the logarithmic scale of the distance in our sampling design. Interactions between the proportion of arable land, field margin and trap distance were also tested. We accounted for the nested design of our study by including the landscape identity ($n = 12$) and the transect identity within each landscape ($n = 24$) as random factors. The analyses were performed using the packages “glmmADMB” (Fournier et al. 2012) for generalized

and “nlme” (Pinheiro et al. 2015) for general mixed models, implemented in R 3.0.2 (R Development Core Team 2013).

To compare the fit of all the possible combinations of predictors in our models we used the second-order Akaike’s information criterion (AICc) corrected for small samples (Whittingham et al. 2006). We first built a global model containing all the interactions among the proportion of arable land, field margin and trap distance. We compared all the models using ΔAICc and Akaike weights ($\sum w_i$). The best fitting model was the one with the lowest AICc. In a set of n models, each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\text{minimum}}$). The difference in AICc values indicated the relative support for the different models. A model was considered plausible if its ΔAICc was below two (Burnham & Anderson 2002). To evaluate the relative importance of each predictor, we summed the w_i across the models in the set in which the predictor occurred. The model inference analyses were performed using the “MuMIn” package (Barton 2013) implemented in R (R Development Core Team 2013).

Results

A total of 3,411 individuals were collected belonging to 30 species of Syrphidae (Table S1). The species *Melanostoma mellinum* (L.) accounted for more than 70% of the total hoverfly abundance. *Melanostoma mellinum* is an aphidophagous species commonly found in disturbed habitats (Speight 2013). For Tachinidae, a total of 370 individuals were collected belonging to 47 species (Table S2). Three species of tachinids were dominant and accounted for more than 60% of the total abundance. *Dinera grisescens* (Fallén), *Microphthalma europaea* Egger and *Voria ruralis* (Fallén) represented 32, 17 and 13% of the individuals collected, respectively. *Dinera grisescens* and *M. europaea* are parasitoids of coleopteran larvae, while *V. ruralis* is a parasitoid of lepidopteran larvae (Cerretti & Tschorsnig 2010; Cerretti 2010).

Table 1. Plausible candidate models (within 2 ΔAICc of the top model) explaining the abundance and species richness of (a) Syrphidae and (b) Tachinidae. Models are ranked according to their second-order Akaike's information criterion (AICc). For each tested variable $\sum w_i$ indicates the sum of model weights.

(a) Syrphidae							
	Abundance					Species richness	
	$\sum w_i$	Best	2nd	3rd	4th	$\sum w_i$	Best
ΔAICc	-	0	0.45	1.36	1.49	-	0
Model weight	-	0.28	0.22	0.14	0.13	-	0.37
Intercept	-	2.67	2.67	2.74	2.67	-	3.27
Arable land	0.54	-	0.29	-	0.2	0.34	-
Distance	1	0.12	0.12	0.12	0.12	0.86	0.21
Field margin	0.37	-	-	*	-	0.35	-
Arable land x Distance	0.28	-	-0.05	-	-	0.08	-
Arable land x Field margin	0.06	-	-	-	-	0.04	-
Distance x Field margin	0.14	-	-	-	-	0.1	-
Arable land x Distance x Field margin	0.01	-	-	-	-	<0.01	-
(b) Tachinidae							
ΔAICc	-	0	1.74	-	-	-	0
Model weight	-	0.47	0.2	-	-	-	0.37
Intercept	-	1.22	1.22	-	-	-	2.13
Arable land	0.45	-	-0.15	-	-	0.44	-
Distance	1	-0.5	-0.45	-	-	1	-0.45
Field margin	0.91	*	*	-	-	0.8	*
Arable land x Distance	0.12	-	-	-	-	0.15	-
Arable land x Field margin	0.15	-	-	-	-	0.15	-
Distance x Field margin	0.87	*	*	-	-	0.69	*
Arable land x Distance x Field margin	0.02	-	-	-	-	0.02	-

* Indicates that the categorical variable was included in the models.

For hoverfly abundance, four plausible models were selected ($\Delta\text{AICc} < 2$, Table 1a). The sum of model weights for each predictor gave support only for an effect of trap distance (Table 1a, Fig. 1a). This indicated that the abundance of hoverflies was higher toward the center of the crop field (edge: 19.8 ± 4.3 , 0 m: 21.3 ± 3.1 , 2 m: 21.7 ± 3.9 , 6 m: 23.7 ± 3.6 , 15 m: 25.9 ± 3.9 , 40 m: 27.5 ± 3.2). For hoverfly species richness, only a single plausible model was selected ($\Delta\text{AICc} < 2$, Table 1a). Similar to the hoverfly abundance, the sum of model weights for each predictor gave support only a strong effect of trap distance (Table 1a, Fig. 1b). This indicated that the species richness of hoverflies was higher toward the center of the crop field (edge: 2.9 ± 0.3 , 0 m: 3.9 ± 0.4 , 2 m: 3.6 ± 0.5 , 6 m: 3.7 ± 0.4 , 15 m: 3.4 ± 0.4 , 40 m: 4.3 ± 0.4).

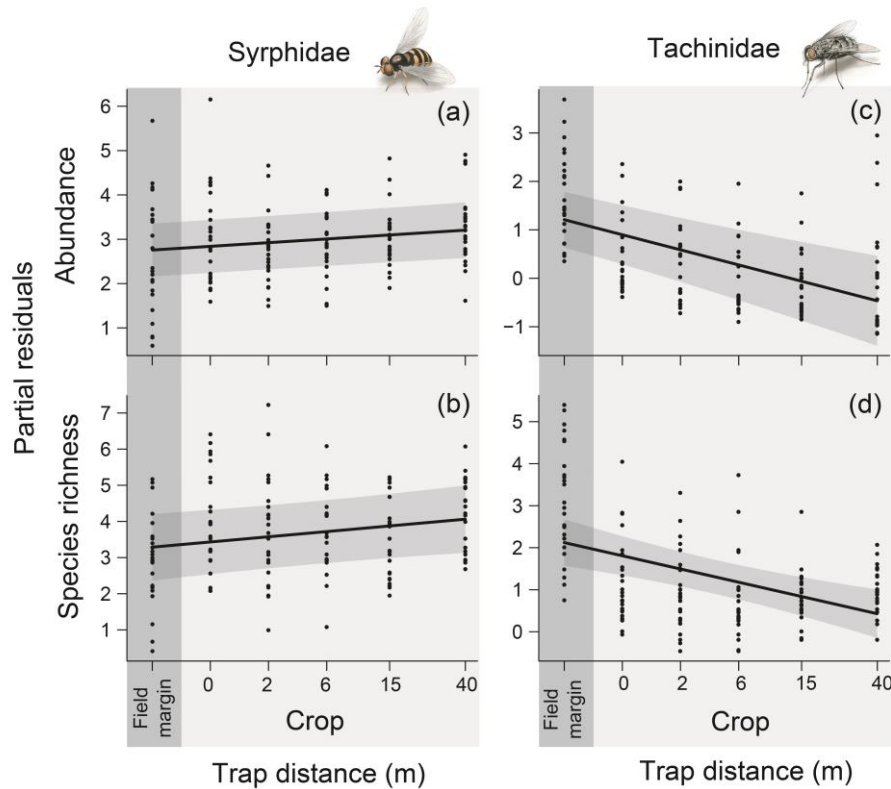


Figure 1. Plots showing the contrasting spillover of two groups of natural enemies from field margin into their adjacent crop field. The left panels show the (a) abundance and (b) species richness of Syrphidae, while the right panels show the (c) abundance and (d) species richness of Tachinidae. For both groups, the fitted line was estimated by a generalized linear mixed model for abundance and by a general linear mixed model for species richness. The points represent the partial residuals from the respective models.

For Tachinidae abundance, two plausible models were selected ($\Delta\text{AICc} < 2$, Table 1b). The sum of model weights for each predictor gave support for a strong effect of trap distance and field margin on tachinid abundance (Table 1b). The effect of the trap distance was negative (Fig. 1c), which indicated that the abundance of tachinids decreased toward the center of the crop field (edge: 7.4 ± 1.4 , 0 m: 2.7 ± 0.7 , 2 m: 2.0 ± 0.5 , 6 m: 1.3 ± 0.4 , 15 m: 1.0 ± 0.3 , 40 m: 1.0 ± 0.3). The abundance of tachinids was slightly higher in hedgerows (2.6 ± 0.5) than in grass margins (2.5 ± 0.5). We also found a good support for the interaction between trap distance and field margin (Fig. 2a). This interaction indicated that the decrease in abundance of tachinids toward the center of the crop field was less evident for grass margins, while it was more pronounced for hedgerows. For Tachinidae species richness, only a single plausible model was selected ($\Delta\text{AICc} < 2$, Table 1b). Similar to the tachinid abundance, the sum of model weights for

each predictor gave support for a strong effect of trap distance and field margin on tachinid species richness (Table 1b). The effect of the trap distance was negative (Fig. 1d), which indicated that the species richness of tachinids decreased toward the center of the crop field (edge: 3.5 ± 0.3 , 0 m: 1.5 ± 0.3 , 2 m: 1.2 ± 0.3 , 6 m: 0.8 ± 0.2 , 15 m: 0.7 ± 0.2 , 40 m: 0.7 ± 0.1). The species richness of tachinids was slightly higher in hedgerows (1.5 ± 0.2) than in grass margins (1.3 ± 0.2). We also found a support for the interaction between trap distance and field margin (Fig. 2b). This interaction indicates that the trend of decrease in species richness toward the center of the crop field is less evident for grass margins than for hedgerows.

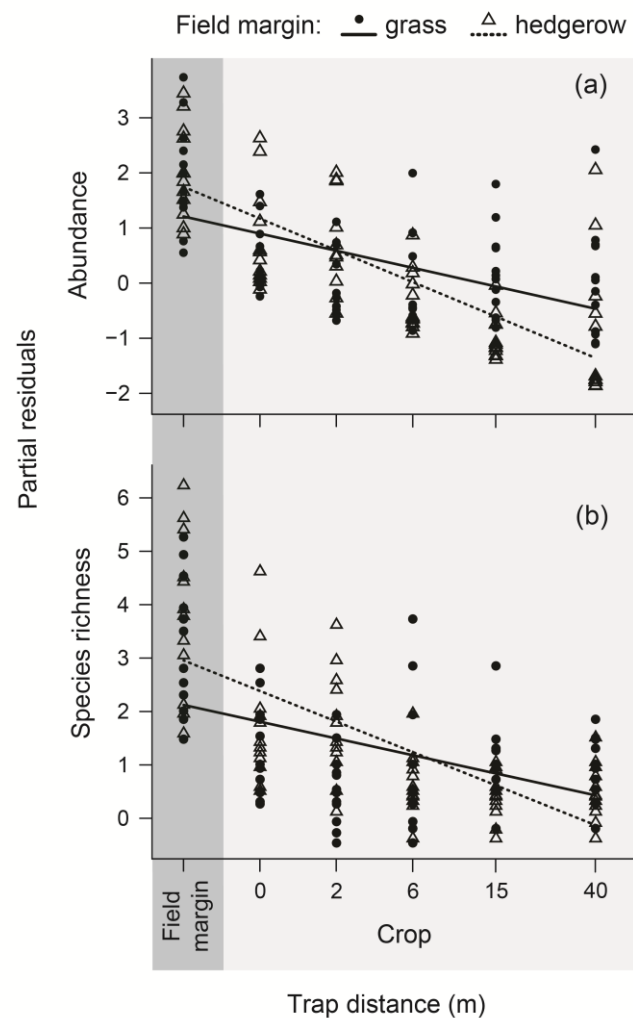


Figure 2. Plots showing the interaction between the field margin and the spillover into their adjacent crop field of tachinid parasitoids. The top and the bottom panel represent the relationship between trap distance and (a) abundance and (b) species richness of tachinids separately for grass and hedgerow. Each fitted line was estimated by a generalized linear mixed model for abundance and by a general linear mixed model for species richness. The partial residuals from the respective models are shown as points for grass margins and as triangles for hedgerows.

Discussion

Our results showed that the spillover of natural enemies can be affected by field margin type, but the response varied significantly between hoverflies and tachinids. Field margins (both grass margins and hedgerows) appeared to not affect the movement of hoverflies, as their abundance and species richness was slightly higher toward the center of the crop fields. Conversely, tachinids were almost restricted to the field margins and their spillover varied depending on the type of margin. The spillover of tachinids appeared to be related to the degree of contrast between the structure of the margin and the crop, as the spillover of this group was more evident on the grass margins. These results have important implications for the conservation of natural enemies in crop fields, as the local spillover of species can be affected by the type of field margins.

The effect of the different field margins on the diversity of natural enemies varied considerably between tachinids and hoverflies. Although we expected that increasing the local complexity will enhance the diversity of both groups of natural enemies, we found only a positive effect of hedgerows on the diversity of tachinid parasitoids. This result is in line with previous studies where increasing the complexity of field margins yielded a higher diversity of tachinids (Olson & Wäckers 2007; Al-Dobai et al. 2012; Dainese et al. 2015). In contrast, the type field margin appeared to have no effect on the diversity of hoverflies. In fact, the diversity of this group was always higher in the crop field rather than in the field margin. These results are not surprising giving that hoverflies, especially the aphidophagous species, are known to be highly associated with the abundance of prey in the crop (Salveter 1998; Meyer et al. 2009).

The spillover also varied between the two groups of natural enemies. Tachinid parasitoids showed a limited spillover as the abundance and species richness of this group at 40 meters in the crop field was at least four times lower than that in the field margin. Similar results have been found by other studies that show a high diversity of tachinids at the field margin, contrasting with the low diversity within the crop fields (Olson & Wäckers 2007; Inclán et al. 2015). In contrast, hoverflies showed large spillover of individuals and species between the field margins and the crop as their abundance and species richness at 40 meters in the crop field was only slightly higher than that in the field margins. This result suggests a strong association of the hoverfly community with the crop fields. A similar pattern has been found in other studies, where the abundance of

species dominated by aphidophagous hoverflies tended to increase in arable land (Salveter 1998; Jauker et al. 2009; Meyer et al. 2009; Haenke et al. 2014). In fact, Wratten et al. (2003) found that field boundaries within agricultural land could even represent a barrier for the movement of hoverflies.

The increase of tachinid parasitoid diversity in hedgerows was not translated into an increasing spillover to the adjacent crop fields. Instead, we found that tachinid parasitoids inhabiting grass margins were more likely to move into their adjacent maize field, contrasting with the lower spillover of tachinids from hedgerows. This result is in line with the “edge-permeability hypothesis” (Stamps et al. 1987) that suggests that species are more likely to move across edges of low contrast (i.e., with similar structure). Tachinids, as many other parasitoids, are known to use diverse combination of cues to forage for resources (i.e., host kairomones and/or visual cues). For instance, finding a suitable habitat is the first approach for the location of host (Godfray 1994; Stireman 2002; Ichiki et al. 2013). Therefore, tachinids occurring in grass margins are likely to go into the maize field, since the community in these margins could perceive the maize field as a similar habitat. In contrast, tachinids occurring in hedgerows may recognize the maize fields as a complete different habitat and they may avoid foraging. Contrary to tachinids, we did not find any interaction between the type of field margin and the trap distance for hoverfly diversity. Independently of the type of field margin, the diversity of hoverflies was always higher toward the center of the crop field, suggesting that the aphidophagous species in this group may even avoid the field margins (Salveter 1998; Wratten et al. 2003; Jauker et al. 2009) as they search for resources (i.e. prey abundance) in the agricultural matrix.

The reduction of the cover of arable land at the landscape scale was expected to enhance the spillover of both groups of natural enemies, but contrary to our expectations we did not find any effect of the increment of arable land on the diversity of tachinids and hoverflies. This may be explained by the generalist host/prey association and the high mobility of tachinids (Stireman 2002; Stireman et al. 2006) and hoverflies (e.g., Wratten et al. 1995; Salveter 1998; Jauker et al. 2009; Alhmedi et al. 2008; Almohamad et al. 2009). In hoverflies, the lack of response to the semi-natural habitats in the landscape is probably related to the response of the aphidophagous species. Several authors have found a positive relationship between the aphidophagous species and the increment of

arable land, as these flies are likely to find their prey mainly in arable fields (Burgio & Sommaggio 2007; Jauker et al. 2009; Meyer et al. 2009; Haenke et al. 2014).

Pest control is an important ecosystem service that often depends on the spillover of natural enemies from the semi-natural areas. Here we demonstrated that the spillover of natural enemies is likely to depend not only on the environmental features such as margin quality, but also on the related life history traits (i.e., dispersal behavior) of each taxon. In fact, the distribution patterns of natural enemies in agricultural landscapes are known to change considerably across different taxa (Dullei & Obrist 2003; Tscharrntke et al. 2005). On the one hand, tachinid parasitoids are likely to follow a “disperser” or “ecotone-species” distribution, as these parasitoids depend mainly on non-crop habitats and their distribution into the crop fields decreases with the distance from the non-crop habitats. On the other hand, hoverflies, especially the aphidophagous species, are likely to follow a “cultural species” distribution, as they depend largely on crop resources and their distribution increases toward the crop area. However, these patterns of distribution may change across different seasons (e.g., Haenke et al. 2014) and further research is still needed to evaluate the temporal variability of the spillover across different taxa.

Conclusions

Our results have important implications for the conservation of natural enemies in agricultural landscapes. In particular, the implementation of field margins to enhance the diversity and spillover of natural enemies needs to consider the local contrast between the field margin and the crop in relation to the dispersal and foraging behavior of the focal taxa. Although several authors have proposed the implementation of complex field margins to improve farmland biodiversity (e.g., Merckx et al. 2012; Dainese et al. 2015), it is clear that this measure can enhance the diversity of some groups with little or no effect on the diversity of crop-specialized natural enemies. While the implementation of both simple and complex field margins clearly enhanced the diversity of tachinid parasitoids, this measure had little effect on cultural-species like aphidophagous hoverflies that are more affected by the management of the crop land. However, it must be considered that species apparently restricted to crop land, like aphidophagous hoverflies, may still use resources from the field margins in different seasons that could

vary depending on the crop phenology (Meyer et al. 2009; Haenke et al. 2014). Our results suggest that different measures should be adopted to enhance the diversity of different groups of natural enemies. Furthermore, farmland interventions, such as the implementation of field boundaries, should focus not only in the enhancement of the local diversity of natural enemies, but also in the spillover of these species into their adjacent field crops. As the spillover of tachinid parasitoids was favored by the low contrast between the grass margins and the maize fields, it appears that the implementation of grass margins may have a greater impact in landscapes with annual crops, while the implementation of hedgerows may have a greater impact in landscapes dominated by perennial crops. However, to justify and facilitate different combinations of field margins, future research is still needed to demonstrate effective spillover between different field margins and crops across multiple spatial and temporal scales.

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Supplementary Material

Table S1. Syrphidae species and their abundance in the study sites.

Species	Total of individuals
<i>Chrysotoxum festivum</i> (Linnaeus, 1758)	2
<i>Episyrphus balteatus</i> (DeGeer, 1776)	85
<i>Eristalinus aeneus</i> (Scopoli, 1763)	29
<i>Eristalinus sepulchralis</i> (Linnaeus, 1758)	29
<i>Eristalis arbustorum</i> (Linnaeus, 1758)	109
<i>Eristalis similis</i> (Fallén, 1817)	2
<i>Eristalis tenax</i> (Linnaeus, 1758)	63
<i>Eumerus amoenus</i> Loew, 1848	1
<i>Eupeodes corollae</i> (Fabricius, 1794)	166
<i>Eupeodes latifasciatus</i> (Macquart, 1829)	1
<i>Helophilus pendulus</i> (Linnaeus, 1758)	8
<i>Helophilus trivittatus</i> (Fabricius, 1805)	7
<i>Lejogaster metallina</i> (Fabricius, 1781)	1
<i>Lejogaster tarsata</i> (Meigen, 1822)	6
<i>Melanostoma mellinum</i> (Linnaeus, 1758)	2696
<i>Meliscaeva auricollis</i> (Meigen, 1822)	1
<i>Merodon avidus</i> (Rossi, 1790)	14
<i>Mesembrius peregrinus</i> (Loew, 1846)	1
<i>Myathropa florea</i> (Linnaeus, 1758)	3
<i>Neoascia podagrica</i> (Fabricius, 1775)	40
<i>Paragus constrictus</i> Šimic, 1986	1
<i>Paragus pecchiolii</i> Rondani, 1857	1
<i>Pipizella viduata</i> (Linnaeus, 1758)	31
<i>Riponnensia splendens</i> (Meigen, 1822)	1
<i>Scaeva pyrastris</i> (Linnaeus, 1758)	1
<i>Sphaerophoria rueppelli</i> (Wiedemann, 1830)	9
<i>Sphaerophoria scripta</i> (Linnaeus, 1758)	42
<i>Syrphus ribesii</i> (Linnaeus, 1758)	3
<i>Syrphus vitripennis</i> Meigen, 1822	7
<i>Volucella zonaria</i> (Poda, 1761)	1

Table S2. Tachinidae species and their abundance in the study sites.

Species	Total of individuals
<i>Bithia immaculata</i> (Herting, 1971)	1
<i>Bithia modesta</i> (Meigen, 1824)	1
<i>Blondelia nigripes</i> (Fallén, 1810)	1
<i>Carcelia lucorum</i> (Meigen, 1824)	1
<i>Chetogena filipalpis</i> Rondani, 1859	1
<i>Compsilura concinnata</i> (Meigen, 1824)	1
<i>Cylindromyia bicolor</i> (Olivier, 1812)	1

Table S2. continued

<i>Dinera grisescens</i> (Fallén, 1817)	117
<i>Drino lota</i> (Meigen, 1824)	1
<i>Eliozeta pellucens</i> (Fallén, 1820)	1
<i>Erycia fatua</i> (Meigen, 1824)	1
<i>Erycia festinans</i> (Meigen, 1824)	1
<i>Exorista fasciata</i> (Fallén, 1820)	2
<i>Exorista larvarum</i> (Linnaeus, 1758)	2
<i>Exorista rustica</i> (Fallén, 1810)	2
<i>Lecanipa leucomelas</i> (Meigen, 1824)	1
<i>Linnaemya comta</i> (Fallén, 1810)	2
<i>Loewia setibarba</i> Egger, 1856	1
<i>Lydella thompsoni</i> Herting, 1959	1
<i>Macquartia tenebricosa</i> (Meigen, 1824)	2
<i>Macquartia tessellum</i> (Meigen, 1824)	1
<i>Medina collaris</i> (Fallén, 1820)	1
<i>Medina separata</i> (Meigen, 1824)	9
<i>Meigenia mutabilis</i> (Fallén, 1810)	11
<i>Meigenia uncinata</i> Mesnil, 1967	1
<i>Microphthalma europaea</i> Egger, 1860	62
<i>Nemoraea pellucida</i> (Meigen, 1824)	4
<i>Nilea innoxia</i> Robineau-Desvoidy, 1863	2
<i>Ocytata pallipes</i> (Fallén, 1820)	7
<i>Paratrixa polonica</i> Brauer & Bergenstamm, 1891	1
<i>Paratryphera barbatula</i> (Rondani, 1859)	2
<i>Peribaea tibialis</i> (Robineau-Desvoidy, 1851)	4
<i>Phania funesta</i> (Meigen, 1824)	45
<i>Policheta unicolor</i> (Fallén, 1820)	3
<i>Pseudoperichaeta palesioidea</i> (Robineau-Desvoidy, 1830)	2
<i>Pseudopericheta nigrolineata</i> (Walker, 1853)	1
<i>Siphona geniculata</i> (De Geer, 1776)	1
<i>Solieria vacua</i> (Rondani, 1861)	1
<i>Spallanzania hebes</i> (Fallén, 1820)	1
<i>Synactia parvula</i> (Rondani, 1861)	1
<i>Thelaira nigripes</i> (Fabricius, 1794)	1
<i>Thelaira solivaga</i> (Harris, 1780)	1
<i>Triarthria setipennis</i> (Fallén, 1810)	2
<i>Vibrissina debilitata</i> (Pandellé, 1896)	1
<i>Vibrissina turrata</i> (Meigen, 1824)	2
<i>Voria ruralis</i> (Fallén, 1810)	47
<i>Zaira cinerea</i> (Fallén, 1810)	1



Chapter VI

**Testing scale-dependent effects
of semi-natural habitats on
farmland biodiversity**

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Abstract

The effectiveness of conservation interventions for maximizing biodiversity benefits from agri-environment schemes (AESs) is expected to depend on the quantity of semi-natural habitats in the surrounding landscape. To verify this hypothesis, we developed a hierarchical sampling design to assess the effects of field boundary type and cover of semi-natural habitats in the landscape at two nested spatial scales. We sampled three types of field boundaries with increasing structural complexity (grass margin – simple hedgerow – complex hedgerow) in paired landscapes with presence or absence of semi-natural habitats (radius 0.5 km), that in turn, were nested within 15 areas with different proportions of semi-natural habitats at a larger spatial scale (10 × 10 km). Overall, 90 field boundaries were sampled across a Mediterranean region (NE Italy). We considered species richness response across three different taxonomic groups: vascular plants, butterflies, and tachinid flies. No interactions between type of field boundary and surrounding landscape were found at either 0.5 and 10 km indicating that the quality of field boundary had the same effect irrespective of the cover of semi-natural habitats. At the local scale, extended-width grass margins yielded higher plant species richness, while hedgerows yielded higher species richness of butterflies and tachinids. At the 0.5 km landscape scale, the effect of the proportion of semi-natural habitats was neutral for plants and tachinids, while butterflies were positively related to the proportion of forest. At the 10 km landscape scale, only butterflies responded positively to the proportion of semi-natural habitats. Our study confirmed the importance of testing multiple scales when considering species from different taxa and with different mobility. We showed that the quality of field boundaries at the local scale was an important factor in enhancing farmland biodiversity. For butterflies, AESs should focus particular attention on preservation of forest patches in agricultural landscapes within 0.5 km as well as the conservation of semi-natural habitats at a wider landscape scale.

Introduction

Since the second half of the 20th century, simplification of agricultural landscapes through the removal of semi-natural habitats and agricultural management intensification aimed at increasing crop yield have caused severe biodiversity losses (Tilman et al. 2001;

Green et al. 2005; Norris 2008). To reverse these negative trends agri-environment schemes (AESs) have been introduced in many European countries (Whittingham 2007), but contrasting results on the benefits of these interventions have been found (Kleijn & Sutherland 2003; Kleijn et al. 2006). In particular the effectiveness of AESs is expected to depend on the quantity of semi-natural habitats in the surrounding landscape (Batáry et al. 2011; Concepción et al. 2012a; Tschardt et al. 2012). According to the ‘intermediate landscape complexity hypothesis’ (Tschardt et al. 2005), the effectiveness of AESs should be higher in intermediate-complexity than in either low- or high-complexity landscapes (Kleijn et al. 2011). On the one hand, complex landscapes already support high biodiversity, so that local conservation management often does not result in a recognizable effect. On the other hand, extremely simplified landscapes with an impoverished regional species pool do not have the capacity to respond to local interventions. When evaluating the effectiveness of introducing high-quality boundaries at the local scale, it is also important to consider that species from different taxa and with different mobility may interact with the environment at different spatial scales (Concepción et al. 2012a).

Understanding the landscape-dependent effect of conservation interventions such as enhancing quality of field boundaries is crucially important for maximizing biodiversity benefits from AESs (Holzschuh et al. 2008; Rundlöf et al. 2008, 2010; Gabriel et al. 2006, 2010; Kleijn et al. 2011; Concepción et al. 2012b). Since most species are influenced by factors acting at the regional, landscape and field scale, conservation of farmland biodiversity needs a multiple-scale perspective (Gonthier et al. 2014). So far, this potential scale dependence has been mainly tested by measuring the proportion of high-quality habitat in the landscape within nested circular buffers (e.g., Steffan-Dewenter et al. 2002) that result in correlated landscape metrics between small and large radii (but see Gabriel et al. 2010; Benjamin et al. 2014). For this reason it is crucial to verify whether the effect of increasing the quality of field boundaries at the local spatial scale depends on the landscape context.

Conservation and restoration of hedgerows is becoming a prominent farmland intervention in several AESs. Indeed, these landscape elements, together with scattered forest patches, are often the only remaining refuges for biodiversity in agricultural landscapes (Forman & Baudry 1984). Recent studies indeed confirm that the presence of hedgerows may help to mitigate the negative effects of agricultural intensification on

insect diversity (Kuussaari et al. 2007; Merckx et al. 2012; Haenke et al. 2014). In addition, the effect of changes in hedgerow structural complexity and/or plant species diversity (e.g., Pywell et al. 2004) may be important to consider in these studies. The effectiveness of introducing a hedgerow to improve farmland biodiversity may depend, however, not only on the quality of the hedgerow, but also on the surrounding landscape.

In this study, we developed an innovative hierarchical sampling design to assess the effects of field boundary quality (i.e., structural complexity and plant species diversity) and semi-natural habitats at multiple scales on the diversity of taxa across three taxonomic groups. Specifically, we have addressed three main questions. First, do field boundaries with increasing complexity enhance farmland biodiversity? At the local scale, three types of field boundary (grass margin – simple hedgerow – complex hedgerow) were chosen to represent different levels of structural complexity and plant species diversity. This comparison will determine if hedgerows provide a further benefit to biodiversity conservation compared with grass margins, the most common field boundary. Second, at which spatial scale do semi-natural habitats most strongly affect farmland biodiversity? To address this question we have considered three nested and uncorrelated spatial scales. Specifically, field boundaries (local scale) were nested within landscape pairs with or without semi-natural habitats (landscape at 0.5 km radius) and landscapes were, in turn, nested within 15 areas with different proportions of semi-natural habitats at a larger spatial scale (landscape at 10 × 10 km). We expected that the effectiveness of local management in terms of enhanced species richness would be maximal at intermediate levels of landscape complexity (Tscharntke et al. 2005). Third, do the effects of field boundary type and landscape factors differ among taxa? To address this question, we examine the response of vascular plants, butterflies and tachinid parasitoids. Plants as primary producers could have a bottom-up control on higher trophic levels (Siemann et al. 1998). Butterflies that are herbivores at the larval stage or potential pollinators in the adult stage can be considered as a sensitive indicator groups for measuring biodiversity in terrestrial ecosystems (Thomas 2005). Tachinid parasitoids are an important taxon for biological control of insect pests (Letourneau et al. 2012). Among natural enemies, relatively little is known about how tachinid diversity varies at different spatial scales. Furthermore, butterflies and tachinids are known to use multiple resources that are spatially separated (Thomas et al. 2001; Stireman 2008; Flick et al. 2012; Inclán et al. 2014), making these groups also ideal for multi-scale studies.

Methods

Study area

The investigated area extends for about 10,000 km² in the Venetian-Friulian Plain (north-eastern Italy). The climate is humid sub-Mediterranean with annual rainfall ranging between 1200–1500 mm year⁻¹ and a mean annual temperature of 13°C. About 65% of the study area is dominated by intensive agriculture (maize, wheat, and soybean are the dominant crops), interspersed by fragments of semi-natural habitats such as forests, grasslands and hedgerows.

Sampling design

To identify the effect of semi-natural habitats at different spatial scales, a multi-scale sampling design was applied (Fig. 1). At the 10 km scale, we firstly divided our study region into a regular grid of 10 × 10 km cells where we measured the cover of semi-natural habitats derived from a detailed vector-based land-cover map (Regione Autonoma Friuli Venezia Giulia 2003; Regione Veneto 2009). Semi-natural habitats included forest and open natural or semi-natural habitats. The proportion of semi-natural habitats within the cells was quantified and ranged between 1 and 30%. We tried to verify the effects of forest and grassland separately in the analysis, however, due to the limited cover of grasslands (the proportion within the cells was always less than 2%), we found no effect of grasslands alone. We then defined three classes on the basis of proportion of semi-natural habitats: (i) simple cells characterized by a low proportion of semi-natural habitats (< 3%); (ii) cells with intermediate characteristics between those of the previous and the next class (8 < proportion of semi-natural habitats < 12%); (iii) complex cells characterized by a high proportion of semi-natural habitats (> 20%). The 20% threshold to define complex landscapes was based on earlier studies (Tscharntke et al. 2005, Batáry et al. 2010). We could not select ‘cleared’ landscapes (< 1% of non-crop habitat), as defined by Tscharntke et al. (2005), as these landscapes are not present in our region. Therefore, for simple landscapes, we used a threshold of 3% to find a balanced number of sample cells. For each class, five cells were selected (Fig. 1a). We tried to obtain an interspersed distribution of the three classes in the study region.

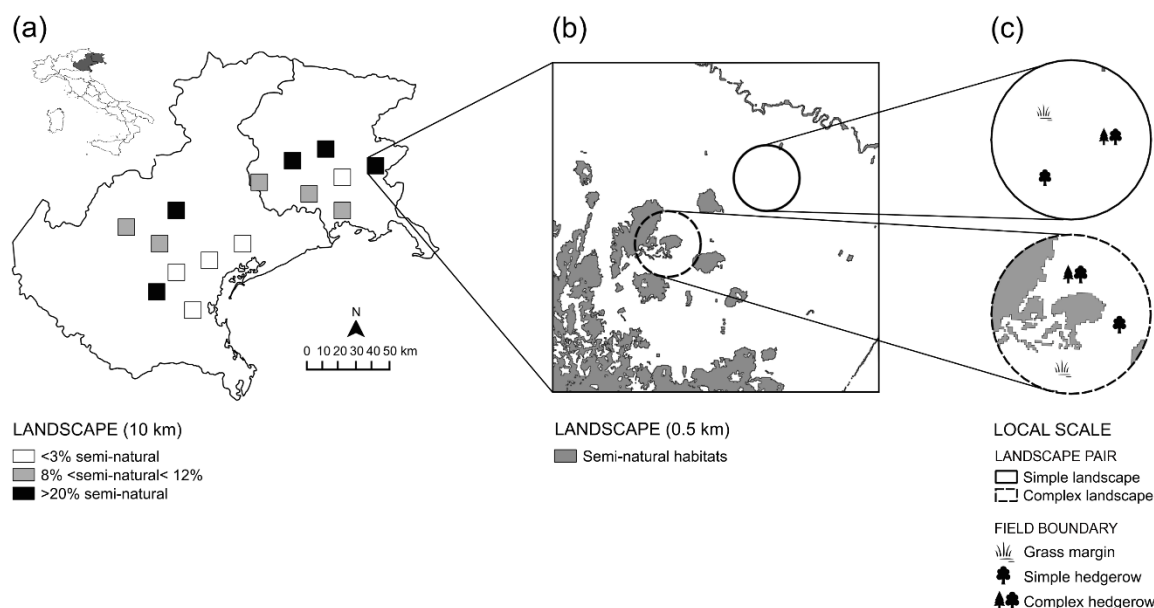


Figure 1. Hierarchical sampling design used to select the 90 field boundaries at three spatial scales: (a) Landscape at 10 km. Fifteen cells (10×10 km) were sampled on the basis of proportion of semi-natural habitat (simple, $< 3\%$; intermediate, $8\text{--}12\%$; complex, $> 20\%$). (b) Landscape at 0.5 km. A landscape pair of one complex and simple landscape, based on presence or absence of semi-natural habitats, was selected within each cell. (c) Local scale. Three field boundaries with increasing structural complexity were chosen within each landscape (grass margin, simple hedgerow, and complex hedgerow). Overall, 30 field boundary triplets were sampled.

At the 0.5 km scale, a landscape pair was selected within each cell on the basis of presence or absence of semi-natural habitats (Fig. 1b, S1). In each landscape three field boundaries were sampled. Around each field boundary, landscape composition was assessed using a buffer with a 500 m radius. In each buffer hedgerow, forest, and grassland (mainly hay-meadows belonging to *Arrhenatherion elatioris* communities) patches were manually digitised from a visual inspection of high-resolution satellite images (Google Earth). In GIS (Quantum GIS 1.7, Open Source Geospatial Foundation Project, <http://qgis.osgeo.org>), we quantified the area of each patch and then we calculated the proportion of the different land-use classes within the buffers.

At the local scale, three types of field boundary with increasing structural complexity (see also the description by Sitzia et al. 2013) were chosen within each landscape at 0.5 km: (i) grass margin, a perennial grass buffer strip without any nearby tree; (ii) simple hedgerow, a grass buffer strip adjacent to a single storied hedge (a so-called ‘treeline – full grown trees’, formed by a few dominant species, either plane tree *Platanus hybrida* Brot., white mulberry *Morus alba* L., or white willow *Salix alba* L.);

(iii) complex hedgerow, a grass buffer strip with a multi-storied hedgerow on the edge (averaged number of trees and shrubs species 10.7 ± 2.9) (Fig. S2). We only selected hedgerows having a grass margin associated with them. For each field boundary, we obtained from interviews the number of cuts executed yearly in each grass buffer strip and we used it as measure of management intensity. We also measured the width of the grass buffer strip to control the unequal habitat area (Table 1), although we found no significant difference between the three types of field boundary (Table S1). Then, within each landscape at 0.5 km a field boundary belonging to each of the three types was sampled (Fig. 1c). In total, 30 field boundary triplets were sampled. We focused the effort on selecting field boundaries adjacent to the three main arable crops cultivated in the study region, i.e. maize, wheat, and soybean. The occurrence of the adjacent arable crops within the different scale was done to obtain an interspersed arrangement. In fact, we found that the occurrence of the adjacent arable crops was independent of landscape at 10 km (Pearson's chi-squared test: $\chi^2 = 6.26$, $P = 0.181$), landscape at 0.5 km ($\chi^2 = 0.33$, $P = 0.955$), and field boundary type ($\chi^2 = 1.98$, $P = 0.923$). Overall, 90 field boundaries were sampled across the study region.

We tested for collinearity between our local and landscape factors. The three spatial scales (field boundary – landscape at 0.5 km – landscape at 10 km) were independent among them (Table S1, S2). Only local factors differed significantly, with a higher number of cuts in grass margin than both hedgerow types. As the collinearity between local and landscape factors was very low, we included all the factors in the same models.

Table 1. Descriptive statistics of the continuous factors used in the models.

	Mean \pm SD	Min	Max
Semi-natural 10 km (%)	11.6 \pm 9.1	1	26
Hedgerow 0.5 km (%)	5.3 \pm 2.3	1	12
Forest 0.5 km (%)	6.4 \pm 8.4	0	33
Grassland 0.5 km (%)	5.3 \pm 7.0	0	30
Margin width (cm)	237.7 \pm 125.7	80	500
Plant species richness ^a	14.6 \pm 4.0	7	25
Number of cuts per year	1.4 \pm 1.3	0	5

^a Plant species richness was used as predictor for butterfly and tachinid models.

Vascular plant, butterfly and tachinid surveys

We estimated vascular plant species richness once before the first cut of the grass buffer strip in June 2013. Sampling was conducted in the grass buffer strip along a transect parallel to the field boundary. We established three plots of 1 \times 2 m²: one plot was placed in the middle part of the transect and the other plots at the two margins at least 10 m apart along transect. Within each sampling plot, we recorded vascular plants to species level (presence/absence data).

We sampled butterflies (diurnal Lepidoptera: *Hesperioidea* and *Papilionidea*) using a linear transect survey (Pollard 1977). A transect length of 50 m was established parallel to the field boundary and was patrolled back and forth for 10 min. We identified and counted all of the butterflies within 2.5 m along the transect. Surveys took place between 9:30 and 17:30 under suitable weather conditions (temperature > 17° C and cloud cover < 25%). Sampling was repeated five times from mid-May to the first half of September 2013. For each survey round all the field boundaries were sampled within four or five days. To avoid any systematic effect of time of day the sequence of surveys was randomized.

We sampled tachinid flies using a passive sampling with pan-traps (750 ml plastic bowl). Within each field boundary, six pan-traps were placed in three clusters with two traps in each cluster. Each cluster was composed of one pan-trap painted with UV-bright yellow and one painted with standard yellow. Yellow pan-traps have been used effectively for sampling tachinid flies (e.g., Stireman 2008; Inclán et al. 2014). The three clusters were placed along the grass buffer strip in the plant sampling plots. The traps were placed directly on the ground among open or low-growing vegetation and were filled with water and a drop of detergent (2% dilution). Sampling was done under stable sunny weather and was repeated four times from the end of May until the beginning of September 2013. During each sampling round the pan-traps were left out for 72 h. Tachinid specimens were kept in alcohol and later identified to species level using Cerretti et al. (2012).

Data analysis

Species richness was calculated by pooling together the samples for each taxonomic group within each field boundary. Vascular plant species richness was the pooled number of species found in the three plots. Butterfly species richness was the cumulative number of species found during the five visits. Tachinid species richness was the cumulative number of species found in the three clusters of traps during the four visits. We used generalized linear mixed models (GLMMs) to test the effect of field boundary, landscape composition at the two scales on species richness of the three groups. We employed a Poisson-distribution with log-link function. The likelihood of the models was computed with the Laplace approximation, as suggested by Bolker et al. (2009). In each model, field boundary type was entered as categorical fixed factor, while number of cuts, margin width (grass buffer strip), proportion of land use classes at 0.5 km (hedgerow, forest, and grassland), and proportion of semi-natural habitats at cell level (10×10 km) as continuous fixed factors. At the cell level (10×10 km) we used a unique measure of semi-natural habitats cover due to the low proportion of grasslands within each cell (< 2%). We also included plant species richness as fixed factor in butterfly and tachinid models since we expected a positive relationship between plant diversity and species richness of flower-visiting insects. Interactions between field boundary and landscape variables at the two scales were also tested. A significant interaction between field boundary type and landscape composition would indicate that the effectiveness of the local intervention depends on the quality of landscape. In particular we expected that the

high-quality boundaries would be more effective in intermediate complexity landscapes. We accounted for the nested design by including the following random factors: cell identity and landscape identity within cell. All the models showed no sign of overdispersion (plants: $\chi^2/\text{residual d.f.} = 0.57$; butterflies: $\chi^2/\text{residual d.f.} = 0.49$; tachinids: $\chi^2/\text{residual d.f.} = 0.70$).

We used an information-theoretic model selection procedure to evaluate alternative competing models (Burnham & Anderson 2002). We compared the fit of all possible candidate models obtained by the combination of the predictors using second-order Akaike's information criterion (AICc). The best fitting model is the one with the lowest AICc. In a set of n models, each model i can be ranked using its difference in AICc score with the best-fitting model ($\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\text{minimum}}$). The difference in AICc values indicates the relative support for the different models. We identified the best subset of candidate models as those with a $\Delta\text{AICc} < 2$. We also derived the model weight (w_i) as the weight of evidence in favour of each model being the best within the set. To measure the relative importance of each predictor, we summed the w_i across the models in the set ($\sum w_i$) in which the predictor occurred. Individual predictor variables that had an Akaike weight > 0.80 were considered as most important predictors. Tukey contrasts were calculated from the best plausible models to test for differences between field boundary types. All statistical analyses were performed in R version 3.0.2 (R Development Core Team 2013). GLMMs were implemented using the 'lme4' package (Bates et al. 2014), model comparison using the 'MuMIn' package (Barton 2013), and Tukey contrasts using the 'glht' function in the 'multcomp' package (Hothorn et al. 2008).

Results

During the surveys, 177 plant, 42 butterfly, and 89 tachinid species were recorded in the 90 field boundaries. Overall, 1522 butterfly and 832 tachinid individuals were sampled. The average species richness per field boundary was 14.6 (range between 7 and 25) for plants, 7.5 (range between 3 and 17) for butterflies, and 5.1 (range between 0 and 12) for tachinid flies.

Table 2. Plausible candidate models ($\Delta\text{AICc} < 2$) explaining (a) plant, (b) butterfly, and (c) tachinid species richness. Models (columns) are ranked from left to right according to their ΔAICc . Variables (rows) are ranked according to their Σw_i . Standardized parameter estimates, number of parameters (k), R^2 (based on the likelihood-ratio test), adjusted R^2 (based on the Nagelkerke's modified statistic) and model weights (w_i) are reported. Individual predictor variables that had a sum of Akaike weights > 0.80 were considered as the most important predictors. Models were generalized linear mixed models (GLMMs).

	Σw_i	1 st mod.	2 nd	3 rd	4 th	5 th	6 th	7 th	8 th
(a) Plant species									
$k^{(1)}$	-	7	6	7	7	8	8		
R^2	-	0.29	0.26	0.28	0.27	0.29	0.29		
adj R^2	-	0.29	0.26	0.28	0.28	0.29	0.29		
ΔAICc	-	0.00	0.57	1.30	1.41	1.48	1.57		
Model w_i	-	0.27	0.20	0.14	0.13	0.13	0.12		
Intercept	-	2.61	2.61	2.61	2.61	2.61	2.61		
Margin width	0.98	0.21	0.20	0.20	0.18	0.20	0.21		
Field boundary	0.92	+	+	+	+	+	+		
Hedgerow 0.5 km	0.51	-0.12				-0.11	0.10		
Forest 0.5 km	0.35				0.08	0.06			
Semi-natural 10 km	0.34			0.10			0.07		
(b) Butterfly species									
$k^{(1)}$	-	8	9	9	10	9	9	10	10
R^2	-	0.46	0.47	0.47	0.48	0.46	0.46	0.48	0.48
adj R^2	-	0.46	0.47	0.47	0.48	0.47	0.47	0.48	0.48
ΔAICc	-	0.00	0.82	1.04	1.15	1.39	1.58	1.94	1.98
Model w_i	-	0.22	0.15	0.13	0.12	0.11	0.10	0.08	0.08
Intercept	-	2.25	2.25	2.23	2.20	2.23	2.25	2.23	2.18

Table 2. continued

Field boundary	1.00	+	+	+	+	+	+	+	+
Forest 0.5 km	0.89	0.21	0.28	0.19	0.17	0.21	0.22	0.25	0.18
Semi-natural 10 km	0.84	0.21	0.22	0.22	0.20	0.19	0.19	0.23	0.17
Plant richness	0.70	0.21	0.20	0.18	0.17	0.22	0.20	0.16	
Margin width	0.59			0.11	0.16			0.10	0.23
Number of cuts	0.47					-0.15	-0.10		-0.16
Hedgerow 0.5 km	0.39							-0.08	-0.13
Grassland 0.5 km	0.35		-0.11						-0.11
(c) Tachinid species									
$k^{(1)}$	-	7	6	8	8				
R^2	-	0.21	0.17	0.21	0.21				
adj R^2	-	0.21	0.17	0.21	0.21				
ΔAICc	-	0	1.77	1.78	1.83				
Model w_i	-	0.45	0.19	0.18	0.18				
Intercept	-	1.79	1.79	1.79	1.80				
Field boundary	0.93	+	+	+	+				
Forest 0.5 km	0.65	-0.22		-0.24	-0.22				
Hedgerow 0.5 km	0.64	-0.23	-0.22	-0.21	-0.24				
Plant richness	0.30			0.09					
Number of cuts	0.29					0.09			

⁽¹⁾ k is higher than the number of model parameters as AICc requires the estimation of sample σ^2 . In multi-model inference, k is equal to the number of parameters estimated in the model (intercept + slopes) + 1 (for σ^2) (Burnham and Anderson 2002).

+ Indicated that the categorical variable, Field boundary, was included in the model.

In GLMMs, we found no interactions between field boundary type and landscape variables for the three investigated groups. The interactions were then removed from the models ($P > 0.05$) and only the main effects were presented. For plant species richness there was support for six plausible models (i.e. $\Delta\text{AICc} < 2$) including mostly margin width and field boundary type (Table 2). For butterfly species richness, we found eight plausible models which included mostly field boundary type, the proportion of forest within landscape at 0.5 km, and the proportion of semi-natural habitats within landscape at 10 km. Concerning the tachinid species richness, we found four plausible models which included mostly field boundary type. All the three taxonomic groups were affected by field boundary type. Plant species richness was higher in grass margins (Fig. 2a) and responded also to the margin width positively (Fig. 3a). For butterflies and tachinids, complex hedgerows yielded higher species richness (Fig. 2). Specifically, butterfly species richness was significantly higher in complex hedgerows, while there was no difference between grass margins and simple hedgerows (Fig. 2b). Tachinid species richness significantly decreased from the complex hedgerows to grass margins while the two woody hedgerows were similar (Fig. 2c). At the landscape scales (0.5 and 10 km), the effect of proportion of semi-natural habitats had a marginal support for both plant and tachinid species richness, while for butterflies we found a positive effect of the proportion of forest within landscape at 0.5 km (Fig. 3b), and a positive effect of the proportion of semi-natural habitats within landscape at 10 km (Fig. 3c).

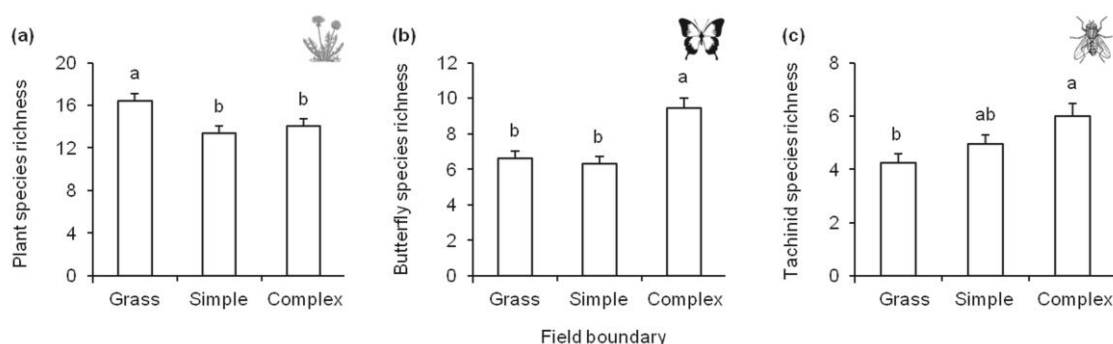


Figure 2. Mean \pm SE of (a) plant, (b) butterfly, and (c) tachinid species richness in relation to field boundary type (grass margin, simple hedgerow, and complex hedgerow). Different letters indicate significant differences according to the Tukey multiple comparison test based on the best plausible model of Table 2.

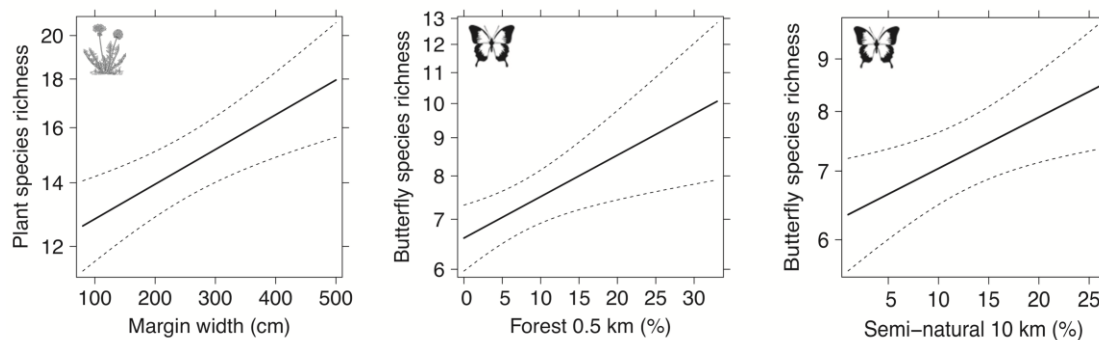


Figure 3. Plots showing the relationships between (a) plant species richness and grass margin width, (b) butterfly species richness and the proportion of forest within landscape at 0.5 km, and (c) butterfly species richness and the proportion of semi-natural habitats within landscape at 10 km. The fitted line and 0.95 confidence intervals is a generalized linear mixed models (GLMMs) estimate calculated from the best plausible model. Plots were performed using the package ‘effects’ in R.

Discussion

In this study, we developed an innovative hierarchical sampling design that allowed us to evaluate the effectiveness of introducing field boundaries of different quality along a gradient of semi-natural habitats in the surrounding area. We found that the introduction of complex field boundaries was a key intervention to support high farmland biodiversity. Contrary to our expectations that the effectiveness of local intervention would be maximal at intermediate levels of landscape complexity (Tschardt et al. 2005), no interactions between local field boundary type and proportion of semi-natural habitats at both 0.5 and 10 km were found. This suggests that the quality of field boundary had the same effect irrespective of the landscape context. This result could be due to the absence of a complete landscape gradient where these interactive effects between landscape and local management factors can be more easily detected. For instance, in our study area there was a lack of ‘cleared’ landscapes (extremely simple and structurally homogeneous), such as large-scale agricultural monocultures, that have been considered in previous studies (Tschardt et al. 2005; Batáry et al. 2011; Concepción et al. 2012a). Hence, according to the ‘intermediate landscape complexity hypothesis’ (Tschardt et al. 2005) the effect found in this study can be located at intermediate levels of landscape complexity where the effectiveness of local management for improving biodiversity, such as the introduction of high-quality boundaries, reaches its maximum (Concepción et al. 2012a).

Our results showed also differences in the effect of landscape context for the three taxonomic groups, highlighting the importance of testing multiple scales when considering species from different taxa and with different mobility (Tscharrntke et al. 2005; Concepción et al. 2012a). For example, plants are all non-mobile organisms, while butterflies and tachinids are capable of foraging across several habitats and over larger spatial scales (e.g., Weibull et al. 2000; Stireman 2008; Flick et al. 2012; Inclán et al. 2014). Specifically, plant and tachinid species richness were only affected by local conditions, while butterflies responded at all spatial scales (local – landscape at 0.5 km – landscape at 10 km).

At the local scale, the contrasting effect of field boundary type on different taxonomic groups could have interesting implications for farmland biodiversity conservation. For plants, grass margins yielded higher species richness compared to woody hedgerows. This was to be expected as grass margins support greater diversity of transient plant species than woody hedgerows (Boutin et al. 2002). Therefore, increasing grass margin width may have benefits for other taxonomic groups providing, for instance, refuge sites for flower-visiting insects (Feber et al. 1996; Pywell et al. 2004; Merckx et al. 2012). Conversely, complex hedgerows yielded higher species richness of butterflies. Complex hedgerows dominated by a variety of shrubs and trees may increase the provision of host plants and nectar resources for adults, and thus contribute to higher diversity. In addition, the greater structural complexity of hedgerows may provide a higher number of refuge sites against predator and unfavorable abiotic conditions such as strong wind. Compared to grass margin, hedgerows can also act as better dispersal corridors (Dover & Sparks 2000; Maudsley 2000). Hedgerows also had positive benefits on tachinid species richness. Hedgerows may provide higher and more stable availability of hosts, nectar and pollen resources for adults and shelter from adverse weather conditions (Landis et al. 2000; Olson & Wäckers 2007; Letourneau et al. 2012).

The different effects of field boundary type on plants and insects could also be due to management intensity of grass buffer strip. Generally, plants tolerate much higher intensities, such as mowing or coppicing (Sitzia et al. 2014), than insects, which showed a weaker disturbance tolerance (Pöyry et al. 2006). Although several studies have recognized hedgerows as important elements to enhance farmland biodiversity (e.g., Burel 1996; Dover & Sparks 2000; Hannon & Sisk 2009; Batáry et al. 2010; Merckx et

al. 2012), they have not controlled for the quality of the hedgerow and the landscape structure.

Consistent with some previous studies, landscape composition at 0.5 km seemed to have only marginal effects on plant species richness (Dauber et al. 2003; Marini et al. 2007), although other studies have found a landscape effect (Gabriel et al. 2006, 2010; Rundlöf et al. 2010; Concepción et al. 2012b). The lack of a landscape effect on plant species richness could be linked to the short dispersal distance of perennial herbaceous plants inhabiting field boundaries (Sitzia 2007), which are mostly limited by the availability of microsites for reproduction rather than by the propagule pressure (Tscharntke et al. 2005). As for plants, tachinids showed marginal effect of landscape at 0.5 km. In this case, the expected large dispersal capacity of dipterans and the generalist parasitism strategy of this group (Stireman & Singer 2003; Inclán et al. 2014) may explain the lack of a landscape effect. For butterflies we found an additive effect of the proportion of forest at 0.5 km landscape scale on species richness. The same pattern has been reported in other studies (e.g., Pywell et al. 2004; Kivinen et al. 2007; Marini et al. 2009). Forest habitat seems to play a key role in maintaining butterfly diversity in agricultural landscapes dominated by arable land, as it may provide alternative food sources and host plants, and stable microhabitats for overwintering (Dover et al. 1997; Pywell et al. 2004).

Although the presence of complex hedgerows was associated with higher butterfly diversity at the local scale, overall hedgerow cover at the landscape scale had no effect. This result highlights the key importance to butterfly diversity of habitat quality rather than habitat cover since our landscape measure of hedgerow cover did not take into account the quality of the hedgerow margin. Indeed, the presence of high-quality field boundary (complex hedgerows) at the local scale and forest cover at 0.5 km landscape scale were the key determinants of butterfly species richness. Since single-storied hedgerows are the most common woody hedges in the study region (Sitzia et al. 2013), the absence of hedgerow cover effect may further suggest the importance of habitat quality. The complex hedgerow may therefore be considered a surrogate of native woodland in intensive agricultural landscapes (Hannon & Sisk 2009).

At the largest spatial scale (10 km), only butterfly species richness was affected by the cover of semi-natural habitats. This is in accordance with the 'regional species pool

hypothesis' (Zobel 1997). At broader spatial scale, complex landscapes sustain a larger species pool than simple landscapes that may permit greater opportunity for recurrent spillover among habitats and therefore may benefit local species richness (Ekroos & Kuussaari 2012; Tschardtke et al. 2012). Although species with different mobility may interact with the environment at different spatial scales (Concepción et al. 2012a), only a few studies have attempted to disentangle broader landscape scale effects on butterflies from factors acting on smaller scales (see Weibull et al. 2000; Casner et al. 2014). Previous studies have focused mainly on smaller scales (< 3 km), ignoring that semi-natural habitats at larger spatial scale could also influence butterfly species richness, although in a recent study Casner et al. (2014) found a large-scale effect of farmland cover on butterfly species richness in California. Our results confirm the likelihood of butterflies to respond at multiple scales (from field boundary to landscape at 10 km). One reason for such an effect may be that butterflies require multiple resources (e.g., host plants for larvae and nectar plants for adults) that are separated spatially (Thomas et al. 2001; Krauss et al. 2005; Flick et al. 2012), especially in agricultural landscapes. Moreover, local species richness may at least partly be dependent on dispersal from surrounding semi-natural habitats (Öckinger & Smith 2006).

Conclusions

The quality of semi-natural habitats at the local scale had an effect on farmland biodiversity. This result has important implications for the design of effective AESs. Hedgerows resulted in higher species richness of both butterflies and parasitoid flies, with butterflies showing a significantly higher species richness in complex hedgerows. Extended-width grass margins had higher plant species richness. Measures focusing not only on the creation and management of field boundaries but also on their quality (i.e., complex hedgerows rather than single-storied hedgerows) would be more effective for conserving farmland biodiversity. At the same time, the management of grass buffer strip (i.e., extended-width grass margins rather than standard margins) could also be important for farmland biodiversity, especially for plants. Although several studies indicate that AESs should preferentially be applied in landscapes with intermediate complexity (Tschardtke et al. 2005; Rundlöf & Smith 2006; Batáry et al. 2011; Concepción et al. 2012a), our results suggest that their overall benefits are not dependent on the landscape

context. Our results also demonstrated that complex agricultural landscapes have much larger species pools of mobile taxa, such as butterflies. The AESs should therefore promote measures aimed at the conservation of semi-natural habitats at large spatial scales (Kleijn et al. 2009; Gabriel et al. 2010; Concepción et al. 2012a; Gonthier et al. 2014). Specifically, the AESs should pay particular attention to the conservation of forest patches in the landscape that are likely to play a key role in maintaining butterfly diversity. In conclusion, the approach utilized in this study could be adopted in future research in order to clearly disentangle the scale effect of farming management on biodiversity patterns.

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Supplementary Material



Figure S1. Example of landscape pair of one a) simple and b) complex landscape (radius 1 km) within each cell. The field boundary triplets for each landscape are pictured: i) grass margin in yellow, ii) simple hedgerow in blue, and iii) complex hedgerow in red. Satellite images from Google Earth.

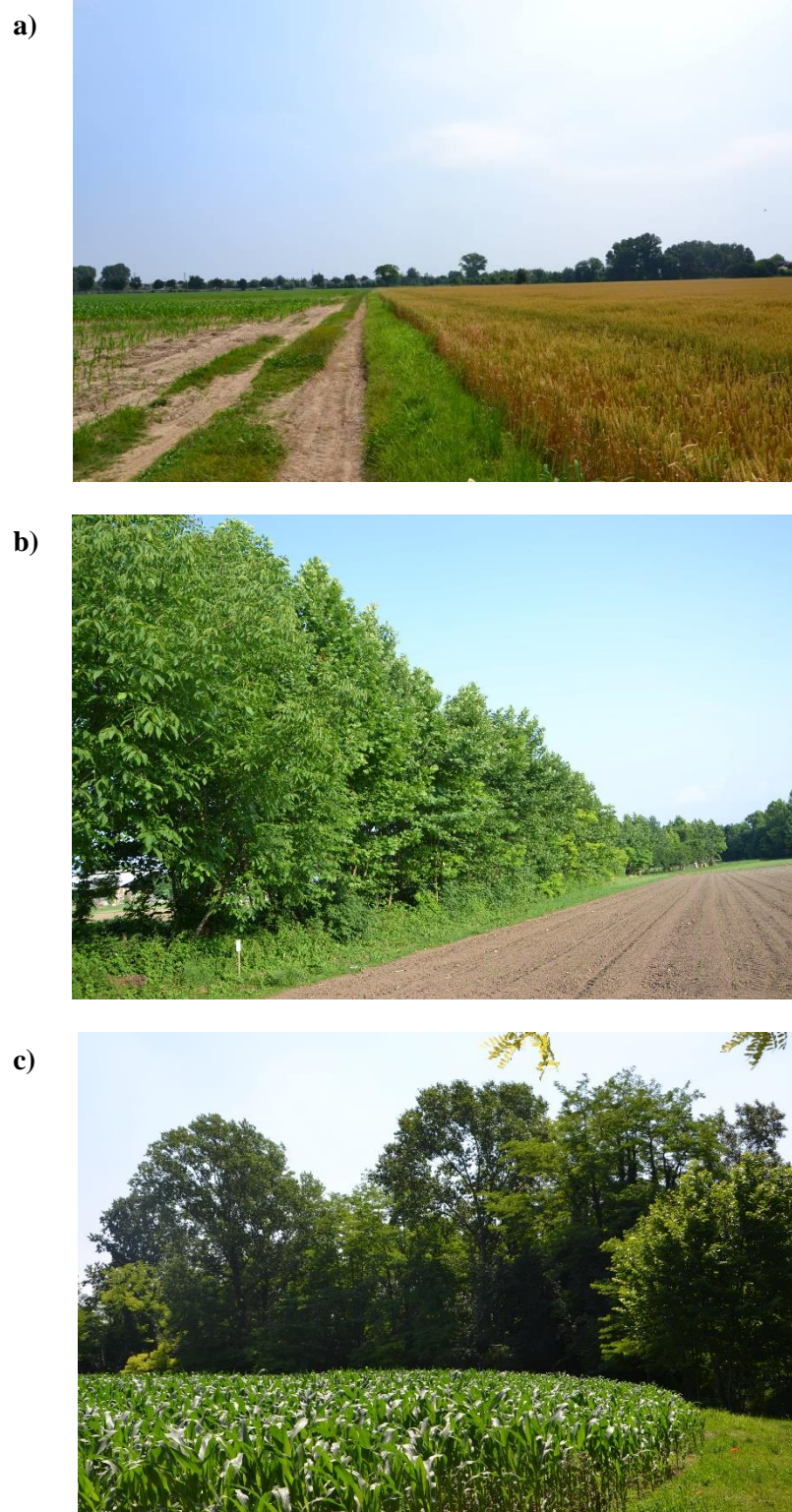


Figure S2. Examples of a a) grass margin, b) simple hedgerow, and c) complex hedgerow. Photo credit: Dainese M.

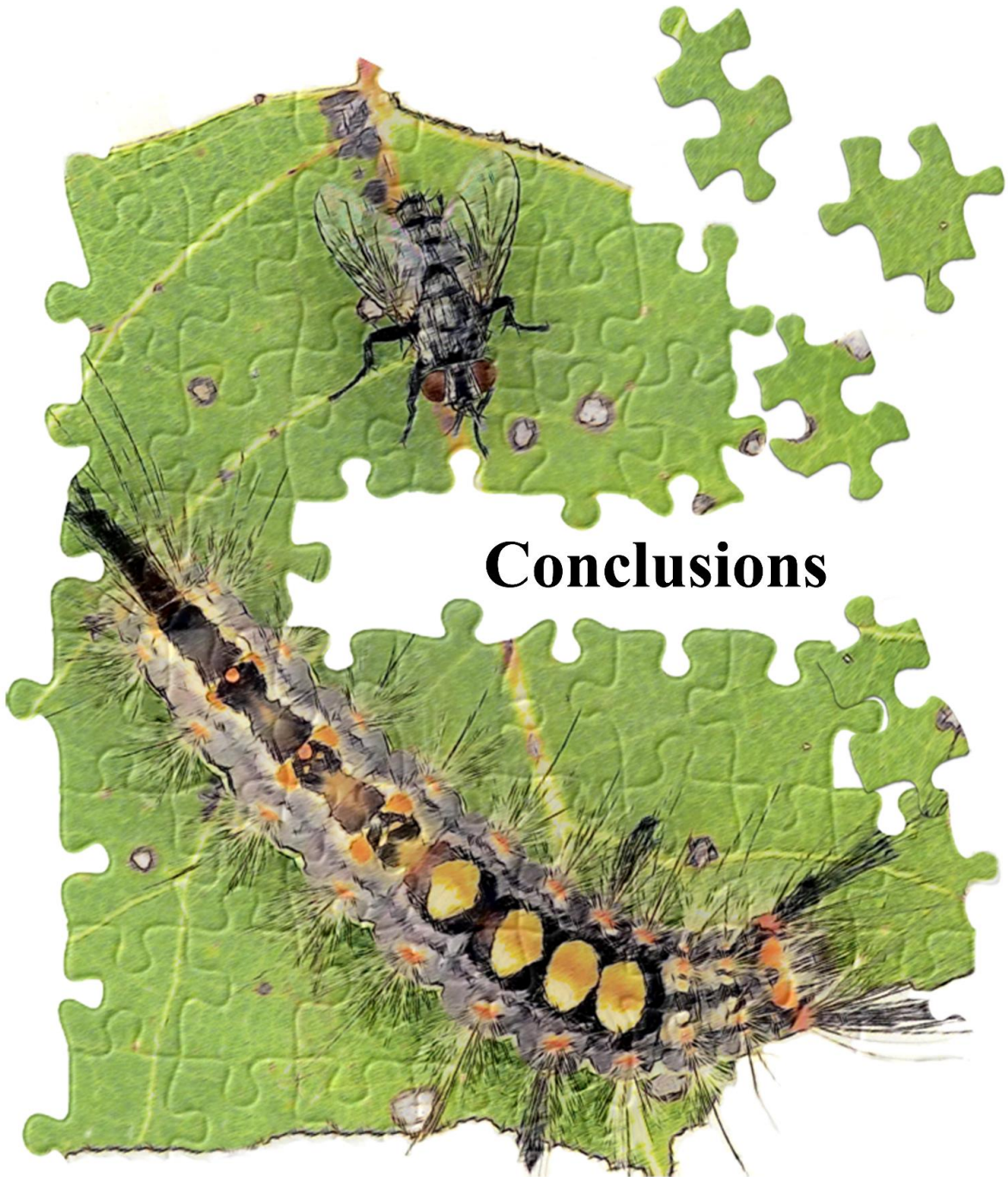
Table S1. Mean values \pm standard deviation and results of the analysis of variance (ANOVA) testing differences in landscape and local conditions between the three classes of field boundary.

	Grass margin (<i>n</i> = 30)	Simple hedgerow (<i>n</i> = 30)	Complex hedgerow (<i>n</i> = 30)	<i>F</i>	<i>P</i>
Hedgerow 0.5 km (%)	5.2 \pm 2.1	5.1 \pm 2.0	5.7 \pm 2.8	0.55	0.577
Forest 0.5 km (%)	6.9 \pm 8.3	6.1 \pm 9.3	6.2 \pm 7.6	0.09	0.912
Grassland 0.5 km (%)	5.6 \pm 7.2	4.3 \pm 6.1	5.9 \pm 7.8	0.45	0.639
Margin width (cm)	230.2 \pm 127.8	213.0 \pm 118.5	270.1 \pm 127.7	1.65	0.198
Number of cuts	2.2 \pm 1.1	1.1 \pm 1.3	1.0 \pm 1.1	10.55	< 0.001

Table S2. Pearson correlations between explanatory variables.

	Semi-natural (10 km)	Hedgerow (0.5 km)	Forest (0.5 km)	Grassland (0.5 km)	Width	Plant richness
Hedgerow (0.5 km)	-0.289**					
Forest (0.5 km)	0.247*	-0.022 ^{ns}				
Grassland (0.5 km)	0.146 ^{ns}	0.283**	0.493***			
Width	0.025 ^{ns}	0.180 ^{ns}	0.260*	0.143 ^{ns}		
Plant richness	0.194 ^{ns}	-0.172 ^{ns}	0.197 ^{ns}	0.047 ^{ns}	0.331**	
Cut	-0.208*	0.105 ^{ns}	-0.033 ^{ns}	-0.006 ^{ns}	0.252*	0.189 ^{ns}

^{ns} not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$



Conclusions

The research presented in this dissertation makes a significant contribution to the understanding of the landscape dynamics of tachinid parasitoids. In general, ecological research on tachinids has been restricted to a few studies and our knowledge on the consequences of habitat fragmentation and intensification of agricultural landscapes on the diversity of this group is very limited. This work demonstrates how the diversity of tachinid parasitoids is affected by diverse factors such as the habitat loss and fragmentation of semi-natural habitats (Chapter II), the agricultural management at the local and landscape scales (Chapter III), the proportion and type of semi-natural habitats in the landscape (Chapter IV), and by local interventions such as the management and implementation of field margins (Chapter V & VI). This study highlights the important role of habitat conservation to maintain and enhance the diversity of tachinid parasitoids.

This study demonstrates the negative impact of habitat fragmentation on tachinid parasitoids. The results from Chapter II show that the strength of this effect depends on the degree of habitat connectivity as the processes of habitat loss and loss of connectivity significantly interact. This suggests that management practices aimed to mitigate the negative effect of habitat loss at the local scale need to consider the surrounding landscape. Specifically, the conservation of habitat connectivity needs to be particularly considered in landscapes with small remnant habitats. In addition, Chapter IV demonstrates that the community of tachinids was affected not only by the proportion of semi-natural habitats in the landscape, but also by the specific type of semi-natural habitats. Therefore, strategies to conserve semi-natural habitats in agricultural landscapes needs to take into account the area, connectivity and type of habitats.

While it is clear that the fragmentation of semi-natural habitats affected the diversity of tachinid parasitoids (Chapter II & IV), my research also shows the significance of considering the effects of the agricultural matrix. In Chapter III the effect of contrasting farming systems indicates that parasitoids were affected by agricultural management at different spatial scales. Thus, any attempt to enhance parasitoid diversity in agricultural landscapes needs to consider the local management in relation to habitat type, location within the field and agricultural management in the surrounding landscape. In particular, this study demonstrates that organic management in arable fields clearly enhanced tachinid diversity, while the management of organic grasslands needs to be reconsidered. To increase the biodiversity of grasslands, organic management should aim to enhance habitat heterogeneity and to reduce practices like mowing frequency and

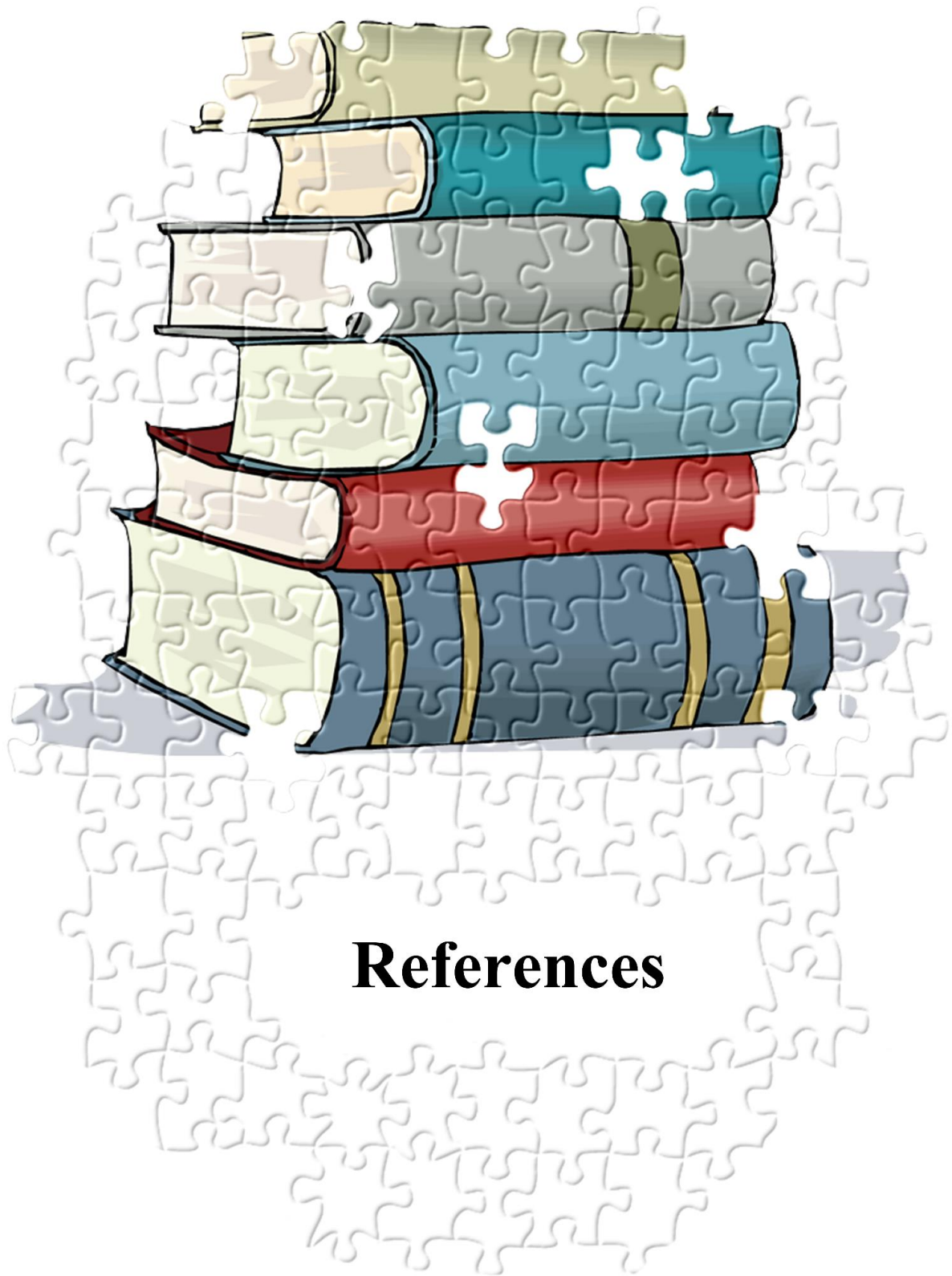
grazing intensity. As organic management had a positive effect also at the landscape scale, the promotion of organic agriculture as an alternative to enhance farmland biodiversity should aim to increase both the total extent of organic farming and the connectivity of individual organic farms.

The recognition of the farmed-matrix as an important component of agricultural landscapes highlights the need of alternative measures that consider the matrix to enhance the overall diversity of these landscapes. For example, the conservation and implementation of semi-natural elements such as field margins and hedgerows have been proposed as a feasible alternative to work within farms. This research demonstrated the positive effect of field margins to enhance the diversity of different taxa (Chapters V & VI). In addition, the quality of field margins should be also considered (e.g., hedgerows vs. grass margins, simple vs. complex hedgerows) as this could be more effective for conserving farmland biodiversity.

The implementation of measures to enhance local farmland diversity should focus not only on the local diversity, but also on how these measures affect the movement of species into the crop fields. To enhance the spillover of species into the crop, the results from Chapter V show that the local contrast between the field margin and the crop in relation to the dispersal behavior of the focal taxa should be considered. Given that the spillover of tachinid parasitoids was favored by the low contrast between grass margins and maize fields, it appears that grass margins could facilitate higher spillover of species in landscapes with annual crops. In contrast, hedgerows may enhance higher spillover of species in landscapes dominated by perennial crops.

The diverse interactions found in this study between crop and non-crop habitats (e.g., Chapters IV, V & VI) emphasize the importance to consider these interactions to enhance biodiversity in agricultural landscapes. The conservation of natural and semi-natural habitats cannot be sustained if these habitats are perceived as incompatible systems with the agricultural matrix. The planning and design of alternative measures to conserve biodiversity in fragmented landscapes need to take in account the ecological dynamics of both the crop and non-crop habitats. In this way, practices implemented for the conservation of biodiversity could also benefit with the provision of ecosystem services to the agricultural matrix.

This research provides new insights into the consequences of landscape changes on the diversity of a key functional group that has been long overlooked in ecological and conservation studies. The results found in this dissertation on tachinid parasitoids could be extended to other groups of insect parasitoids. Consequently, this study provides relevant information to land managers in fragmented agricultural landscapes. However, to fully understand how fragmentation and intensification of agricultural systems affects the complex multi-trophic interactions of parasitoids, further research is still needed to understand the dynamics and consequences of the loss of parasitoid diversity on ecosystem functioning.



References

A

- Al-Dobai, S., Reitz, S. & Sivinski, J. (2012). Tachinidae (Diptera) associated with flowering plants: Estimating floral attractiveness. *Biological Control*, *61*, 230–239.
- Alexandratos, N. & Bruinsma, J. (2012). *World agriculture towards 2030/2050: the 2012 revision*. ESA Working paper No. 12–03. FAO, Rome, IT.
- Alhmedi, A., Haubruge, E. & Francis, F. (2008). Role of prey-host plant associations on *Harmonia axyridis* and *Episyrphus balteatus* reproduction and predatory efficiency. *Entomologia Experimentalis et Applicata*, *128*, 49–56.
- Almohamad, R., Verheggen, F. & Haubruge, É. (2009). Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. *Biotechnology, Agronomy, Society and Environment*, *13*, 467–481.
- Andrén, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, *71*, 355–366.
- Arnaud, P. H. Jr. (1978). *A Host-Parasite Catalog of North American Tachinidae (Diptera)*. USDA Misc. Publ. 1319. 860 pp.
- Askew, R. R. & Shaw, M. R. (1986). Parasitoid communities: their size, structure and development. In: Waage, J. & Greathead, D. (eds) *Insect parasitoids*. Academic Press, London, pp. 237–264.

B

- Bacaro, G., Gioria, M. & Ricotta, C. (2013). Beta diversity reconsidered. *Ecological Research*, *28*, 537–540.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*, 51–57.
- Barton, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. <http://CRAN.R-project.org/package=MumIn>
- Bartsch, H. (2009). *Diptera: Syrphidae: Syrphinae*. ArtDatabanken, Sweden. 406 pp.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143.
- Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society of London Series B - Biological Sciences*, *278*, 1894–902.
- Batáry, P., Holzschuh, A., Orsi, K. M., Samu, F. & Tscharntke, T. (2012). Responses of plant, insect and spider biodiversity to local and landscape scale management

- intensity in cereal crops and grasslands. *Agriculture, Ecosystems and Environment*, *146*, 130–136.
- Batáry, P., Matthiesen, T. & Tscharrntke, T. (2010). Landscape-moderated importance of hedges in conserving farmland bird diversity of organic vs. conventional croplands and grasslands. *Biological Conservation*, *143*, 2020–2027.
- Batchelor, T. P., Hardy, I. C., Barrera, J. F. & Pérez-Lachaud, G. (2005). Insect gladiators II: Competitive interactions within and between bethylid parasitoid species of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control*, *33*, 194–202.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0–6. <http://CRAN.R-project.org/package=lme4>
- Baudry, J., Burel, F., Aviron, S., Martin, M., Ouin, A., Pain, G. & Thenail, C. (2003). Temporal variability of connectivity in agricultural landscapes: do farming activities help? *Landscape Ecology*, *18*, 303–314.
- Belshaw, R. (1993). *Tachinid flies. Diptera: Tachinidae. Handbooks for the identification of British Insects 10*, Part 4a (i). Royal Entomological Society of London, London.
- Bengtsson, J., Ahnström, J. & Weibull, A. C. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, *42*, 261–269.
- Benjamin, F. E., Reilly, J. R. & Winfree, R. (2014). Pollinator body size mediates the scale at which land use drives crop pollination services. *Journal of Applied Ecology*, *51*, 440–449.
- Bennett, A. B. & Gratton, C. (2013). Floral diversity increases beneficial arthropod richness and decreases variability in arthropod community composition. *Ecological Applications*, *23*, 86–95.
- Benton, T. G., Vickery, J. A. & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, *18*, 182–188.
- Bianchi, F. J. J. A., Booij, C. J. H. & Tscharrntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B*, *273*, 1715–1727.
- Blackshaw, R. P. & Coll, C. (1999). Economically important leatherjackets of grassland and cereals: biology, impact and control. *Integrated Pest Management Reviews*, *4*, 145–162.
- Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A. & Tscharrntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems and Environment*, *146*, 34–43.
- Boatman, N. D., Parry, H. R., Bishop, J. D. & Cuthbertson, A. G. (2007). Impacts of agricultural change on farmland biodiversity in the UK. In: Hester, R. E. & Harrison, R. M. (eds) *Biodiversity under threat*. RSC Publishing, Cambridge, UK, pp. 1–32.

- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. (2008). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*, 127–135.
- Bommarco, R., Kleijn, D. & Potts, S. G. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology and Evolution*, *28*, 230–238.
- Borcard, D. & Legendre, P. (2012). Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. *Ecology*, *93*, 1473–1481.
- Boutin, C., Jobin, B., Bélanger, L. & Choinière, L. (2002). Plant diversity in three types of hedgerows adjacent to crop fields. *Biodiversity and Conservation*, *11*, 1–25.
- Brown, B. V. (2001). Flies, gnats, and mosquitoes. In: Levin, S. A. (ed), *Encyclopedia of Biodiversity*, Vol. 2. Academic Press, London, pp. 815–826.
- Burel, F. (1996). Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences*, *15*, 169–190.
- Burgio, G. & Sommaggio, D. (2007). Syrphids as landscape indicators in Italian agroecosystems. *Agriculture, Ecosystems and Environment*, *120*, 416–422.
- Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd ed. Springer, New York, USA.
- C**
- Cagnolo, L., Valladares, G. R., Salvo, A., Cabido, M. & Zak, M. (2009). Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Conservation Biology*, *23*, 1167–1175.
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67.
- Carvalho, J. C., Cardoso, P., Borges, P. A., Schmera, D. & Podani, J. (2013). Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos*, *122*, 825–834.
- Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D. & Nowakowski, M. (2007). Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, *44*, 29–40.
- Casner, K. L., Forister, M. L., O'Brien, J. M., Thorne, J., Waetjen, D. & Shapiro, A. M. (2014). Contribution of urban expansion and a changing climate to decline of a butterfly fauna. *Conservation Biology*, *28*, 773–82.
- Cerretti, P. (2010). *I tachinidi della fauna italiana (Diptera Tachinidae), con chiave interattiva dei generi uest paleartici*, Vol. I & II + CD-rom (in Italian with English interactive key). Cierre Edizioni, Verona, IT.

- Cerretti, P., O'Hara, J. E., Wood, D. M., Shima, H., Inclán, D. J. & Stireman, J. O. III (2014). Signal through the noise? Phylogeny of the Tachinidae (Diptera) as inferred from morphological evidence. *Systematic Entomology*, *39*, 335–353.
- Cerretti, P. & Tschorsnig, H.-P. (2010). Annotated host catalogue for the Tachinidae (Diptera) of Italy. *Stuttgarter Beiträge zur Naturkunde, A, Neue Serie*, *3*, 305–340.
- Cerretti, P., Tschorsnig, H.-P., Lopresti, M. & Di Giovanni, F. (2012). MOSCHweb - A matrix-based interactive key to the genera of the Palearctic Tachinidae (Insecta, Diptera). *Zookeys*, *205*, 5–18.
- Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I., Kleijn, D. & Tschardt, T. (2007). Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. *Journal of Applied Ecology*, *44*, 804–812.
- Colwell, R. K. (2013). EstimateS: statistical estimation of species richness and shared species from samples. Version 9. Available from: <http://purl.oclc.org/estimates> (accessed November 2012).
- Concepción, E. D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E. J. P., Tschardt, T. & Verhulst, J. (2012a). Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, *49*, 695–705.
- Concepción, E. D., Fernández-González, F. & Díaz, M. (2012b). Plant diversity partitioning in Mediterranean croplands: effects of farming intensity, field edge and landscape context. *Ecological Applications*, *22*, 1005–1014.
- Coudrain, V., Herzog, F. & Entling, M. H. (2013). Effects of habitat fragmentation on abundance, larval food and parasitism of a spider-hunting wasp. *PLoS ONE*, *8*, e59286.
- Cronin, J. T. (2007). From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology*, *88*, 2966–2976.
- Cronin, J. T. & Reeve, J. D. (2005). Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 2225–2235.
- Crowder, D. W., Northfield, T. D., Strand, M. R. & Snyder, W. E. (2010). Organic agriculture promotes evenness and natural pest control. *Nature*, *466*, 109–112.
- D**
- Dainese, M., Inclán, D. J., Sitzia, T. & Marini, L. (2015). Testing scale-dependent effects of semi-natural habitats on farmland biodiversity. *Ecological Applications* (in press).
- Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A. & Wolters V. (2003). Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment*, *98*, 321–329.

- Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R. & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Frontiers in Ecology and the Environment*, *12*, 212–217.
- Díaz, S., Fargione, J., Chapin, F. S. III & Tilman, D. (2006). Biodiversity Loss Threatens Human Well-Being. *PLoS Biology*, *4*, e277.
- Dodson, C. H. (1962). The importance of pollination in the evolution of the orchids of tropical America. *American Orchid Society Bulletin*, *31*, 525–735.
- Donald, R. F., Green, R. E. & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*, 25–29.
- Dover, J. W. & Sparks T. H. (2000). A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, *60*, 51–63.
- Dover, J. W., Sparks, T. H. & Greatorex-Davies, J. (1997). The importance of shelter for butterflies in open landscapes. *Journal of Insect Conservation*, *1*, 89–97.
- Duelli, P. & Obrist, M. K. (2003). Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology*, *4*, 129–138.
- Dunning, J. B., Danielson, B. J. & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, *65*, 169–175.

E

- Eggleton, P. & Belshaw, R. (1993). Comparisons of dipteran, hymenopteran and coleopteran parasitoids: provisional phylogenetic explanations. *Biological Journal of the Linnean Society*, *48*, 213–26.
- Eggleton, P. & Gaston, K. J. (1992). Tachinid host ranges: a reappraisal (Diptera: Tachinidae). *Entomologist's Gazette*, *43*, 139–43.
- Ekroos, J., Rundlöf, M. & Smith, H. G. (2013). Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. *Landscape Ecology*, *28*, 1–10.
- Ekroos, J. & Kuussaari M. (2012). Landscape context affects the relationship between local and landscape species richness of butterflies in semi-natural habitats. *Ecography*, *35*, 232–238.
- Elsen van, T. (2000). Species diversity as a task for organic agriculture in Europe. *Agriculture, Ecosystems and Environment*, *77*, 101–109.
- Elzinga, J. A., van Nouhuys, S., van Leeuwen, D. J. & Biere, A. (2007). Distribution and colonization ability of three parasitoids and their herbivorous host in a fragmented landscape. *Basic and Applied Ecology*, *8*, 75–88.

- Ewers, R. M. & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, *81*, 117–142.
- Eyre, M. D. & Leifert, C. (2011). Crop and field boundary influences on the activity of a wide range of beneficial invertebrate groups on a split conventional/organic farm in northern England. *Bulletin of Entomological Research*, *101*, 135–144.
- Eyre, M. D., Luff, M. L. & Leifert, C. (2013). Crop, field boundary, productivity and disturbance influences on ground beetles (Coleoptera, Carabidae) in the agroecosystem. *Agriculture, Ecosystems and Environment*, *165*, 60–67.

F

- FAOSTAT (2014). FAO statistics division. Available from: <http://faostat3.fao.org> (accessed on 09 December 2014).
- Feber, R. E., Smith, H. & Macdonald, D. W. (1996). The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, *33*, 1191–1205.
- Fenoglio, M. S., Salvo, A., Videla, M. & Valladares, G. R. (2010). Plant patch structure modifies parasitoid assemblage richness of a specialist herbivore. *Ecological Entomology*, *35*, 594–601.
- Fenoglio, M. S., Srivastava, D., Valladares, G., Cagnolo, L. & Salvo, A. (2012). Forest fragmentation reduces parasitism via species loss at multiple trophic levels. *Ecology*, *93*, 2407–2420.
- Ferraz, G., Russell, G. J., Stouffer, P. C., Bierregaard, R. O., Pimm, S. L. & Lovejoy, T. E. (2003). Rates of species loss from Amazonian forest fragments. *Proceedings of the National Academy of Sciences*, *100*, 14069–14073.
- Finke, D. L. & Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature*, *429*, 407–410.
- Fischer, J. & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, *16*, 265–280.
- Flick, T., Feagan, S. & Fahrig, L. (2012). Effects of landscape structure on butterfly species richness and abundance in agricultural landscapes in eastern Ontario, Canada. *Agriculture, Ecosystems and Environment*, *156*, 123–133.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005). Global consequences of land use. *Science*, *309*, 570–574.
- Forman, R. T. T. & Baudry, J. (1984). Hedgerows and hedgerow networks in landscape ecology. *Environmental Management*, *8*, 495–510.
- Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. & Sibert, J. (2012). AD Model Builder: using automatic

differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27, 233–249.

Frost, C. M., Didham, R. K., Rand, T. A., Peralta, G. & Tylianakis, J. M. (in press). Community-level net spillover of natural enemies from managed to natural forest. *Ecology*.

Fuller, R. J., Norton, L. R., Feber, R. E., Johnson, P. J., Chamberlain, D. E., Joys, A. C., Mathews, F., Stuart, R. C., Townsend, M. C., Manley, W. J., Wolfe, M. S., Macdonald, D. W. & Firbank, L. G. (2005). Benefits of organic farming to biodiversity vary among taxa. *Biology Letters*, 1, 431–434.

G

Gabriel, D., Carver, S. J., Durham, H., Kunin, W. E., Palmer, R. C., Sait, S. M., Stagl, S. & Benton, T. G. (2009). The spatial aggregation of organic farming in England and its underlying environmental correlates. *Journal of Applied Ecology*, 46, 323–333.

Gabriel, D., Roschewitz, I., Tschardtke, T. & Thies, C. (2006). Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. *Ecological Applications*, 16, 2011–2021.

Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E. & Benton, T. G. (2010). Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, 13, 858–869.

Gagic, V., Hänke, S., Thies, C. & Tschardtke, T. (2014). Community variability in aphid parasitoids versus predators in response to agricultural intensification. *Insect Conservation and Diversity*, 7, 103–112.

Gaujour, E., Amiaud, B., Mignolet, C. & Plantureux, S. (2012). Factors and processes affecting plant biodiversity in permanent grasslands. A review. *Agronomy for Sustainable Development*, 32, 133–160.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W. W., Emmerson, M., Morales, M. B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L. W., Dennis, C., Palmer, C., Oñate, J. J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P. W. & Inchausti, P. (2010). Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology*, 11, 97–105.

Geiger, F., Wäckers, F. L. & Bianchi, F. J. J. A. (2008). Hibernation of predatory arthropods in semi-natural habitats. *Biocontrol*, 54, 529–535.

Géneau, C. E., Wäckers, F. L., Luka, H., Daniel, C. & Balmer, O. (2012). Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic and Applied Ecology*, 13, 85–93.

Godfray, H. C. J. (1994). *Parasitoids: behavioral and evolutionary ecology*. Princeton University Press, Princeton.

- Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M. & Toulmin, C. (2010). Food security: the challenge of feeding 9 billion people. *Science*, *327*, 812–818.
- Gonthier, D. J., Ennis, K. K., Farinas, S., Hsieh, H.-Y., Iverson, A. L., Batáry, P., Rudolphi, J., Tschardtke, T., Cardinale, B. J. & Perfecto, I. (2014). Biodiversity conservation in agriculture requires a multi-scale approach. *Proceedings of the Royal Society of London Series B - Biological Sciences*, *281*, 20141358.
- Green, R. E., Cornell, S. J., Scharlemann, J. P. W. & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, *307*, 550–555.
- Grenier, S. (1988). Applied biological control with tachinid flies (Diptera, Tachinidae): a review. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, *61*, 49–56.
- ## H
- Haaland, C., Naisbit, R. E. & Bersier, L. F. (2011). Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, *4*, 60–80.
- Haenke, S., Kovács-Hostyánszki, A., Fründ, J., Batáry, P., Jauker, B., Tschardtke, T. & Holzschuh, A. (2014). Landscape configuration of crops and hedgerows drives local syrphid fly abundance. *Journal of Applied Ecology*, *51*, 505–513.
- Hance, T. (1997). Do aphids survive over summer in maize crops in Belgium? A test of the “aphid reservoir” hypothesis. *Biological Agriculture & Horticulture*, *15*, 191–201.
- Hannon, L. E. & Sisk, T. D. (2009). Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation*, *142*, 2140–2154.
- Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press, New York.
- Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio*, *40*, 248–255.
- Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology*, *16*, 666–673.
- Haraldseide, H. & Tschorsnig, H. P. (2014). On the biology of *Loewia foeda* (Meigen) (Diptera: Tachinidae). *Tachinid Times*, *27*, 15–19.
- Heisswolf, A., Reichmann, S., Poethke, H. J., Schrader, B. & Obermaier, E. (2009). Habitat quality matters for the distribution of an endangered leaf beetle and its egg parasitoid in a fragmented landscape. *Journal of Insect Conservation*, *13*, 165–175.
- Holland, J. M., Winder, L. & Perry, J. N. (2000). The impact of dimethoate on the spatial distribution of beneficial arthropods in winter wheat. *Annals of Applied Biology*, *136*, 93–105.
- Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. (1999). Trophic rank and the species–area relationship. *Ecology*, *80*, 1495–1504.

- Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2008). Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, *117*, 354–361.
- Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, *79*, 491–500.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3–35.
- Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363.
- Humbert, J. Y., Ghazoul, J. & Walter, T. (2009). Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems and Environment*, *130*, 1–8.

I

- Ichiki, R. T., Kainoh, Y., Yamawaki, Y. & Nakamura, S. (2011). The parasitoid fly *Exorista japonica* uses visual and olfactory cues to locate herbivore-infested plants. *Entomologia Experimentalis et Applicata*, *138*, 175–183.
- Inclán, D. J., Cerretti, P. & Marini, L. (2014). Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes. *Landscape Ecology*, *29*, 879–889.
- Inclán, D. J., Cerretti, P., Gabriel, D., Benton, T. G., Sait, S. M., Kunin, W. E., Gillespie, M. A. K. & Marini, L. (accepted for publication). Organic farming enhances parasitoid diversity at the local and landscape scale. *Journal of Applied Ecology*.

J

- Jauker, F. & Wolters, V. (2008). Hoverflies are efficient pollinators of oilseed rape. *Oecologia*, *156*, 819–823.
- Johnson, M. T. J., Lajeunesse, M. J. & Agrawal, A. A. (2006). Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters*, *9*, 24–34.
- Johnson, P. C. D. (2014). Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution*, *5*, 944–946.
- Jonsson, M., Buckley, H. L., Case, B. S., Wratten, S. D., Hale, R. J. & Didham, R. K. (2012). Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. *Journal of Applied Ecology*, *49*, 706–714.

K

- Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R. & Daily, G. C. (2012). Intensive agriculture erodes β -diversity at large scales. *Ecology Letters*, *15*, 963–970.
- Kindt, R. & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi
- Kivinen, S., Luoto, M., Kuussaari, M. & Saarinen, K. (2007). Effects of land cover and climate on species richness of butterflies in boreal agricultural landscapes. *Agriculture, Ecosystems and Environment*, *122*, 453–460.
- Klapwijk, M. J. & Lewis, O. T. (2012). Host–parasitoid dynamics in a fragmented landscape: Holly trees, holly leaf miners and their parasitoids. *Basic and Applied Ecology*, *13*, 94–105.
- Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E. J. P., Steffan-Dewenter, I., Tschardtke, T., Verhulst, J., West, T. M. & Yela, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, *9*, 243–54.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E. J. P., Tschardtke, T. & Verhulst, J. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society of London Series B - Biological Sciences*, *276*, 903–9.
- Kleijn, D., Rundlof, M., Scheper, J., Smith, H. G. & Tschardtke, T. (2011). Does conservation on farmland contribute to halt biodiversity decline? *Trends in Ecology and Evolution*, *26*, 474–481.
- Kleijn, D. & Sutherland, W. J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, *40*, 947–969.
- Klein, A., Steffan-Dewenter, I. & Tschardtke, T. (2003). Fruit set of highland coffee depends on the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B - Biological Sciences*, *270*, 955–961.
- Krauss, J., Steffan-Dewenter, I., Müller, C. B. & Tschardtke, T. (2005). Relative importance of resource quantity, isolation and habitat quality for landscape distribution of a monophagous butterfly. *Ecography*, *28*, 465–474.
- Kruess, A. (2003). Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography*, *26*, 283–290.
- Kruess, A. & Tschardtke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, *264*, 1581–84.

Kruess, A. & Tscharntke, T. (2002). Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation*, *106*, 293–302.

Kuussaari, M., Heliölä, J., Luoto, M. & Pöyry, J. (2007). Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. *Agriculture, Ecosystems and Environment*, *122*, 366–376.

L

Lambin, E. & Geist, H. (2006). *Land Use and Land Cover Change: Local Processes, Global Impacts*. Springer, New York.

Landis, D. A., Menalled, F. D., Costamagna, A.C. & Wilkinson, T. K. (2005). Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, *53*, 902–908.

Landis, D. A., Wratten, S. D. & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, *45*, 175–201.

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*, 1324–1334.

Legendre, P., Borcard, D. & Peres-Neto, P. R. (2005). Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, *75*, 435–450.

Legendre, P. & Legendre, L. (1998). *Numerical ecology*. Elsevier, Amsterdam.

Lenteren van, J. C., & Bueno, V. H. (2003). Augmentative biological control of arthropods in Latin America. *BioControl*, *48*, 123–139.

Lenth, R. V. (2013). lsmeans: least-squares means. R package version 1.10-4.

Letourneau, D. K. & Bothwell, S. G. (2008). Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, *6*, 430–438.

Letourneau, D. K., Bothwell-Allen, S. G. & Stireman, J. O. III (2012). Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. *Journal of Applied Ecology*, *49*, 1405–1416.

Lohaus, K., Vidal, S. & Thies, C. (2013). Farming practices change food web structures in cereal aphid-parasitoid-hyperparasitoid communities. *Oecologia*, *171*, 249–259.

Longley, M. (1999). A review of pesticide effects upon immature aphid parasitoids within mummified hosts. *International Journal of Pest Management*, *45*, 139–145.

M

MacArthur, R. H. (1967). *The theory of island biogeography* (Vol. 1). Princeton University Press.

- Maccherini, S., Chiarucci, A. & De Dominicis, V. (2000). Structure and species diversity of *Bromus erectus* grasslands of biancana badlands. *Belgian Journal of Botany*, *133*, 3–14.
- Macfadyen, S. & Muller, W. (2013). Edges in agricultural landscapes: species interactions and movement of natural enemies. *PloS ONE*, *8*, e59659.
- Macfadyen, S., Craze, P. G., Polaszek, A., van Achterberg, K. & Memmott, J. (2011). Parasitoid diversity reduces the variability in pest control services across time on farms. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 3387–3394.
- Macfadyen, S., Gibson, R., Polaszek, A., Morris, R. J., Craze, P. G., Planqué, R., Symondson, W. O. C. & Memmott, J. (2009). Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters*, *12*, 229–238.
- Magurran, A. E. & McGill, B. J. (2010). *Biological diversity: frontiers in measurement and assessment*. Oxford University Press, Oxford.
- Marini, L., Fontana, P., Klimek, S., Battisti, A. & Gaston, K. J. (2009). Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biological Conservation*, *142*, 394–403.
- Marini, L., Bommarco, R., Fontana, P. & Battisti, A. (2010). Disentangling effects of habitat diversity and area on orthopteran species with contrasting mobility. *Biological Conservation*, *143*, 2164–2171.
- Marini, L., Fontana P., Scotton, M. & Klimek, S. (2007). Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *Journal of Applied Ecology*, *45*, 361–370.
- Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J. B. & Bommarco, R. (2012). Landscape context and elevation affect wild bee communities in intensive apple orchards. *Basic and Applied Ecology*, *13*, 681–689.
- Marini, L., Scotton, M., Klimek, S. & Pecile, A. (2008). Patterns of plant species richness in Alpine hay meadows: Local vs. landscape controls. *Basic and Applied Ecology*, *9*, 365–372.
- Marshall, E. J. R. & Moonen, A. C. (2002). Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems and Environment*, *89*, 5–21.
- Martinson, H. M. & Fagan, W. F. (2014). Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecology Letters*, *17*, 1178–1189.
- Matesanz, S., Gimeno, T. E., de la Cruz, M., Escudero, A. & Valladares, F. (2011). Competition may explain the fine-scale spatial patterns and genetic structure of two co-occurring plant congeners. *Journal of Ecology*, *99*, 838–848.
- Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, *277*, 504–509.

- Maudsley, M. J. (2000). A review of the ecology and conservation of hedgerow invertebrates in Britain. *Journal of Environmental Management*, *60*, 65–76.
- Mendenhall, C. D., Karp, D. S., Meyer, C. F., Hadly, E. A. & Daily, G. C. (2014). Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, *509*, 213–217.
- Merckx, T., Marini L., Feber R. E. & Macdonald, D. W. (2012). Hedgerow trees and extended-width field margins enhance macro-moth diversity: implications for management. *Journal of Applied Ecology*, *49*, 1396–1404.
- Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009). Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, *10*, 178–186.
- Millenium Ecosystem Assessment (2005). *Ecosystems and Human Well-Being*. World Resources Institute, Washington, DC.
- Moilanen, A. & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, *83*, 1131–1145.
- N**
- Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.
- Nihei, S. S. & Schwarz, E. D. A. (2011). On the first tachinid fly (Diptera, Tachinidae) carrying Asclepiadoideae pollinaria in the Neotropical Region. *Revista Brasileira de Entomologia*, *55*, 441–444.
- Norris, K. (2008). Agriculture and biodiversity conservation: opportunity knocks. *Conservation Letters*, *1*, 2–11.
- Nouhuys van, S. (2005). Effects of habitat fragmentation at different trophic levels in insect communities. *Annales Zoologici Fennici*, *42*, 433–447.
- O**
- Ó hUallacháin, D., Anderson, A., Fritch, R., McCormack, S., Sheridan, H. & Finn, J. A. (2013). Field margins: a comparison of establishment methods and effects on hymenopteran parasitoid communities. *Insect Conservation and Diversity*, *7*, 289–307.
- O'Hara, J. E. (2012). World genera of the Tachinidae (Diptera) and their regional occurrence. Version 7.0. PDF document, 75 pp. Available from: http://www.nadsdiptera.org/Tach/Genera/Gentach_ver7.pdf (accessed November 2013).
- O'Hara, J. E. (2013). History of tachinid classification (Diptera, Tachinidae). *ZooKeys*, *316*, 1–34.

- O'Hara, J. E. (2014). World genera of the Tachinidae (Diptera) and their regional occurrence. Version 8.0. PDF document, 87 pp. Available from: http://www.nadsdiptera.org/Tach/WorldTachs/Genera/Gentach_ver8.pdf (accessed December 9, 2014).
- Öckinger, E. & Smith, H. G. (2006). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*, 50–59.
- Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H. (2013). Vegan: Community Ecology Package. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B. & Stevens, M. (2007). Vegan: community ecology package. R package version 1.15–4. (<http://r-forge.r-project.org/projects/vegan>).
- Ollerton, J. & Liede, S. (2014). The ASCLEPOL Database. Available from: http://www.bio.uni-bayreuth.de/planta2/research/pollina/as_pol_d.html (accessed December 9, 2014).
- Olson, D. M., Takasu, K. & Lewis, W. J. (2005). Food needs of adult parasitoids: behavioral adaptations and consequences. In: Wäckers, F. L., van Rijn, P. C. J. & Bruin, J. (eds), *Plant-provided Food for Carnivorous Insects*. Cambridge University Press, Cambridge, pp. 137–147.
- Olson, D. M. & Wäckers, F. L. (2007). Management of field margins to maximize multiple ecological services. *Journal of Applied Ecology*, *44*, 13–21.
- P**
- Pardini, R., Bueno, A. A., Gardner, T. A., Prado, P. I. & Metzger, J. P. (2010). Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*, *5*, e13666.
- Paston, S. & Rotheray, G. E. (2009). *Eriothrix rufomaculata* (De Geer, 1776) (Diptera, Tachinidae) reared from *Chrysoteuchia culmella* (Linnaeus) (Lepidoptera, Pyralidae) – a first British host record. *Dipterists Digest*, *16*, 3–6.
- Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Acholes, R. J., Sumaila, U. R. & Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, *330*, 1496–1501.
- Pérez-Lachaud, G., Batchelor, T. P. & Hardy, I. C. (2004). Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps. *Biological Control*, *30*, 149–155.

- Perfecto, I. & Vandermeer, J. (2010). The agroecological matrix as alternative to the land sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences*, *107*, 5786–5791.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–111, <http://CRAN.R-project.org/package=nlme>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2015). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-119, <http://CRAN.R-project.org/package=nlme>.
- Podani, J. & Schmera, D. (2011). A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. *Oikos*, *120*, 1625–1638.
- Podani, J. & Schmera, D. (2012). A comparative evaluation of pairwise nestedness measures. *Ecography*, *35*, 889–900.
- Polis, G. A., Anderson, W. B. & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, *28*, 289–316.
- Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*, 115–134.
- Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K. & Kuussaari, M. (2006). Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos*, *115*, 401–412.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist*, *132*, 652–661.
- Pywell, R., Warman, E., Sparks, T., Greatorex-Davies, J., Walker, K., Meek, W., Carvell C., Petit, S. & Firbank, L. (2004). Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, *118*, 313–325.
- R**
- R Development Core Team (2013). The R foundation for Statistical Computing, ver 3.0.2 Vienna University of Technology, Vienna. Available at: <http://www.r-project.org/>
- Radford, J. Q., Bennett, A. F. & Cheers, G. J. (2005). Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological conservation*, *124*, 317–337.
- Rand, T. A. & Louda, S. M. (2006). Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conservation Biology*, *20*, 1720–1729.
- Rand, T.A. & Tschardtke, T. (2007). Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos*, *116*, 1353–1362.

- Rand, T. A., Tylianakis, J. M. & Tscharntke, T. (2006). Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology Letters*, *9*, 603–614.
- Regione Autonoma Friuli Venezia Giulia (2003). *Usa del suolo aggiornato all'anno 2000 realizzato nell'ambito del Progetto "MOLAND FVG - Consumo ed uso del territorio del Friuli Venezia Giulia" (2001-2002)*. Regione Autonoma Friuli Venezia Giulia, Servizio Pianificazione Territoriale, Trieste, IT.
- Regione Veneto (2009). *Banca Dati della Copertura del Suolo della Regione Veneto*. Regione del Veneto, Unità di Progetto per il SIT e la cartografia, Venezia, IT.
- Robinson, R. A. & Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, *39*, 157–176.
- Roland, J. & Taylor, P. (1997). Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, *386*, 710–713.
- Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2013). Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology*, *50*, 387–394.
- Rosen, C. (ed) (2000). *World Resources 2000-2001: People and ecosystems: The fraying web of life*. Elsevier, Oxford, UK.
- Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rundlöf, M., Bengtsson J. & Smith, H. G. (2008). Local and landscape effects of organic farming on butterfly species richness and abundance. *Journal of Applied Ecology*, *45*, 813–820.
- Rundlöf, M., Edlund, M. & Smith H. G. (2010). Organic farming at local and landscape scales benefits plant diversity. *Ecography*, *33*, 514–522.
- Rundlöf, M. & Smith, H. G. (2006). The effect of organic farming on butterfly diversity depends on landscape context. *Journal of Applied Ecology*, *43*, 1121–1127.
- Rusch, A., Valantin-Morison, M., Sarthou, J. P. & Roger-Estrade, J. (2010). Biological control of insect pests in agroecosystems: effects of crop management, farming systems, and semi natural habitats at the landscape scale: a review. *Advances in Agronomy*, *109*, 219–389.

S

- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, R., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. & Wall, D. H. (2000). Biodiversity – global biodiversity scenarios for the year 2100. *Science*, *287*, 1770–1774.

- Salveter, R. (1998). The influence of sown herb strips and spontaneous weeds on the larval stages of aphidophagous hoverflies (Dipt., Syrphidae). *Journal of Applied Entomology*, *122*, 103–114.
- Schellhorn, N. A., Bianchi, F. J. J. A. & Hsu, C. L. (2014). Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annual Review of Entomology*, *59*, 559–581.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. & Kleijn, D. (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecology Letters*, *16*, 912–920.
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Schulze, E. D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Fischer, M. S., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., König, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V. D., Milcu, A., Müller, R., Partsch, S., Petermann, J. S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V. M. & Tschardt, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, *468*, 553–556.
- Schröter, L. & Irmeler, U. (2013). Organic cultivation reduces barrier effect of arable fields on species diversity. *Agriculture, Ecosystems and Environment*, *164*, 176–180.
- Segoli, M. & Rosenheim, J. A. (2013). The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats. *Functional Ecology*, *27*, 1224–1232.
- Shaw, M. (2006). Habitat Considerations for Parasitic Wasps (Hymenoptera). *Journal of Insect Conservation*, *10*, 117–127.
- Showers, W. B. (1993). Diversity and variation of European corn borer populations. In: Kim, K. C. & McPherson, B. A. (eds) *Evolution of Insect Pests/Patterns of Variation*. John Wiley and Sons, New York, pp. 287–309.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998). Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, *152*, 738–750.
- Sitzia, T. (2007). Hedgerows as corridors for woodland plants: a test on the Po Plain, northern Italy. *Plant Ecology*, *188*, 235–252.
- Sitzia, T., Trentanovi, G., Marini, L., Cattaneo, D. & Semenzato, P. (2013). Assessment of hedge stand types as determinants of woody species richness in rural field margins. *iForest - Biogeosciences and Forestry*, *6*, 201–208.
- Sitzia, T., Dainese, M. & McCollin, D. (2014). Environmental factors interact with spatial processes to determine herbaceous species richness in woody field margins. *Plant Ecology*, *215*, 1323–1335.

- Soares-Filho, B. S., Nepstad, D. C., Curran, L. M., Cerqueira, G. C., Garcia, R. A., Ramos, C. A., Voll, E., McDonald, A., Lefebvre, P. & Schlesinger, P. (2006). Modelling conservation in the Amazon basin. *Nature*, *440*, 520–523.
- Sotherton, N. W. (1998). Land-use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biological Conservation*, *83*, 259–268.
- Speight, M. C. D. (2013). Species accounts of European Syrphidae (Diptera), 2013. *Syrph the Net, the database of European Syrphidae*, vol.72, Syrph the Net publications, Dublin, 316 pp.
- Speight, M. C. D. & Sarthou, J.-P. (2010). StN keys for the identification of adult European Syrphidae (Diptera). *Syrph the Net, the database of European Syrphidae*, Vol. 60, Syrph the Net publications, Dublin, 107 pp.
- Stamps, J. A., Buechner, M. & Krishnan, V. V. (1987). The effects of edge permeability and habitat geometry on emigrations from patches of habitat. *American Naturalist*, *129*, 533–552.
- Steffan-Dewenter, I. & Tschardtke, T. (2002). Insect communities and biotic interaction on fragmented calcareous grasslands—a mini review. *Biological Conservation*, *104*, 275–284.
- Steffan-Dewenter, I., Münzenberg, U., Bürger C., Thies, C. & Tschardtke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*, 1421–1432.
- Stireman, J. O. III (2002). Host location and selection cues in a generalist tachinid parasitoid. *Entomologia Experimentalis et Applicata*, *103*, 23–34.
- Stireman, J. O. III (2005). The evolution of generalization? Host range in parasitoid flies. *Journal of Evolutionary Biology*, *18*, 325–336.
- Stireman, J. O. III (2008). α and β diversity of a tachinid parasitoid community over space and time. *Annals of the Entomological Society of America*, *101*, 362–370.
- Stireman, J. O. III, Cerretti P., Whitmore, D., Hardersen, S. & Gianelle, D. (2012). Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest. *Insect Conservation and Diversity*, *5*, 346–357.
- Stireman, J. O. III & Singer, M. S. (2003). What determines host range in parasitoids? An analysis of a tachinid parasitoid community. *Oecologia*, *135*, 629–638.
- Stireman, J. O. III, O'Hara, J. E. & Wood, D. M. (2006). Tachinidae: evolution, behavior, and ecology. *Annual Review of Entomology*, *51*, 525–555.
- Stoate, C., Boatman, N. D., Borralho, R. J., Carvalho, C., De Snoo, G. R. & Eden, P. (2001). Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, *63*, 337–365.
- Swift, M. J., Vandermeer, J., Ramakrishnan, P. S., Anderson, J. M., Ong, C. K. & Hawkins, B. A. (1996). Biodiversity and agroecosystem function. In: Cushman, J.

H., Mooney, H. A., Medina, E., Sala, O. E. & Schulze, E. D. (eds) *Functional Roles of Biodiversity: A Global Perspective*. Wiley, Chichester, pp. 261–298.

T

- Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, *68*, 571–573.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*, 79–92.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L. W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W. W., Winqvist, C. & Tscharntke, T. (2011). The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecological Applications*, *21*, 2187–2196.
- Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2003). Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, *101*, 18–25.
- Thies, C. & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, *285*, 893–895.
- Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2008). Interannual landscape changes influence plant-herbivore-parasitoid interactions. *Agriculture, Ecosystems and Environment*, *125*, 266–268.
- Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences*, *360*, 339–57.
- Thomas, J. A., Bourn, N. A., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., Curtis, R. & Goodger, B. (2001). The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London Series B - Biological Sciences*, *268*, 1791–1796.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D. & Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science*, *292*, 281–284.
- Tooker, J. F., Hauser, M. & Hanks, L. M. (2006). Floral host plants of Syrphidae and Tachinidae (Diptera) of central Illinois. *Annals of the Entomological Society of America*, *99*, 96–112.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., van Nouhuys, S. & Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, *43*, 294–309.

- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, *151*, 53–59.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, *8*, 857–874.
- Tscharntke, T., Rand, A. T. & Bianchi, J. J. A. F. (2005). The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Annales Zoologici Fennici*, *42*, 421–432.
- Tscharntke, T., Sekercioglu, C. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P. & Tylianakis, J. M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, *89*, 944–951.
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. & Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, *87*, 661–85.
- Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A. & Bengtsson, J. (2014). Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *Journal of Applied Ecology*, *51*, 746–755.
- Tylianakis, J. M., Klein, A.-M. & Tscharntke, T. (2005). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*, *86*, 3296–3302.
- ## V
- Valladares, G., Salvo, A. & Cagnolo, L. (2006). Habitat fragmentation effects on trophic processes of insect–plant food webs. *Conservation Biology*, *20*, 212–217.
- Veres, A., Petit, S., Conord, C. & Lavigne, C. (2013). Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems and Environment*, *166*, 110–117.
- Vickery, J. A., Feber, R. E. & Fuller, R. J. (2009). Arable field margins managed for biodiversity conservation: a review of food resource provision for farmland birds. *Agriculture, Ecosystems and Environment*, *133*, 1–13.
- Vinatier, F., Gosme, M. & Valantin-Morison, M. (2013). Explaining host–parasitoid interactions at the landscape scale: a new approach for calibration and sensitivity analysis of complex spatio-temporal models. *Landscape Ecology*, *28*, 217–231.

W

- Weibull, A.-C., Bengtsson, J. & Nohlgren, E. (2000). Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, *23*, 743–750.
- Whittingham, M. J. (2007). Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, *44*, 1–5.
- Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, *75*, 1182–1189.
- Wilby, A. & Thomas, M. B. (2002). Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters*, *5*, 353–360.
- Williams, S. C., Arnaud, P.H. & Lowe, G. (1990). Parasitism of *Anuroctonus phaiodactylus* (Wood) and *Vaejovis spinigerus* (Wood) (Scorpiones: Vaejovidae) by *Spilochaetosoma californicum* Smith (Diptera: Tachinidae), and a review of parasitism in scorpions. *Myia*, *5*, 11–27.
- Wratten, S. D., Bowie, M. H., Hickman, J. M., Evans, A. M., Sedcole, J. R. & Tylianakis, J. M. (2003). Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia*, *134*, 605–611.
- Wratten, S. D., White, A. J., Bowie, M. H., Berry, N. A. & Weigmann, U. (1995). Phenology and ecology of hoverflies (Diptera: Syrphidae) in New Zealand. *Environmental Entomology*, *24*, 595–600.
- Wright, H. L., Lake, I. R. & Dolman, P. M. (2012). Agriculture — a key element for conservation in the developing world. *Conservation Letters*, *5*, 11–19.

Z

- Zobel, M. (1997). The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, *12*, 266–269.

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Publications

Dissertation

- Inclán, D. J.**, Cerretti, P. & Marini, L. (2014). Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes. *Landscape Ecology*, 29, 879–889.
- Dainese, M., **Inclán, D. J.**, Sitzia, T. & Marini, L. (in press). Testing scale-dependent effects of semi-natural habitats on farmland biodiversity. *Ecological Applications*.
- Inclán, D. J.**, Cerretti, P., Gabriel, D., Benton, T. G., Sait, S. M., Kunin, W. E., Gillespie, M. A. K. & Marini, L. (accepted). Organic farming enhances parasitoid diversity at the local and landscape scale. *Journal of Applied Ecology*.
- Inclán, D. J.**, Cerretti, P. & Marini, L. (submitted). Landscape effect on parasitoid spillover between crop and non-crop habitats.
- Inclán, D. J.**, Dainese, M., Cerretti, P., Paniccia, D. & Marini, L. (submitted). Spillover of natural enemies between contrasting field margins and crops.

Other publications

- Inclán, D. J.** & Stireman J. O. III (2014). A new species and synonymy of the Neotropical *Eucelatoria* Townsend and redescription of *Myiodoriops* Townsend. *ZooKeys*, 464, 63–97.
- Inclán, D. J.** (2014). A new range extension for *Erythromelana distincta* Inclán (Tachinidae). *The Tachinid Times*, 27, 32–33.
- Cerretti, P., Di Giulio, A., Romani, R., **Inclán, D. J.**, Whitmore, D., Di Giovanni, F., Scalici, M. & Minelli, A. (2014). First report of exocrine epithelial glands in oestroid flies: the tachinid sexual patches (Diptera: Oestroidea: Tachinidae). *Acta Zoologica*. (online first).
- Cerretti, P., O'Hara, J., Wood, M., Shima, H., **Inclán, D. J.** & Stireman, J. O. III (2014). Signal through the noise? Phylogeny of the Tachinidae (Diptera) as inferred from morphological evidence. *Systematic Entomology*, 39, 335–353.
- Inclán, D. J.** & Stireman, J. O. III (2013). Revision of the genus *Erythromelana* Townsend (Diptera: Tachinidae) and analysis of its phylogeny and diversification. *Zootaxa*, 3621: 1–82.
- Inclán, D. J.** & Stireman, J. O. III (2011). Tachinid (Diptera: Tachinidae) parasitoid diversity and temporal abundance at a single site in the Northeastern United States. *Annals of the Entomological Society of America*, 104, 287–296.

- Inclán, D. J.** (2010). Revisión del Género *Erythromelana* Townsend, 1919 (Díptera: Tachinidae) con notas en su filogenia y diversificación. M.S. Thesis, Wright State University, Dayton, OH, USA.
- Inclán, D. J.** & Stireman, J. O. III (2009). A preliminary study of the diversity and temporal patterns of abundance of Tachinidae in Southwestern OH. *The Tachinid Times*, 22, 1–4.
- Inclán, D. J.**, Bermúdez, F. J., Alvarado, E., Ellis, M. A., Williams, R. N. & Acosta, N. (2008). Comparison of biological and conventional insecticide treatments for the management of the pineapple fruit borer, *Strymon megarus* (LEPIDOPTERA: LYCAENIDAE) in Costa Rica. *Ecological Engineering*, 34, 328–331.
- Inclán, D. J.**, Alvarado, E. & Williams, R. N. (2007). Evaluación de cuatro insecticidas naturales para el control de Tecla, *Strymon megarus* (Godart) (LEPIDOPTERA: LYCAENIDAE), en el cultivo de la piña. *Tierra Tropical*, 3, 199–210.
- Inclán, D. J.** (2006). Evaluación de Insecticidas Naturales en el Control de *Strymon megarus*. (LEPIDOPTERA: LYCAENIDAE) en Piña. *Proyecto de Graduación*, Universidad EARTH. Guácimo, Limón, Costa Rica.
- Inclán, D. J.**, Williams, R. N., Ellis, M. A., Fickle, D. S. & McClure, K. B. (2006). Managing the multicoloured Asian lady beetle in grapes, 2005. *Arthropod Manag Tests*, 31, L7.
- Williams, R. N., Fickle, D. S., McClure, K. B., **Inclán, D. J.** (2006). Chemical evaluations for control of the multicoloured Asian lady beetle on grapes. *Arthropod Manag Tests*, 31, C11.