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Bridging applied ecology and network theory to improve landscape management for conservation

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Legnaro (PD), September 27th 2019   Francesco Lami

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Summary

Agricultural intensification is widely considered a major threat to biodiversity and ecosystem services. To better protect biological communities, it is necessary to gain a more detailed understanding of the way species use habitats and move across increasingly simplified landscapes. Traditional landscape ecology approaches are mainly based on the dichotomy between focal semi-natural habitat patches and the surrounding agricultural matrix. While the advances made possible by the landscape mosaic model are undeniable, this approach fails to account for real-world complexity, as many species are known to use multiple habitat types (natural and disturbed) during their life cycle. In addition to landscape changes, many local factors (including management such as soil disturbance or pest control) can impact biodiversity, often interacting with each other. In order to inform efficient biodiversity management actions in the future, it is crucial to increase our knowledge on the way local and landscape factors can impact biodiversity at multiple spatial scales. The general aim of this thesis was to develop a novel approach to the study of species-habitat interactions, and to apply the approach to answer some pressing questions about the way landscape simplification influences important arthropod functional groups. Additionally, we studied the effects of local factors on an arthropod-mediated ecosystem service (weed seed predation) in the same area. Arthropods were chosen as they are among the most abundant and ecologically relevant organisms in agroecosystems, providing a wide variety of pivotal services. The new approach, based on network theory, showed that landscape simplification reduces habitat specialization in low-mobility insect groups, and allowed us to pinpoint the most important habitat types for the facilitation of arthropod movement through the landscape mosaics. Our local-level study, on the other hand, highlighted how multiple factors can interact in a complex way in shaping ecosystem services. This study demonstrates the potential of the novel species-habitat network approach as a complementary tool for investigating landscape-biodiversity interactions, while simultaneously unveiling new information on the way landscape changes and local factors influence key arthropod groups. This enabled us to provide a series of recommendations for biodiversity management actions, varying depending on the target group. Overall, our research is a reminder of the importance of taking into account multiple potentially interacting factors at different spatial scales to correctly understand and manage biodiversity-related processes.

Riassunto

L'intensificazione agricola è ampiamente considerata una grave minaccia per la biodiversità ed i servizi ecosistemici ad essa connessi. Per meglio gestire le comunità biologiche naturali, è necessaria una più dettagliata comprensione del modo in cui le specie usano gli habitat e si muovono attraverso un paesaggio sempre più semplificato. I tradizionali approcci dell'ecologia del paesaggio sono principalmente basati sulla dicotomia fra le patch target di habitat semi-naturale e la matrice agraria circostante. Nonostante sia stato fonte di innegabili progressi, questo approccio non può accuratamente rappresentare la complessità del mondo reale, in quanto è ormai noto che molte specie usano diversi tipi di habitat, sia naturali che disturbati, nel corso del loro ciclo vitale. Oltre alle alterazioni del paesaggio, molti fattori locali (incluse tecniche di gestione quali il disturbo del suolo o la lotta ai fitofagi) possono causare impatti sulla biodiversità, anche interagendo fra di loro. Per poter formulare in futuro efficienti strategie di gestione della biodiversità, è fondamentale incrementare la nostra conoscenza del modo in cui fattori di paesaggio e locali possono influenzare la biodiversità a diverse scale spaziali. Lo scopo di questa tesi è quello di testare un nuovo approccio allo studio delle interazioni specie-habitat, applicandolo per rispondere ad alcune importanti domande sul modo in cui la semplificazione del paesaggio influenza degli importanti gruppi funzionali di artropodi. Inoltre, abbiamo studiato gli effetti di fattori locali su un servizio ecosistemico legato agli artropodi (la predazione dei semi di infestanti) nella stessa area. Gli artropodi sono stati scelti in quanto sono fra gli organismi più abbondanti ed ecologicamente rilevanti negli agroecosistemi, e forniscono una grande varietà di servizi fondamentali. Il nuovo approccio, basato sulla teoria dei network, ha dimostrato che la semplificazione del paesaggio riduce la specializzazione per gli habitat nei gruppi di insetti a bassa mobilità, e ci ha consentito di identificare i tipi di habitat più importanti per facilitare gli spostamenti di artropodi attraverso il paesaggio. Il nostro studio a livello locale ha inoltre evidenziato come fattori multipli possono interagire in modo difficilmente prevedibile nell'influenzare i servizi ecosistemici. La nostra ricerca dimostra il potenziale del nuovo approccio di network specie-habitat come strumento complementare per lo studio delle interazioni paesaggio-biodiversità, rivelando nel contempo nuove informazioni sull'impatto delle trasformazioni del paesaggio e dei fattori locali su gruppi chiave di artropodi. Questo ci ha permesso di fornire una serie di consigli per la gestione della biodiversità, diversi a seconda del gruppo target. Nel complesso, la nostra ricerca sottolinea l'importanza di tenere conto di molteplici fattori potenzialmente interagenti a diverse scale spaziali per poter comprendere appieno e gestire funzioni e processi legati alla biodiversità.

Chapter 1

Introduction

Agriculture and biodiversity: a landscape perspective

Agriculture represents a major threat to biodiversity and ecosystem services (McLaughlin & Mineau, 1995; Reidsma *et al.*, 2006). In order to ensure long-term sustainability and human well-being, it is recognized that new, environmentally friendly agricultural practices are to be pursued (Rockström *et al.*, 2017). This, in turn, requires a deeper understanding of the main environmental impacts of agriculture. A great deal of attention has been paid to practices and technologies that affect biodiversity at the field level, such as pesticides (Geiger *et al.*, 2010) and soil disturbance (Shearin *et al.*, 2007). However, in recent years an increasing body of research has been focused on larger-scale impacts and management actions.

It is now widely recognized that one of the most important consequences of agricultural intensification is landscape simplification, which can in turn have dramatic effects on biodiversity (Tscharntke *et al.*, 2005a). As an ecological concept, landscape can be defined as a mosaic of interacting ecosystems (Aronson, 2011) with a defined spatial scale, usually depending on the size and biology of the studied organisms (Wiens & Milne, 1989). The aim of landscape ecology is to understand how landscape structure influence organism distribution and abundance, as well as the related biological functions (Fahrig, 2005).

Different approaches to landscape ecology

Traditionally, landscape ecology has been heavily influenced by the classic theory of island biogeography (MacArthur & Wilson, 1963), which led to the patch-mosaic or patch-corridor-matrix model (Wiens *et al.*, 1993; Forman, 1995), based on the idea of landscape elements as discrete entities. According to this interpretation, habitat patches (usually consisting of natural habitats) can be seen as islands surrounded by a lower-quality or hostile matrix, such as cropland. The structure of populations and communities on each habitat "island" heavily depends on the size of the patches (which makes them more or less able to support large populations and be found by migrating individuals) and on their connectivity (which makes organisms more or less able to move from patch to patch). The matrix has traditionally been ignored in the explanation of these dynamics, but more recent approaches recognize that there are matrices of varying quality, which in turn can influence the ability of organisms to move through and take advantage of the landscape (Quesnelle *et al.*, 2015; Ruffell *et al.*, 2017).

While the advancements made possible by the patch-mosaic model are widely recognized (Turner, 2005), recently an increasing number of researchers have been criticizing this approach as being inconsistent with ecological theory and real-world scenarios (Kedron *et al.*, 2018). These authors advocate for models that take into account scenarios in which spatial heterogeneity is continuous, rather than represented by clearly divided patches (McIntyre & Barrett, 1992; Manning *et al.*, 2004; Fischer & Lindenmayer, 2006). A sizeable body of work on gradient models and related promising metrics that describe landscape processes has been accumulating (McGarigal & Cushman, 2005; McGarigal *et al.*, 2009; Lausch *et al.*, 2015).

Another commonly criticized aspect of the patch-mosaic model is the implicit dichotomy of a focal habitat patch vs. the surrounding matrix, that does not represent well the fact that many organisms are known to use more than one habitat type during their life cycle (Ricketts, 2001; Driscoll *et al.*, 2013). Some theoretical frameworks have moved past the patch-matrix dichotomy, but they tend to be still too detached from empirical research to find actual applications (Gounand *et al.*, 2018).

Landscape simplification: mechanisms and effects

Negative effects of landscape simplification include reduction of species diversity (Flynn *et al.*, 2009; Gámez-Virués *et al.*, 2015), deterioration of related ecosystem services (Power, 2010; Allan *et al.*, 2015), and increases in the abundance and spread of pests and pathogens (Margosian *et al.*, 2009). The two main aspects of landscape usually investigated from this point of view are landscape composition (the abundance of one or more habitat types in the landscape, irrespective of their shape) and landscape configuration (the geometry of habitat patches within the landscape) (Holzschuh *et al.*, 2010). Habitat destruction reduces the resources available to organisms that rely on natural habitats for at least a part of their life cycle, while habitat fragmentation is the division of large, uninterrupted habitat patches into smaller patches, often surrounded by agricultural fields or urban areas, and thus isolated from similar habitat patches. Fragmentation can impact biodiversity in two main ways; first, smaller patches can only sustain smaller populations, which are more prone to fluctuations and local extinctions. Second, fragmentation increases the amount of edges, which often represents a lower-quality habitat compared to the core portions of the habitat patches (Fahrig, 2003; Laurance, 2008; Haddad *et al.*, 2015).

While the effects of landscape composition have been intensively studied (Tscharntke *et al.*, 2012; Kennedy *et al.*, 2013; Shackelford *et al.*, 2013; Karp *et al.*, 2018), unveiling the effects of landscape configuration changes can be more challenging (Duflot *et al.*, 2017; Martin *et al.*, 2019). Investigations on the subject, in fact, have sometimes yielded seemingly contradictory or mixed responses (Gámez-Virués *et al.*, 2015; Martin *et al.*, 2019). This variability can be explained by the fact that specialist species might perceive configurational heterogeneity as habitat fragmentation, while generalist species might be even facilitated in their movement and resource acquisition by complex configurations (Mitchell *et al.*, 2015), which increase contact points between habitat patches and the chance of spillover (Fahrig *et al.*, 2011). Additionally, it is sometimes difficult to disentangle the effects of habitat fragmentation from the effects of habitat loss, as the two processes are often coupled (Fahrig, 2003). Studying independent gradients of composition and configuration (Holzschuh *et al.*, 2010; Coudrain *et al.*, 2014) and taking into account the functional traits that might influence the way organisms react to those gradients (Smith *et al.*, 2014) might help overcome those challenges and improve predictions of community-level reactions to landscape changes.

Ecosystem services: the role of arthropods in agroecosystems

Ecosystem services are usually defined as the direct and indirect benefits mankind derives from ecosystem functions and processes (Costanza *et al.*, 1997), and are widely considered pivotal not only for agriculture, but for human life and long-term well-being in general (Butler & Oluoch-Kosura, 2006; Harrison *et al.*, 2010). Examples include food provisioning, water and air quality regulation, nutrient cycling and psychological benefits (MA, 2005). The state of biodiversity, which is the source of ecosystem services, has long been known to be deeply linked with the effectiveness and stability of the services themselves (Naeem & Li, 1997; Isbell *et al.*, 2011), to the point that many authors argue for ecosystem services to be one of the main reasons to conserve biodiversity (Balvanera *et al.*, 2006; Díaz *et al.*, 2006). Even more than taxonomic diversity, in recent years it is functional diversity (i.e. the diversity of biological traits linked with ecological functions) that is thought to be instrumental in the provision and stability of ecosystem services (de Bello *et al.*, 2010; Gagic *et al.*, 2015; Wood *et al.*, 2015).

A particularly interesting group from this point of view is represented by insects and other terrestrial arthropods, as they are the most diversified, abundant and ecologically relevant land animals (Schowalter, 2011), and are widespread in agricultural and natural habitats alike.

Arthropods, and in particular insects, are amongst the most important providers of ecosystem services (Losey & Vaughan, 2006). Pollination services of wild and domesticated plants (Biesmeijer, 2006; Cane *et al.*, 2007; Ollerton *et al.*, 2011) provided by pollinator insects, for instance, are so vital to economy and well-being that are widely perceived as such even by the general public (Domroese & Johnson, 2017). Equally important is the biological control service provided by many arthropod guilds against harmful organisms in agroecosystems (Westerman *et al.*, 2003; Jonsson *et al.*, 2008; Begg *et al.*, 2017). Ground beetles (Coleoptera: Carabidae), for example, prey on both invertebrate pests and weed seeds (Lövei & Sunderland, 1996; Honek *et al.*, 2003). Arthropods are also pivotal decomposers, accelerating nutrient cycling, maintaining soil structure and reducing the amount of potentially pathogen-harboring waste (Nichols *et al.*, 2008; Culliney, 2013; Bagyaraj *et al.*, 2016).

Interactions between landscape simplification and local factors on functional biodiversity

Given the increasing body of knowledge about the effects of landscape changes on biodiversity, landscape-level management strategies to enhance ecosystem services over large areas are quickly becoming a priority (Thies & Tscharntke, 1999; Martin *et al.*, 2019). A main focus of this type of research is on semi-natural habitats, which are commonly considered source habitats from which beneficial organisms can spill over to crop fields (Blitzer *et al.*, 2012; Inclán & Marini, 2015), sources of alternate food and refuge for beneficial organisms (Burgio *et al.*, 2006). In spite of the unquestionable importance of semi-natural habitats for functional biodiversity (Morandin & Winston, 2006; Dainese *et al.*, 2017), however, evidence points out that in some cases they are not enough to significantly enhance ecosystem services (Tscharntke *et al.*, 2016; Karp *et al.*, 2018) or even promote spillover (Gaigher *et al.*, 2015). Other landscape variables or different factors altogether are thus to be investigated.

Landscape-level processes can interact with local factors, leading to different effects on biodiversity and ecosystem services depending on the context (Concepcion *et al.*, 2012; Kennedy *et al.*, 2013). It has been shown, for instance, that conservation tillage can significantly mitigate the negative effects of landscape simplification on soil arthropods and the related ecosystem services (Tamburini *et al.*, 2016b, 2016a), which is not surprising considering that soil disturbance generated by conventional tillage is often detrimental to soil invertebrates (Blubaugh and Kaplan, 2015; Shearin et al., 2007). Similarly, other wildlife-friendly practices

such as organic farming and the sowing of flower strips adjacent to fields are known to have higher effectiveness in simplified landscapes than in complex landscapes rich in alternative resources (Holzschuh *et al.*, 2007; Haenke *et al.*, 2009). A growing body of evidence shows that these interactions between local and landscape factors, while not universally present (Dainese *et al.*, 2015), are potentially very important in conservation planning. A better understanding of the effects of both landscape changes and local management on functional biodiversity should thus be achieved.

Research objectives and thesis structure

The main aim of this thesis is to introduce a new theoretical framework to study habitat use by arthropod communities, and to apply the same framework, along with investigations of local-level factors, to understand how to better manage functionally important arthropod groups impacted by landscape simplification. The thesis is divided into three parts: in Part 1 I introduced the framework and presented some case studies that show its application in the conservation and management of important arthropod groups, including ground beetles. In Part 2 I focused on weed seed predation, a pivotal ecosystem service provided by ground beetles, and how it is influenced by field features and arthropod community composition. In Part 3 I provided general conclusions and implications for management.

Part 1: A novel approach to landscape-level management of functionally important arthropod groups

Chapter 2 introduces the species-habitat network, a theoretical framework aimed at better explaining habitat use by multiple species, thus complementing traditional landscape ecology approaches. The framework is based on analytical techniques and existing tools normally employed to study mutualistic interactions, making it highly versatile and easy to apply and interpret. We provide several possible applications of the method, as well as a simple worked example using real data.

Chapter 3 applies the species-habitat network concept to elucidate the effects of landscape simplification on the level of habitat specialization of functionally important arthropods. We focused on 3 different guilds with varying degrees of mobility: predators (ground beetles), herbivores (leafhoppers *sensu latu*) and pollinators (wild bees). Arthropods were sampled in habitat patches across multiple landscape mosaics representing gradients of landscape

complexity. We took into account the effects on two elements potentially influencing specialization: shifts in community composition, and behavioral changes in individual species.

Chapter 4 explores the potential of the species-habitat network approach to devise landscape-level management actions aimed at functionally important arthropods. The case study was represented by ground-dwelling spiders. We investigated the network structure of spider communities across a gradient of landscape complexity, its interactions with landscape features, and the role of each habitat type in the network. Finally, we focused on the implications of these results for the management of spider assemblages in agroecosystems.

Part 2: Local factors influencing ecosystem services provided by arthropods

Chapter 5 investigates the local factors affecting weed seed predation by ground beetles and other arthropods. Seed predation intensity and seed predator community features were assessed in a field experiment comparing conventional tillage and conservation tillage fields. Soil disturbance and distance from field margin were taken into account as explanatory variables. Additionally, we also investigated the effects of the functional composition of local seed predator communities, to check for potential intra-guild predation interference.

Part 3: Conclusions

Chapter 6 provides a summarizing discussion of the results, focusing on their theoretical implications and their possible applications to the management of functionally important arthropods in agroecosystems.

Chapter 2

Species-habitat networks: A tool to improve landscape management for conservation

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Abstract

Land-use change is reshaping terrestrial ecosystems world-wide and is recognized as a key driver of biodiversity loss with negative consequences on ecosystem functioning. Understanding how species use resources across landscapes is essential for the design of effective management strategies. Despite recent advances in network ecology, there is still a gap between theory and applied ecological science, and we lack the information to manage entire landscapes to maximize biodiversity conservation and ecosystem service delivery. While several pioneering approaches have tried to link ecological networks and conservation science, applied ecologists still struggle to incorporate these models into research due to their inherent complexity. We propose the application of bipartite networks principles to create species–habitat networks. This approach explicitly links multiple species and habitat resources, provides tools to estimate the importance of particular species or specific habitat in a given landscape, and quantifies emerging properties of entire habitat networks. Most existing metrics used to study properties of bipartite ecological networks can easily be adapted to investigate species–habitat relationships. The tool use is relatively simple and does not require advanced computational expertise.

Synthesis and applications. One of the biggest challenges in applied ecology is managing multiple habitats for the effective conservation of multiple species. One key advantage of this proposed approach is that the scale of the derived ecological information could match the scale of landscape management interventions. The versatility, visualization power and ease of interpretation of these networks will enable application of the species–habitat network concept to a wide array of real-world problems, such as multispecies conservation, habitat restoration, ecosystem services management or invasion ecology. In particular, species–habitat networks could be applied to identify optimal landscape compositions and configurations to design effective interventions at the landscape scale. This approach also enables the detection of emerging network properties that could also be used to test the effects of large-scale drivers of global change upon ecosystem structure and stability.

Landscape management for conservation

One of the biggest challenges in applied ecology is to manage multiple habitats for the effective conservation of multiple species. The field of landscape ecology has indeed made significant inroads towards understanding community responses to landscape processes, providing a solid evidence base for managers and policy makers to protect biodiversity and ecosystem services (Tscharntke *et al.*, 2012; Mayer *et al.*, 2016). However, most of these studies are based on a simple dichotomy, that is, a focal local habitat versus the surrounding landscape or matrix. Often the species community of interest is only sampled in one habitat and related to the landscape by using the proportion of suitable or unsuitable habitats (Figure 1a). Many applications of this approach exist and recent advances in ecosystem services research have successfully applied the same approach to study key functions such as seed dispersal, biocontrol (Schellhorn *et al.*, 2015) or pollination (Kennedy *et al.*, 2013). While this research has pioneered the use of landscape ecology to understand biodiversity patterns, it lacks a mechanistic understanding about how community-level processes are affected by multiple habitats, indicating the need for complementary tools to study complex spatial patterns.
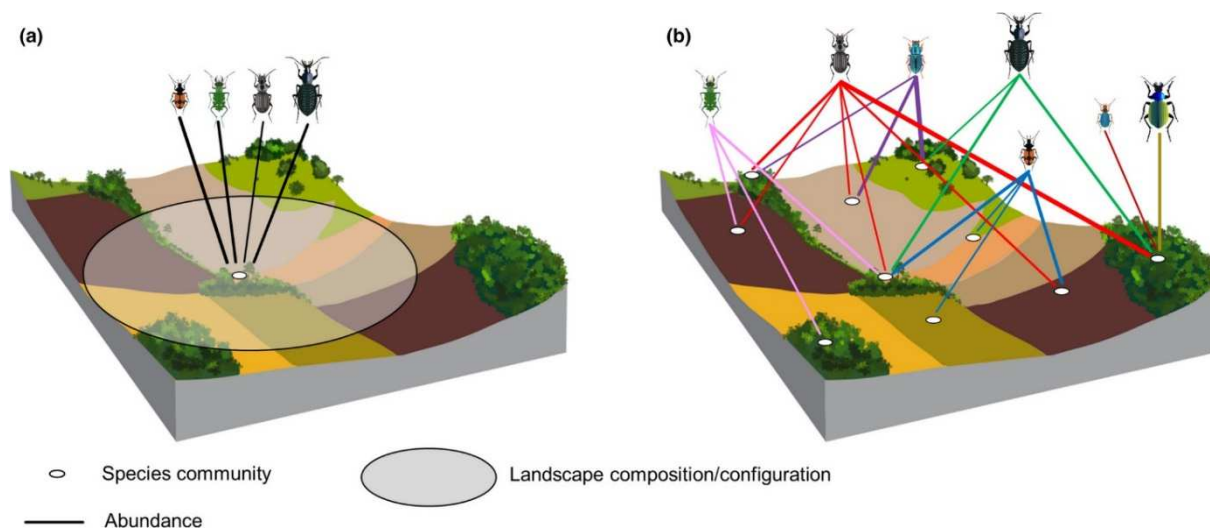

Fig. 1. (a) Traditional approach to study species communities across heterogeneous landscapes. Most empirical research in landscape ecology focuses on the local habitat versus surrounding landscape dichotomy, where the landscape is quantified in terms of composition and/or configuration around a central point (circular buffer) where the community is sampled; (b) the species–habitat network whereby the whole landscape is sampled and the species are sampled at multiple sites (line width proportional to species abundance). The landscape can be classified in patches according to the functional role of the different habitats for the target species community.

Traditionally, landscapes have been defined as complex and heterogeneous mosaics, constituted of many interacting discrete habitat patches. More recently, several gradient models

of landscape structure have challenged the mosaic paradigm, suggesting that landscape heterogeneity should be modelled using multiple, continuous environmental gradients (Fischer & Lindenmayer, 2006). In both cases, explicitly accounting for species resource use requires the sampling of target species in multiple sites across the landscape. These ideas have led us to consider the whole landscape as a unit to quantify and analyse community response to landscape processes and/or management interventions (Figure 1b). Integrating and analysing species use of multiple sites corresponding to different habitat types within a landscape may seem a daunting task. Fortunately, tools developed from ecological network theory can be used to analyse and describe such complex interactions. In particular, we advocate the modelling of species–habitat interactions as bipartite networks, analogous to those describing antagonistic or mutualistic interactions (Bascompte & Jordano, 2007). Ecological networks based on graph theory have been increasingly applied to the problem of describing complex and dynamic community-level changes in ecology (Bascompte & Jordano, 2007; Memmott, 2009; Burkle *et al.*, 2013; Gilarranz *et al.*, 2017). While several pioneering approaches have tried to link ecological networks and conservation science (Kaiser-Bunbury & Blüthgen, 2015; Albert *et al.*, 2017; Harvey *et al.*, 2017; Tylianakis & Morris, 2017; Pellissier *et al.*, 2018), applied ecologists still struggle to incorporate these models into research due to their inherent complexity. While there is the potential to expand the network concept beyond species–species networks to include habitat networks (Gonzalez *et al.*, 2011; Baguette *et al.*, 2013), there are still little applications of these ideas. Against this background, we propose to apply the principles of bipartite networks to create species–habitat networks to explicitly link multiple species and habitat resources across heterogeneous landscapes.

Beyond the focal habitat: Building species-habitat networks

In the simplest case, habitat types and the species occurring within each habitat constitute the two types of nodes of a species–habitat network. The focal species community would usually share a similar functional role, with examples being lichens, pollinators, ground-dwelling predatory arthropods or insectivorous mammals. The flexibility of the proposed approach allows habitat nodes to be further defined as individual sites where the community was sampled (Burns & Zotz, 2010), similar to ecological interaction networks downscaled from species to individual levels (Tur *et al.*, 2014; Koch *et al.*, 2018). That is, each individual site could affect network topology and stability depending on attributes such as habitat quality, management or connectivity. Note that the links need to be carefully formulated as they can affect the ecological

interpretation of the species–habitat network. Here, we use the operational definition of a link as the occurrence/abundance of a particular species in a certain site.

The spatial extent in which the community is sampled should be selected according to species' foraging ranges (e.g. for mobile organisms) or propagule dispersal (e.g. for sessile organisms) and to the ecological hypotheses underpinning the study. This issue is similar to the selection of buffer radii when adopting a traditional approach to quantify landscape composition or configuration. It is important to stress that, as the spatial extent of the habitat mosaic used by the species is generally large (e.g. 1–10 km for mobile organisms), it is likely that most surveyed species–habitat networks would be subunits of much larger networks (Jordano, 2016). While the definition of species as nodes is usually straightforward, the way in which habitats are defined as nodes can be more complex. Spatial grain and habitat classification can affect the topology (and hence interpretation) of the network. In heavily modified landscapes, different habitats are often organized in patches, which can be defined as discrete areas with a definite shape, size and configuration. The focal species community may be used to guide the identification of habitat types that are functionally relevant. From an operational point of view, we suggest that habitat nodes are defined according to the dominant vegetation, accounting for differences in structure and function for different communities.

Tools for analysing species-habitat networks

Most existing metrics used to study properties of bipartite ecological networks can easily be adapted to the study of species–habitat networks. These metrics can address key applied questions and can be broadly divided into two groups: emergent properties of the whole network and node-level metrics that measure the role of single nodes (i.e. single habitats, sites or species) in the network (Dormann, Frund, Bluthgen, & Gruber, 2009; Figure 2). Here, we provide examples of a few commonly used metrics, while several comprehensive reviews of different metrics are available (Blüthgen *et al.*, 2006; Dormann *et al.*, 2009a). For a simple, technical application of the metrics described below we present a worked example in Appendix A using R.
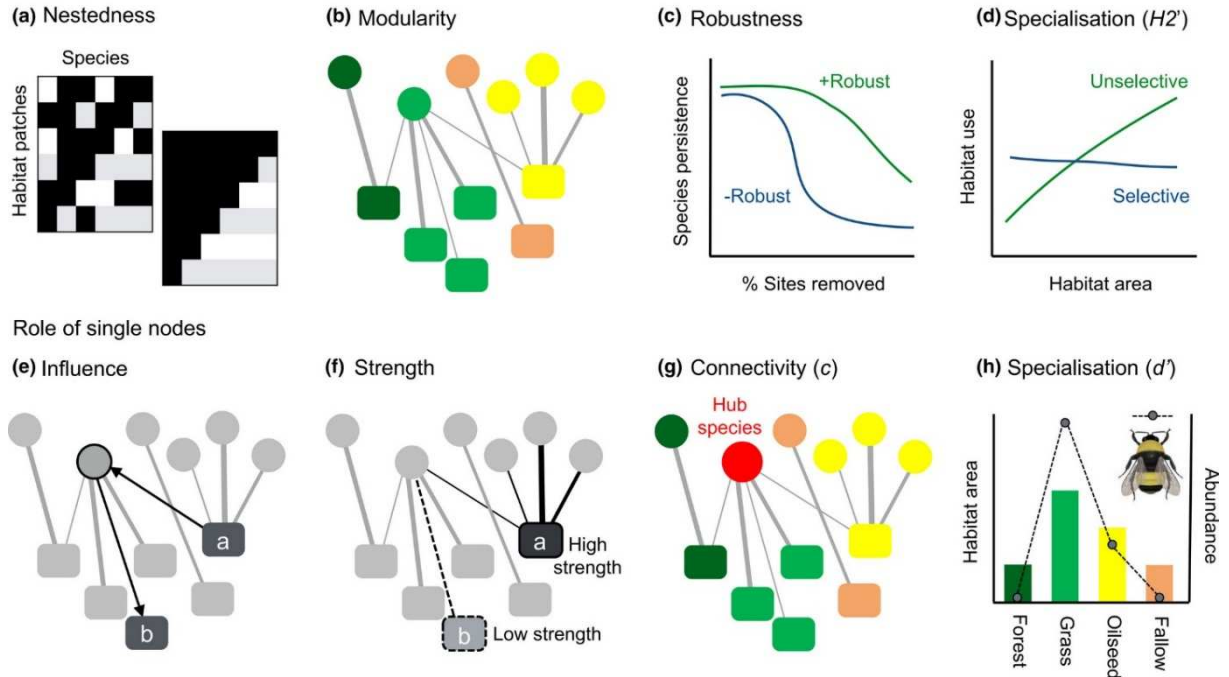
Whole network topology

(a) Nestedness

(b) Modularity

(c) Robustness

(d) Specialisation (H2')

Role of single nodes

(e) Influence

(f) Strength

(g) Connectivity (c)

(h) Specialisation (d')

Fig. 2. An untapped network toolbox for assessing species–habitat links. Bipartite network analysis is a mature field able to identify emerging properties of a system (a–d) as well as the roles that individual nodes (species or habitat sites) play in the network (e–h). Circles and rectangles represent species and habitat sites, respectively. Here, we present only a few examples of the metrics that can be computed (Blüthgen et al., 2006; Dormann et al., 2009). See text for details.

In bipartite networks, *nestedness* is a central property that describes network structure. A network is said to be nested when the communities of sites that have a few links (i.e. species) are a subset of the communities of sites with more links (Baselga, 2010; Figure 2a). In a nested species–habitat network, the entire system will likely be affected if the most species-rich habitat or site is removed. In contrast, the removal of species-poor habitats that only interact with a few habitat generalists is unlikely to have significant ripple effects. In a bipartite network, it is also possible to quantify *modularity* that measures the strength of division of a network into modules. A module comprises a set of habitat sites and species that interact more with each other than with other sites and species outside the module (Figure 2b). Often, networks with a modular structure are expected to have a lower risk of collapse due to their buffering capacity to system perturbations (Dormann *et al.*, 2017; Gilarranz *et al.*, 2017). However, the loss of specific sites may also affect the associated species in the same module due to low redundancy. Hence, the degree of both *nestedness* and *modularity* can have profound conservation implications.

A common way to assess the implications of habitat loss is to look at network *robustness*. The *robustness* of a network can be a key metric for conservation prioritization of

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high value sites and ecosystem management (Sole & Montoya, 2001), as it is defined as the network resilience to the loss of habitat patches or species. For instance, simple simulations that remove habitats randomly or in realistic sequences are one way to quantify community robustness to habitat loss (Figure 2c).

Understanding species selectivity is central to assess the extent of habitat generalization. For instance, *network specialization* (*H2′*) can be useful for comparisons across different networks. The more selective the species are the greater the value of *H2′* for the network: 0 (no specialization) and 1 (complete specialization; Blüthgen et al., 2006). Unselective species used habitats proportionally to their size (green line in Figure 2d), while selective species used sites irrespective of habitat area (blue line in Figure 2d). This metric can be used to test the effect of different drivers (e.g. landscape intensification, climate change) on habitat preferences.

Species–habitat network analysis can also provide insights into the roles of specific habitat sites or species in the network. First, the influence of one site upon another site can be assessed using *apparent influence* metrics (Muller *et al.*, 1999). This index quantifies how much one habitat site contributes to sustaining the species present in another site (Figure 2e). This a typical problem in applied ecology when practitioners introduced novel habitats or interventions in a landscape mosaic.

Another useful metric is node *strength* (Bascompte *et al.*, 2006). This metric captures a single site importance taking into account how much the species depend on this site. A site has high *strength* if it supports a high number of species with high dependency (i.e. specialists) on it (node *a* in Figure 2f). Conversely, sites that only host a few generalist species (node *b*) have low *strength* playing a minor role in the landscape.

Finally, we can also assess the contribution of particular nodes to network level metrics like modularity or nestedness. For example, using among-module *connectivity* (*c*) we can identify hub species connecting different modules (Figure 2g). This can help to identify key-stone sites or species that can affect the robustness of the whole network. To quantify habitat specialization at the species level, generality or preference can be also measured at the node level using several selectivity metrics (e.g. *specialization d'*; Figure 2h).

Use and limitations of the framework

There are several important conditions to consider when operationalizing species–habitat networks. First, users must ensure that the data inputs are realistic and relevant to the sampled community to ensure meaningful results are obtained through network analysis. For sessile organisms, such as lichen or plant species, occurrence directly links to resource use and habitat preference (Burns & Zotz, 2010). On the contrary, for mobile organisms that use multiple resources, species occurrence can assume different ecological meanings (Kremen *et al.*, 2007). For instance, if we consider a specific habitat patch, a species can be recorded at that site because individuals can use multiple resources (e.g. host plants for reproduction, prey, nesting site or structure for roosting or shelter) or simply because individuals are using that site as a stepping stone for dispersal. Second, not all taxa can be appropriately studied by species–habitat networks. One situation where the framework might not be applicable is when average species dispersal in the community is too large (e.g. large mammals or birds) compared with the feasibility of field sampling. Third, the species–habitat networks may be limited in use when the landscape structure is characterized by very high habitat heterogeneity at a spatial scale much smaller than the average species dispersal. However, human-impacted landscapes often present high contrast between habitat types providing ideal conditions to apply the framework. Fourth, in its present form species–habitat networks are not spatially explicit and therefore information on the spatial relationships between patches (e.g. connectivity) cannot be derived. Finally, as for most empirical interaction networks, species–habitat networks would suffer to some extent from under-sampling. This limitation is particularly challenging in situations where the communities host many rare species or when species are inherently difficult to sample or observe. Similar to ecological networks, this raises the concern that rare species of high conservation concern may not be appropriately represented in the data. Increasing sampling effort is, therefore, recommended to minimize these biases. At the data analysis stage, when interaction networks contain many singletons, the role of these single observations needs to be carefully explored with the available tools (Vizentin-Bugoni *et al.*, 2016).

Implications for ecosystem management and policy

An urgent question in conservation ecology is to understand how to manage whole landscapes to maximize biodiversity conservation or ecosystem services delivery (Mendenhall *et al.*, 2016; Albert *et al.*, 2017; Harvey *et al.*, 2017). The flexibility of the proposed approach is that it can

easily be applied across a range of ecological fields such as species conservation, habitat restoration, ecosystem services management, or invasion ecology (Memmott *et al.*, 2007). Here, we provide as an example four important research directions that could be addressed by adopting species–habitat networks:

1. Conservation prioritization

Conservation actions often face the trade-off between maximum protection of the environment and a limited budget. Site *strength* values in a landscape or in a protected area network can be used to prioritize which sites to conserve to maximize the biodiversity of any target taxon.

2. Land-use change and community stability

Conservationists often aim to achieve maximum biodiversity representation, without an explicit focus on the long-term stability. Recent studies (Gilarranz *et al.*, 2017) on ecological networks have tried to use architectural patterns such as *modularity* to understand the mechanisms underlying the stability of communities. Similarly, we can investigate if certain species–habitat structures confer stability to the system in order to predict the *robustness* of species–habitat interactions to habitat perturbations.

3. Maximizing biodiversity-based ecosystem services

Landscape interventions to support ecosystem services often require the introduction of new habitats (e.g. hedgerows, mass flowering crops) across a landscape. For instance, pollinators and pest control agents are known to be enhanced by the proximity to semi-natural areas (Kennedy *et al.*, 2013; Schellhorn *et al.*, 2015). Simulations using different landscape configurations of crop fields and green infrastructures can be used to maximize the positive *influence* among sites. For example, placing early mass flowering crops in the right configuration may maximize ecosystem service delivery, without imposing negative effects on natural habitats (Magrach *et al.*, 2018).

4. Impact of invasive species

Landscapes are often invaded by alien plant species with a strong impact on native communities and ecosystem functioning. Here, the application of the species–habitat network will help to better understand the native community response to alien invasions across gradients of landscape composition and configuration. Incorporating a temporal perspective will elucidate how alien species move and use resources across the landscape. For instance, *modularity* or

specialization can provide key information on species spill-over and potential competition between natives and aliens.

One key advantage of the application of the framework is that the scale of the derived ecological information could match the scale of landscape management. In particular, species–habitat networks can help identifying optimal landscape compositions and configurations to design effective conservation interventions. By sampling multiple networks along relevant environmental gradients, these emerging properties can be used to test the effects of large-scale drivers of global change upon ecosystem structure and stability (Schleuning *et al.*, 2012; Tylianakis & Morris, 2017; Pellissier *et al.*, 2018). The versatility, visualization power and ease of interpretation of these networks will enable the application of the species–habitat network concept to a wide array of real-world problems concerning biodiversity conservation and ecosystem service enhancement at different spatial scales.

Chapter 3

Specialization of species-habitat networks in herbivores, predators and pollinators across land-use intensification gradients

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Abstract

Depending on their degree of specialization, most mobile organisms use a complex range of resources across heterogeneous landscapes. Measuring specialization is pivotal for predicting shifts in functional community composition and for quantifying consequences on ecosystem functioning. Here, we applied a species-habitat network approach to elucidate whether land-use induces shifts in habitat specialization of predators, herbivores, and pollinators sampled across multiple landscapes representing independent gradients of composition and configuration. Community specialization declined with loss of semi-natural habitats and increasing patch density, but only in groups with low mobility (predators and herbivores), while pollinators did not change their specialization. The changes in specialization were linked to both species turnover (i.e. replacement of specialists with generalists) and behavioral changes, challenging the assumption that a single species behaves as either a generalist or a specialist irrespective of any environmental variation. Our network approach provided key ecological information to inform landscape management for the conservation of key arthropod guilds across agricultural landscapes.

Introduction

Agricultural intensification has heavily simplified landscapes through the expansion of cropland, causing dramatic declines in farmland biodiversity (Perovic et al. 2015, Flynn et al. 2009) and associated ecosystem services (Power, 2010; Allan *et al.*, 2015). Mitigating these negative effects can only be achieved by a concerted effort to restore green infrastructures, fundamentally redesigning agricultural landscapes at a large spatial scale (Landis, 2017). The subject has been mainly investigated by studying diversity patterns in a focal habitat, and relating them with the composition and configuration of semi-natural habitats in the surrounding landscape mosaic (Leibold *et al.*, 2004; Gámez-Virués *et al.*, 2015; Hadley *et al.*, 2016). While this approach has led towards a better understanding of community responses to landscape processes (Tscharntke *et al.*, 2012; Martin *et al.*, 2019), it is now clear that individual species can use a complex range of resources across multiple habitats depending on their degree of ecological specialization (Ricketts, 2001; Driscoll *et al.*, 2013). Measuring ecological specialization is central for predicting shifts in community functional composition (Devictor *et al.*, 2010; Gámez-Virués *et al.*, 2015) and for quantifying consequences on ecosystem functioning (Ewers & Didham, 2005). However, these complex spatial interactions cannot be

captured by traditional landscape studies, and most of our understanding of specialization shifts is based on expert assessment and/or on literature trait data (Wong *et al.*, 2019). One untested assumption of such approach is that a single species behaves as either a generalist or a specialist irrespective of any environmental variation.
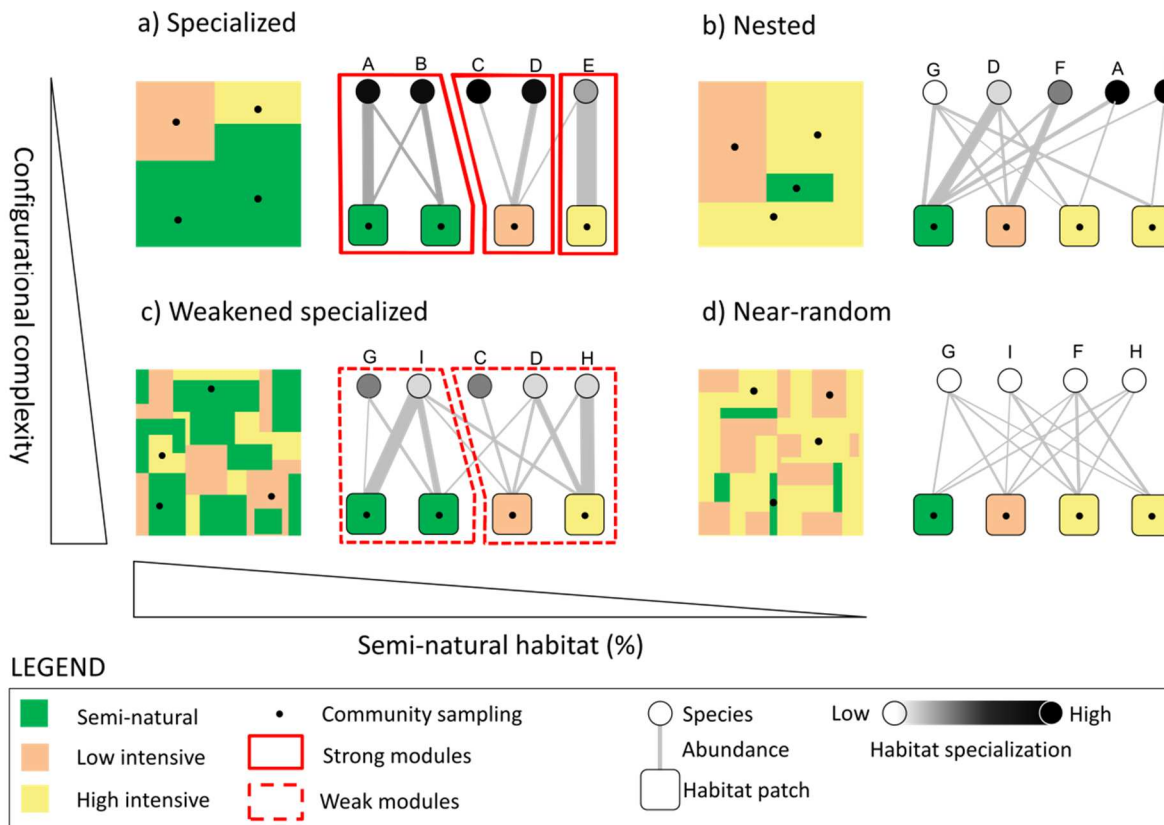

Fig. 1. Hypotheses on how alteration of landscape composition and configuration can modify community habitat specialization.

The degree of habitat specialization of a community can be deeply affected by the loss and fragmentation of natural habitats (Fahrig, 2003; Fischer & Lindenmayer, 2007), through both species turnover and behavioral changes (Barnagaud *et al.*, 2011; CaraDonna *et al.*, 2017) (Fig. 1). Specialization is predicted to be high in undisturbed landscapes with large cover of natural or semi-natural habitats (Fig. 1A), while severe habitat losses are expected to reduce specialization through species turnover, with specialists being progressively lost and replaced by generalists (Fig. 1B) (Gámez-Virués *et al.*, 2015). In this scenario, it is likely for unsuitable habitats to hosts subsets of the species assemblages hosted by species-rich habitats in a nested structure, as predicted by classic island biogeography theory (MacArthur & Wilson, 1963). Similarly, an increase in landscape fragmentation should decrease specialization not only through species turnover, but also by increasing landscape interspersion and thereby resource

accessibility (Fahrig *et al.*, 2011) (Fig. 1C). These effects should be exacerbated when severe habitat loss is coupled with increased fragmentation, with all species having a high chance of moving between different habitats. In the most extreme cases, the community should be composed of super-generalists exhibiting a close-to-random selection of habitats (Fig. 1D). Capturing the complexity of these spatial interactions is challenging, and can be only achieved if the whole landscape is sampled and species occurrence are observed in all the available habitats. Recently, it has been proposed to adapt bipartite network tools to landscape ecology (Marini *et al.*, 2019) to unveil the complexity of species-habitat associations. Such interactions are suited to be envisioned as bipartite networks between species and habitat patches, which can then be described with the specialization metrics developed for traditional ecological networks (Hackett *et al.*, 2019; Pompozzi *et al.*, 2019; Saunders & Rader, 2019).

In this study, we applied a species-habitat network approach to elucidate the way land use influences habitat specialization in three key insect groups with contrasting mobility and functional role: predators (ground beetles, Coleoptera: Carabidae), herbivores (leafhoppers *sensu latu*, Hemiptera: Cicadomorpha), and pollinators (wild bees, Hymenoptera: Apoidea). Specifically, our main goal was to understand how landscape alteration (i.e. loss of semi-natural habitats and increases in patch density) affects the degree of habitat specialization at the level of whole community and individual species. To this end, we sampled the target taxa in 671 sites selected along landscape mosaics, representing independent gradients of composition and configuration in three different regions across Europe.

Materials and methods

Sampling design

The sampling took place in central Germany in 2011 (for pollinators), in north-eastern Italy in 2017 (for predators) and in central Italy in 2018 (for herbivores) (Table 1). In each area, 10 to 15 landscapes were selected, representing gradients of semi-natural habitat cover and patch density, which are common proxies of land use intensification (Chaplin-Kramer *et al.*, 2011; Lizée *et al.*, 2012; Hopfenmüller *et al.*, 2014; Martin *et al.*, 2016). In each landscape, 12 to 25 sampling points (depending on the target organisms) were selected for a total of 671 sites. Landscapes were selected in QGIS 2.18.27 using land-use maps. No landscapes were overlapping each other except in two cases in northern Italy, in which there was a minor overlap between two landscapes (4.01% and 0.66%, respectively). To ensure an even spatial distribution

and aid the selection of the habitat type of sampling points, a grid (350 m in cell side for predators and 200 m for herbivores and pollinators respectively) was used on each landscape. For pollinators, one sampling point was placed roughly at the center of each grid cell, guaranteeing that point selection represented the relative abundancies of all the main habitat types in the landscape. For predators and herbivores, the point in each cell was assigned to either semi-natural habitats or cropland, depending on which macro-habitat type covered more than 50% of the cell according to 2015 Google Satellite images; the final location of each site was kept as close as possible to the original selection (to ensure a degree of even spatial distribution), but it had to be adjusted at the beginning of field work to be near roads and thus guarantee easy access. Exact semi-natural or agricultural habitat category was decided on field, as in most cases it was impossible to determine it beforehand. In all cases, the number of traps per habitat type reflected the relative abundance of the habitat itself. More details about the pollinator sampling can be found in Scherber *et al.* 2018.

Table 1. Information about sampling location, period, technique, number of landscapes and sampling points for each of the target functional groups.

	Predators	Herbivores	Pollinators
Taxonomic group	Carabidae (ground beetles)	Cicadomorpha (leafhoppers *sensu latu*)	Apoidea (wild bees)
Location	Udine (north-eastern Italy)	Pescara (central Italy)	Gottingen (central Germany)
Coordinates	46°4′0″N; 13°14′0″E	42°28′0″N; 13°06′0″E	51° 32′0″N; 9° 56′0″E
Mean annual temperature	13 ºC	24 ºC	8,5 ºC
Mean annual precipitation	*c.* 1300 mm	*c.* 735 mm	*c.* 650 mm
Number of landscapes	15	10	10
Size of sampling area	Circle of 1 km of radius	Circle of 500 m of radius	Square of 1 X 1 km
Number of sampling points	300 (20 per landscape)	121 (12 per landscape, except for one which had 13)	250 (25 per landscape)
Sampling period and duration	May - June 2017 (28 consecutive days of activation)	April - October 2018 (154 total days of activation)	May - June 2011 (3 days in May and 3 in June)

Sampling technique	Pitfall traps (0.5 l, 10 cm in diameter, 14 cm deep, activated with 150-200 ml of ethilene glycol 40%)	Yellow sticky traps (Serbios, 40 X 24.5 cm, 1 m from soil surface)	Yellow pan traps (0.75 l, 15.6 cm in diameter, activated with water, on a wooden pole at vegetation height)
Habitat classification	Annual crops, forest, hedgerow, meadow, perennial crops	Annual crops, forest, meadow, olive, vineyard	Annual crops, forest, meadow, oilseed rape

Insect sampling and identification

Sampling technique varied in each area, because of differences in the ecology and phenology of the target taxa. Ground beetles were sampled with pitfall traps (protected from rain by plastic covers) for 28 consecutive days from the end of May to the end of June of 2017. Traps were emptied and immediately reactivated after the first 14 days to avoid overfilling, resulting in 2 consecutive rounds. Collected ground beetles were stored in 70% ethanol, and then identified to the species level by morphological traits. To account for the fact that certain traps were active for only one sampling round (having been destroyed during the other), a mean between the two sampling rounds was calculated for the other trap. Decimal values were then rounded up, as the calculation of network-level specialization and null models assumes that values are integers (Blüthgen *et al.*, 2006; Dormann *et al.*, 2008). Ground beetles prey upon other invertebrates and seeds, and are thus considered important biocontrol agents of pests and weeds (Lövei & Sunderland, 1996; Honek *et al.*, 2003). These insects preferentially or exclusively move by walking, and as such they have a much lower level of mobility if compared with flying insects (Allema *et al.*, 2015, 2019).

Sap-feeders were sampled with yellow sticky traps for a total of 154 days from the end of April to mid-October of 2018. During the period of highest activity density of sap-feeders (until mid-June) sampling took place for non-consecutive periods of two weeks, with two weeks gaps between them. After that date, the sampling became continuative, with traps being replaced every 2-3 weeks. When collected from field, traps were wrapped in transparent plastic film and stored at room temperature, and insects were identified to the species level. Many *Cicadomorpha* species are important emerging pests in both annual and perennial crops due to their role as vectors of plant pathogens such as such as viruses, phytoplasmas and bacteria (Chuche & Thiéry, 2014; Cornara *et al.*, 2017). Species are often polyphagous and feed on xylem or phloem sap and can use different habitats during their life cycle causing important

economic damages to crops. The average mobility of this group is often relatively low (Lessio & Alma, 2004; Dietrich, 2009).

Native bees were sampled with yellow pan traps for 3 days in May and 3 days in June of 2011. Traps were placed at vegetation height to avoid attracting insects from surrounding habitats. It is known that pan traps underestimate the abundance of certain large pollinators (such as bumblebees), and the outcomes of this method can be influenced by the surrounding habitat context, and especially by floral resource availability (Baum & Wallen, 2011; Saunders & Luck, 2013; O'Connor *et al.*, 2019). However, pan traps are also much easier to standardize, less time consuming, can be used at multiple sites simultaneously, and they are less biased than non-specialist collectors sampling transects (Westphal *et al.*, 2008; Tuell & Isaacs, 2009; O'Connor *et al.*, 2019; Scherber *et al.*, 2019). All these factors contribute to the choice of pan-traps for such a large scale sampling campaign, covering hundreds of sites, simultaneously. Collected specimens were sent to specialists for identification. The European honey bee *Apis mellifera* L. was excluded from the dataset as it is managed and its populations do not depend on nesting availability, but on beekeeper socio-economic factors. The pollination services delivered by wild bees are pivotal for wild and domesticated plants alike (Biesmeijer, 2006; Cane *et al.*, 2007; Ollerton *et al.*, 2011). These insects usually have a relatively high mobility compared with the previous two taxa, with foraging ranges of several kilometers (Walther-Hellwig & Frankl, 2000; Greenleaf *et al.*, 2007). For more details about sampling procedures, see Table 1, and for pollinator sampling in particular see also Scherber *et al.* 2018.

Diversity metrics

For each landscape we calculated two widely employed diversity metrics, species richness and Smith and Wilson's evenness index E_{var} (Smith & Wilson, 1996), as well as the total abundance of each group. Additionally, we evaluated the sampling effort for each group by calculating species rarefaction curves based on 1000 randomizations using the "vegan" package in R 3.5.2 (Oksanen *et al.*, 2019).

Species-habitat networks

While sampling each habitat category proportionally to its abundance ensured a correct representation of the species assemblage and habitat diversity of each landscape, the network analysis was carried out using the single habitat patches (corresponding to each trap) as nodes. This was deemed more correct as patches are differentiated by a variety of factors other than habitat category (i.e. shape, size, position…); additionally, this approach reduces the risk of bias caused by varying sampling effort per node. Species-habitat networks were built from

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bipartite interaction matrices between l habitat patches in rows and J species in columns. Each network corresponded to a single landscape. The strength of the interaction between a species and a patch was represented by the number of individuals of that species that were found in that patch.

Network-level metrics

We focused on network metrics directly relevant to specialization (Schleuning *et al.*, 2012). First, we calculated the network specialization index H_2' (Blüthgen *et al.*, 2006). H_2', derived from Shannon entropy, characterizes the degree of specialization of the entire network, ranging from 0 (maximum generalization) to 1 (maximum specialization). Second, we calculated modularity, defined as the tendency to form modules in which species and habitats interact more strongly with each other than with the rest of the network (Olesen *et al.*, 2007). This property is expected to be positively correlated with specialization (Lewinsohn *et al.*, 2006). We also calculated unweighted NODF (Almeida-Neto *et al.*, 2008) as a measure of nestedness. In highly nested networks, the habitats used by rare species are a subset of the habitats used by more common species (Bascompte *et al.*, 2003). This results in species-rich habitats being the only ones to host specialists, and in species-poor habitats only hosting widespread generalists. Both modularity and nestedness can have profound implications for conservation (Gilarranz *et al.*, 2017; Marini *et al.*, 2019). The significance of the main network-level metrics (H_2', modularity, NODF) was tested by creating 1000 null models per network with the Patefield algorithm and calculating z-scores for each metric and network (Dormann & Strauss, 2014). Network analyses were performed with the package "bipartite" in R 3.5.2 (Dormann *et al.*, 2008).

Node-level metrics

Beside the network specialization index H_2', we computed its species-level counterpart d' (Blüthgen *et al.*, 2006). d' characterizes the level of specialization of each individual node (in our case, the arthropod species) in the network ranging from 0 (maximum generalization) to 1 (maximum specialization). For the calculation of this index, we took into account the abundances (and thus the actual availability) of habitat patches, calculated as the number of traps (1) for each patch. We also computed the normalized degree, which is the number of links per species (Freeman, 1979), scaled by the number of possible partners.

Beta-diversity

As species turnover is expected to be a major factor in shaping network-level specialization, we calculated the mean beta diversity between landscapes for each group, measured as the

Colwell and Coddington index (Colwell & Coddington, 1994) on presence/absence data, as well as its separate components of true species turnover (Williams, 1996; Cardoso *et al.*, 2009) and species richness (Podani & Schmera, 2011; Carvalho *et al.*, 2012). These analyses were performed by using the "betadiver" function in the package "vegan" in R 3.5.2 (Oksanen *et al.*, 2019).

Additionally, we calculated the beta diversity of interactions between species and habitat types considering only the species and habitats shared between each network couple. This allowed us to focus on network rearrangements caused by actual behavioral changes, rather than species turnover. In analogy with species beta diversity, we also calculated the interaction beta diversity turnover and richness components by using a modified version of the "betalink" package in R 3.5.2 (Poisot *et al.*, 2012; Noreika *et al.*, 2019). For both interaction and species beta diversity, the turnover component β_3 between focuses on the true replacement of interactions/species between two landscapes, and it is calculated using the following formula:

$$\beta\_3 = 2 * ((\min(b, c) / (a + b + c))$$

where a is the number of species/interactions shared by both landscapes, and b and c are the number of species/interactions exclusive to the first and to the second landscape, respectively. The richness component of beta diversity β_{Rich} focuses on the difference in interaction/species number between two landscapes, and is is calculated as:

$$\beta_{Rich} = |(b - c)| / (a + b + c)$$

The Coldwell and Coddington index β_{CC} for overall beta diversity results from the sum of β_3 and β_{Rich}, and can also be calculated as:

$$\beta_{CC} = \beta\_3 + \beta_{Rich} = (b + c) / (a + b + c)$$

Landscape metrics

Landscape metrics were calculated in circular buffers of 1 km (for predators and herbivores) or 1.5 km (for the more mobile pollinators) in radius centered on the sampling area. In each buffer, we manually digitized the main habitat categories (forest, meadow, annual crops, etc…), with habitat classification being different for each group, as habitat types can have different importance for taxa with different ecologies (Table 1).

Raster maps (pixel size: 1x1 m) of each landscape were then analyzed in Fragstats 4.2 to calculate the *%* cover of semi-natural land (a proxy for landscape compositional heterogeneity) and patch density (a proxy for landscape configurational heterogeneity), defined as the number of patches per 100 ha (Cushman *et al.*, 2008). For each landscape couple, we calculated the geographical distance between landscape centroids, the Euclidean dissimilarity between the levels of patch density and the Bray-Curtis dissimilarity (Bray & Curtis, 1957) between landscape habitat composition using the "vegan" package in R 3.5.2 (Oksanen *et al.*, 2019).

Statistical analyses

Network-level

For each group, we calculated linear models between network-level metrics and landscape metrics. In addition to semi-natural cover and patch density, we added network size (calculated as the number of cells in each matrix) as an additional explanatory variable in all models (Magrach *et al.*, 2018). We verified the absence of multicollinearity between explanatory variables using Variance Inflation Factors. All VIFs were around 1, indicating very low collinearity.

Node-level

To investigate node-level metrics, we tested the effect of the previously mentioned explanatory variables on *d'* and normalized degree (expressed as 1 – normalized degree, to make it positively linked with specialization) by using linear mixed-effects models, with insect species used as a random factor. We included only species present in at least 5 landscapes, and with more than 3 individuals per landscape. By including species as random factor, the model tested for within-species behavioral shifts in habitat specialization due to habitat use rewiring.

Results

Overall, we identified a total of 30,572 ground beetles, 16,680 leafhoppers *sensu latu* and 4,445 wild bees belonging to 104, 83 and 110 species respectively. The most abundant species in the three groups were the generalist predatory beetle *Pterostichus melas* (Creutzer) (11,184 individuals, more than one third of the captures), the leafhopper *Thamnotettix zelleri* (Kirschbaum) (5,273 individuals, almost one third of the captures) and the sweat bee *Lasioglossum pauxillum* (Schenck) (2,253 individuals, more than half of the captures). The shape of the rarefaction curves (Appendix B Fig. B1) suggests that the sampling effort adequately represented the diversity of predators and herbivores in the studied areas. The

sampling effort for pollinators appeared to be somewhat lacking in comparison, which may be linked with the inherent limitations of the pan trap method and the higher mobility of this group.

Semi-natural habitat cover showed a tendency for positively influencing predator evenness, and it was negatively linked with their abundance. None of the other abundance/diversity metrics for the other groups were influenced by the landscape variables (Table 2).

All networks were significantly more specialized and modular and significantly less nested than expected by chance (except for one case for NODF in pollinators – see Appendix B Table B1). The values of H_2' and modularity tended to be higher for predators compared to the other groups (Fig. 2a – b), while NODF values tended to be higher for herbivores (Fig. 2c).
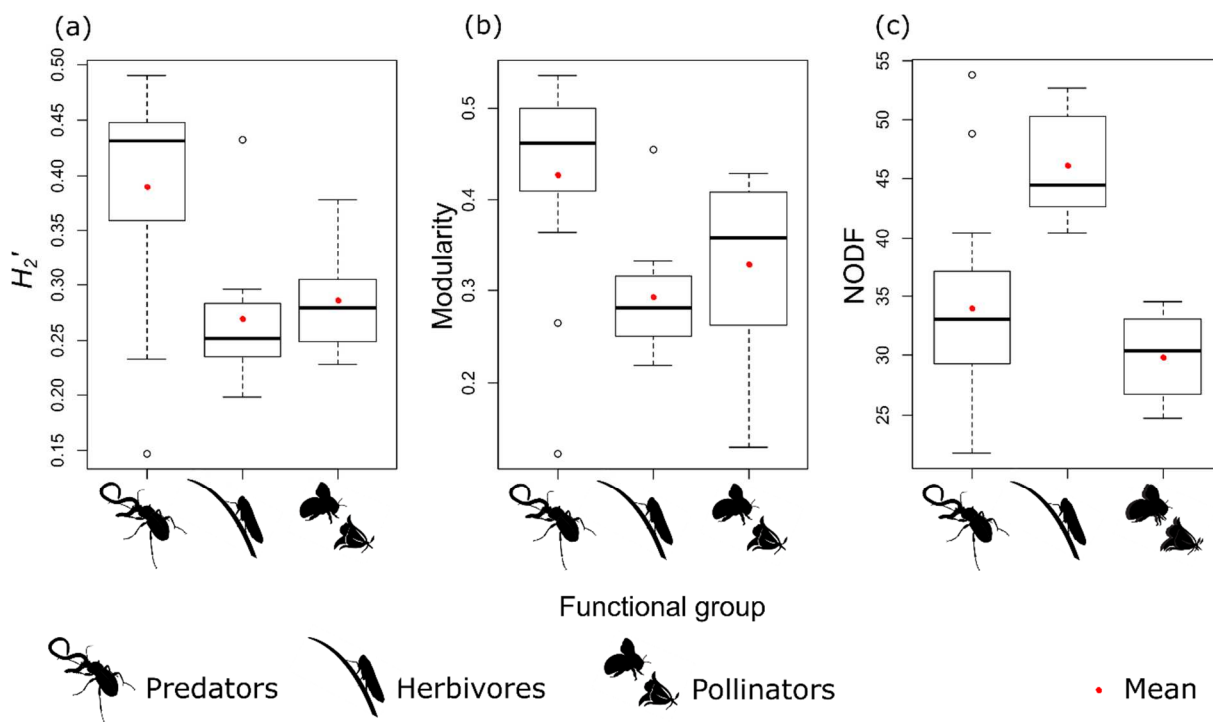

Fig. 2. Box plots representing the values of network-level specialization H_2' (a), modularity (b) and nestedness (NODF) (c) for the three groups.

Effects of landscape composition and configuration on species-habitat networks

Network-level

Predator network-level metrics were influenced by semi-natural cover, with specialization and modularity showing a positive relationship and NODF showing a negative correlation (Table 2, Fig. 3a). Herbivore network-level specialization H_2' and modularity significantly decreased with increasing patch density, while they showed a tendency to increase with semi-natural cover

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(Table 2, Fig. 3b). For pollinators, there were no effects of landscape variables on network-level metrics (Table 2, Fig. 3c).

Species beta diversity between landscapes was relatively high (with assemblages sharing on average less than 50% of the species for predators and pollinators, and around 60% for herbivores), and it appeared to be mainly driven by species turnover, rather than differences in species richness (Table 3).

Table 2. Results of the linear models testing the effects of landscape features (semi-natural cover and patch density) on landscape-level community features, including network-level metrics (for which we also included network size as an explanatory variable). Networks were built between species and individual habitat patches.

			Df	Estimate	Std. Error	t	p
Predators	**Network - level metrics**	**H_2'**					
		Semi-natural cover (%)	1	0.37658	0.14179	2.65596	0.02235
		Patch density	1	-0.00042	0.00173	-0.24090	0.81407
		Network size	1	0.00004	0.00013	0.30103	0.76900
		Modularity					
		Semi-natural cover (%)	1	0.45766	0.15034	3.04427	0.01116
		Patch density	1	-0.00046	0.00183	-0.24987	0.80729
		Network size	1	0.00002	0.00014	0.11725	0.90878
		NODF					
		Semi-natural cover (%)	1	-40.88658	10.06590	-4.06189	0.00188
		Patch density	1	0.00442	0.12286	0.03594	0.97197
		Network size	1	-0.00353	0.00922	-0.38261	0.70930
	Abundance and diversity	**Abundance**					
		Semi-natural cover (%)	1	-4441.90024	2224.02821	-1.99723	0.06899
		Patch density	1	-11.57473	23.72582	-0.48785	0.63445
		Species richness					
		Semi-natural cover (%)	1	-8.9966	13.3314	-0.675	0.513
		Patch density	1	0.2308	0.1422	1.623	0.131
		Evenness					
		Semi-natural cover (%)	1	0.35036	0.09399	3.72751	0.00289
		Patch density	1	0.00096	0.00100	0.96087	0.35558

|							
Herbivores	**Network - level metrics**	***H₂'***					
		Semi-natural cover (%)	1	0.28303	0.18018	1.57075	0.16730
		Patch density	1	-0.00295	0.00096	-3.07802	0.02172
		Network size	1	0.00141	0.00084	1.68229	0.14350
		Modularity					
		Semi-natural cover (%)	1	0.30280	0.20251	1.49526	0.18547
		Patch density	1	-0.00297	0.00108	-2.75687	0.03299
		Network size	1	0.00104	0.00094	1.10561	0.31124
		NODF					
		Semi-natural cover (%)	1	-12.26366	17.74360	-0.69116	0.51530
		Patch density	1	0.06936	0.09434	0.73523	0.48993
		Network size	1	-0.12905	0.08256	-1.56298	0.16909
	Abundance and diversity	**Abundance**					
		Semi-natural cover (%)	1	-1533.37088	2044.41073	-0.75003	0.47768
		Patch density	1	15.90501	10.91197	1.45757	0.18831
		Species richness					
		Semi-natural cover (%)	1	-5.04990	9.11387	-0.55409	0.59677
		Patch density	1	0.00985	0.04864	0.20256	0.84524
		Evenness					
		Semi-natural cover (%)	1	0.14322	0.11399	1.25641	0.24927
		Patch density	1	-0.00074	0.00061	-1.21008	0.26552
Pollinators	**Network - level metrics**	***H₂'***					
		Semi-natural cover (%)	1	0.03531	0.14356	0.24593	0.81393
		Patch density	1	0.00173	0.00595	0.29040	0.78129
		Network size	1	-0.00011	0.00013	-0.79151	0.45878
		Modularity					
		Semi-natural cover (%)	1	0.06874	0.19496	0.35260	0.73645
		Patch density	1	0.00572	0.00808	0.70865	0.50513
		Network size	1	-0.00051	0.00018	-2.79481	0.03138
		NODF					
		Semi-natural cover (%)	1	9.02875	10.44925	0.86406	0.42075
		Patch density	1	-0.09044	0.43288	-0.20893	0.84141
		Network size	1	0.00465	0.00978	0.47521	0.65144
	Abundance and diversity	**Abundance**					
		Semi-natural cover (%)	1	636.32237	918.35553	0.69289	0.51070
		Patch density	1	15.45675	41.55892	0.37192	0.72095
		Species richness					
		Semi-natural cover (%)	1	0.34087	15.29924	0.02228	0.98285
		Patch density	1	0.39490	0.69235	0.57038	0.58625
		Evenness					
		Semi-natural cover (%)	1	-0.22590	0.17825	-1.26737	0.24555
		Patch density	1	-0.00361	0.00807	-0.44758	0.66798
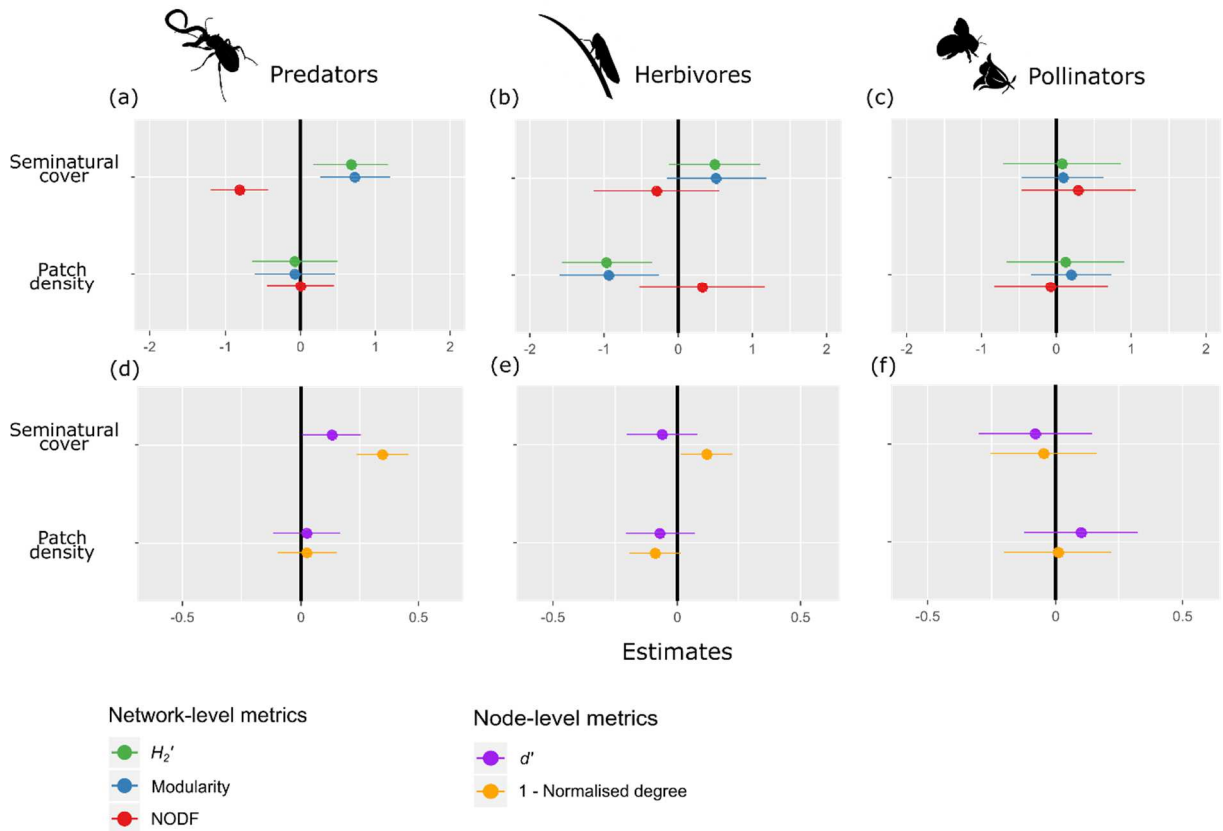
Fig. 3. Effect sizes of semi-natural habitats and patch density on whole-network-level (a – c) and species-level (d – f) network metrics for the three groups.

Table 3. Average beta diversity across all landscapes for the three groups. For species beta diversity, all species were included in the analysis; for interaction beta diversity only species shared between the landscapes of each couple were included. The turnover and richness components of beta diversity are also reported.

	Species beta diversity (all species)			Interaction beta diversity (shared species)		
	Beta diversity	**Turnover component**	**Richness component**	**Beta diversity**	**Turnover component**	**Richness component**
Predators	0.54570	0.39266	0.15304	0.48166	0.35199	0.12967
Herbivores	0.40236	0.35276	0.04961	0.43190	0.34110	0.09080
Pollinators	0.56331	0.40662	0.15669	0.49600	0.33752	0.15848

Species-level specialization

For predators, both *d'* and normalized degree indicated that species-level specialization increased with the amount of semi-natural cover (Table 4, Fig. 3a). For herbivores, the behavior of normalized degree suggests an increase in specialization with semi-natural cover and a tendency for a decrease in specialization with patch density (Table 4, Fig. 3b). For pollinators, we found no effect of landscape variables on species-level specialization (Table 4, Fig. 3c).

Table 4. Results of the linear mixed-effects models testing the effects of landscape features (semi-natural cover and patch density) and network size on node-level network metrics. Insect species was included as a random factor. Networks were built between species and individual habitat patches.

		Value	Std. Error	numDF	denDF	t value	Pr(>|t|)
Predators	***d'***						
	Semi-natural cover (%)	0.19236	0.09421	1	219	2.04177	0.04237
	Patch density	0.00037	0.00105	1	219	0.35649	0.72182
	Network size	-0.00016	0.00009	1	219	-1.80103	0.07307
	1 - Normalised degree						
	Semi-natural cover (%)	0.45861	0.07396	1	219	6.20111	0.00000
	Patch density	0.00033	0.00083	1	219	0.39988	0.68963
	Network size	-0.00004	0.00007	1	219	-0.56444	0.57303
Herbivores	***d'***						
	Semi-natural cover (%)	-0.11362	0.14368	1	180	-0.79079	0.43011
	Patch density	-0.00070	0.00076	1	180	-0.92849	0.35440
	Network size	-0.00005	0.00068	1	180	-0.06705	0.94661
	1 - Normalised degree						
	Semi-natural cover (%)	0.28113	0.12351	1	180	2.27611	0.02402
	Patch density	-0.00110	0.00065	1	180	-1.68730	0.09328
	Network size	0.00024	0.00058	1	180	0.41746	0.67684
Pollinators	***d'***						
	Semi-natural cover (%)	-0.08600	0.12349	1	62	-0.69645	0.48875
	Patch density	0.00447	0.00492	1	62	0.90803	0.36738
	Network size	-0.00006	0.00011	1	62	-0.56614	0.57334
	1 - Normalised degree						
	Semi-natural cover (%)	-0.07581	0.17781	1	62	-0.42632	0.67135
	Patch density	0.00073	0.00710	1	62	0.10282	0.91844
	Network size	-0.00030	0.00016	1	62	-1.86521	0.06689

Even when considering only shared species, all groups show a relatively high level of interaction turnover between landscapes (with values higher than 0.4). Similarly to species beta diversity, the interaction turnover component was more important than the interaction richness difference component (Table 3).

Discussion

Our species-habitat network approach revealed that three key functional groups of arthropods delivering ecosystem services or disservices to agriculture are differentially impacted by either loss of semi-natural habitats or landscape fragmentation. While there was no variation in species richness at the landscape level, network-based metrics offered an unprecedented insight of the

effects of landscape alteration on the way communities use and move across habitats. Overall, landscape alteration affected habitat specialization of the least mobile groups (predators and herbivores), while specialization of the more mobile pollinators was unaffected by landscape features, indicating an opportunistic foraging behavior of this group, which can easily exploit resources at the landscape scale by visiting multiple habitats. Accounting for within-species variation in habitat specialization can increase our understanding of the effects of global changes on species and community dynamics (Hackett *et al.*, 2019).

General topology of species-habitat networks

The species-habitat network approach revealed the complex structure of interactions between multiple habitats and entire communities of predators, pests and pollinators occurring across agricultural landscapes. Similarly to mutualistic ecological networks (Olesen *et al.*, 2007; Dupont & Olesen, 2009; Polidori *et al.*, 2013), species-habitat networks were often more modular and specialized than expected by chance. However, while ecological networks also tend to be more nested than expected by chance (Bascompte *et al.*, 2003; Vázquez *et al.*, 2005), species-habitat networks exhibited an opposite pattern. All of the studied groups included a large proportion of species that show a certain degree of specialization for different habitat types. As a consequence, it is unlikely to find a single habitat that hosts all or even a majority of the species present across the landscape. An often-proposed explanation for the nested structure of plant-pollinator networks is coevolution between species, and the fact that nested assemblages tend to be more robust to perturbations (Bascompte *et al.*, 2003; Memmott *et al.*, 2004; Nielsen & Bascompte, 2007). As coevolution (at least in the traditional sense) cannot act on habitats, this might explain why species-habitat network can stray further from nested structures and support more strictly modular organizations. The fact that modularity and specialization were in general higher for networks of predatory ground beetle can be explained with the lower mobility of these ground-dwelling arthropods, which makes it more difficult for them to move between patches, and links them more strongly to the physical structure of the habitats.

Effects of land-use on specialization: species turnover and habitat use rewiring

For predators, we found a pervasive effect of the loss of semi-natural habitats on community specialization (Fig. 4). As the amount of semi-natural habitats in the landscape decreased, predator assemblages became less specialized and modular, and more nested. For herbivores, networks became less modular and specialized with an increase in patch density (Fig. 4). Changes in species identity were likely a major cause of these patterns (Devictor & Julliard,

2008). This concurs with our initial expectations that both changes in landscape composition and configuration would cause a replacement of specialists with generalists. The negative effect of increased patch density on specialists is probably due to edge effects and the fragmentation of large populations into vulnerable smaller populations (Fahrig, 2003). Pollinator assemblages, on the other hand, appeared to be less sensitive to landscape changes (Fig. 4). Pollinators possess higher mobility than predators and herbivores, which allows them to reach habitat resources even when they become scarcer or more fragmented across the landscapes (Marini *et al.*, 2014).
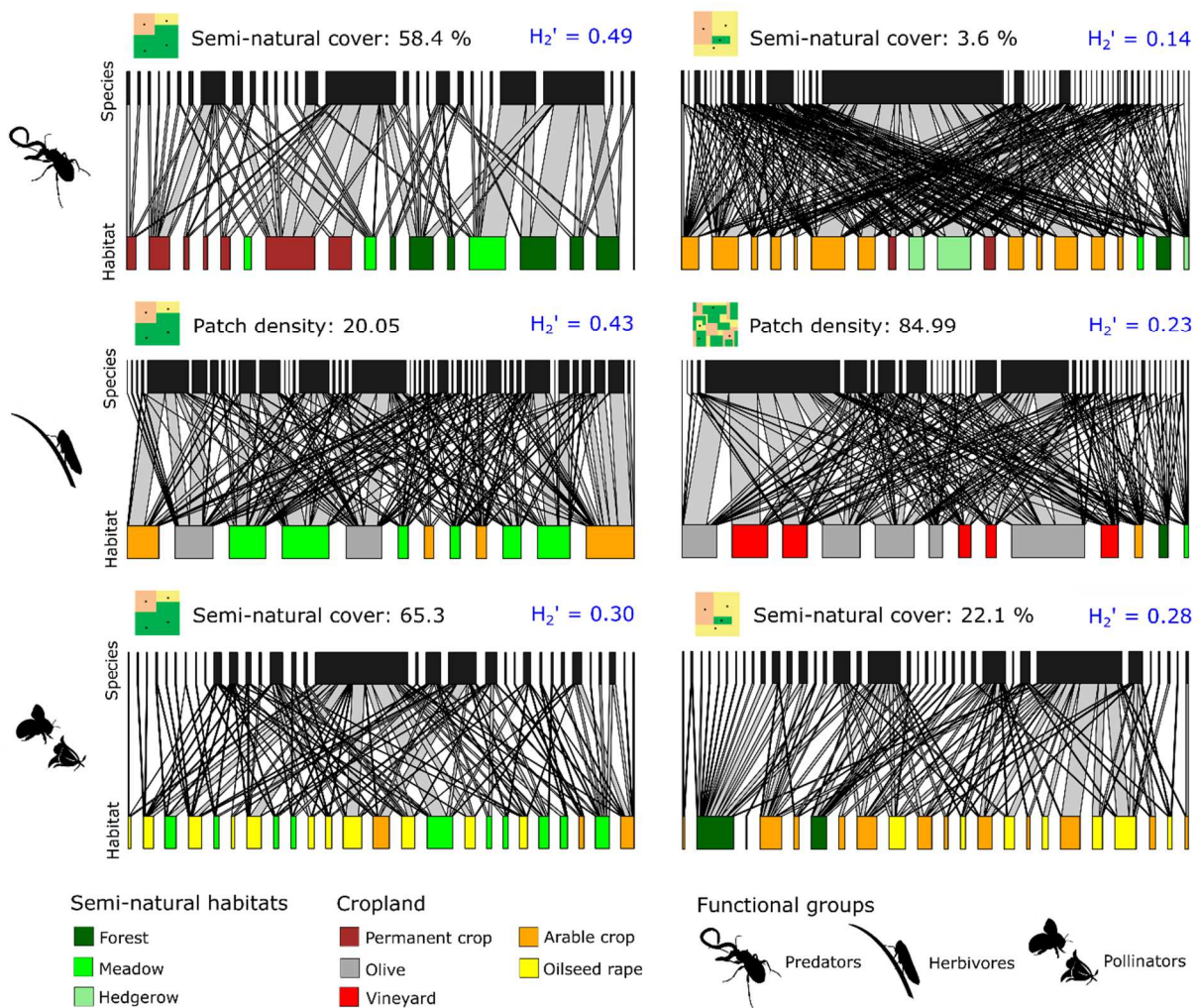
Fig. 4 Examples of species habitat networks in contrasting landscape settings for the three groups.

While species turnover effects on community specialization are well known (Carstensen *et al.*, 2014; Trøjelsgaard *et al.*, 2014), we also observed within species variation in specialization. The relatively high level of interaction turnover suggests that all studied groups can show a degree of behavioral plasticity when it comes to habitat selection. For herbivores,

and even more for predators, species-level metrics reflected the general trends of network-level metrics, corroborating the idea that such plasticity (Barnagaud *et al.*, 2011) can play an important role in network rearrangement, and act as a response to landscape transformations. With increasing semi-natural cover, species tended to only occur in high-quality habitats (i.e. semi-natural habitats) as they became abundant in the landscape. On the contrary, when semi-natural habitats became scarce, the same species adapted to use a wider range of less suitable habitats, thus becoming more generalist. Similarly, we found that patch density could decrease species-level specialization in herbivores, as fragmentation increases the points of contact between different habitat types, thus increasing the chances of spill-over (Fahrig, 2017). We, therefore, challenged the assumption that a single species behaves as either a generalist or a specialist irrespective of any environmental variation. Pollinator species, once again, were not affected by landscape features, probably because of their higher degree of mobility.

Implications for landscape management

The results from our species-habitat networks can also inform landscape management addressing different conservation goals for the three studied groups. First, semi-natural habitats are often considered important source habitats from which beneficial organisms such as **predators** are expected to spill-over to crop fields (Chaplin-Kramer *et al.*, 2011; Duflot *et al.*, 2016). Pristine and large semi-natural areas however, while holding high conservation values and ground beetle diversity, promoted a higher level of specialization in predator communities, reducing the chance of beneficial beetles moving from nearby semi-natural habitats to fields. It follows that, to maximize pest control delivered by this group, it would be better to improve in-field environmental conditions for the open-habitat ground beetle species that already occupy the fields, or to preserve smaller patches of open semi-natural habitats, such as meadows. Our findings also suggest that very simple landscapes dominated by crops sustained very abundant predator populations of species with a low degree of habitat specialization. These species are expected to have positive effects on pest control within crop fields but also potential negative effects on non-pest species in semi-natural habitats (Rand *et al.*, 2006).

Second, concerning low-mobile **herbivores**, landscape mosaics with large, uninterrupted semi-natural habitats and large crop patches tended to host more specialized communities of sap-feeders. Landscape configuration characterized by small patches could have a positive impact on sap-feeding pests, because they are expected to facilitate movements between habitats. For species that are vectors of plant pathogens, these movements are expected to enhance the probability of infection and pathogen spread (Santoiemma *et al.*, 2019). Crops

located in landscapes with high configurational complexity are therefore expected to be more prone to pest colonization from the surrounding habitats, making pest control strategies particularly challenging.

Third, the great interest for the conservation of bees and other **pollinators** (Vanbergen *et al.*, 2013) makes them a top priority for biodiversity management actions (Ricketts *et al.*, 2008). It appears that habitat specialization levels of pollinators were generally low and did not change with landscape simplification. Most of the species appeared able to visit all of the sampled habitat patches, indicating that management strategies should be planned at the landscape scale. For instance, the management of landscape-scale patterns of early and late mass-flowering crops together with semi-natural habitats could be used to sustain vital pollinator communities and crop pollination services (Riedinger *et al.*, 2014) since virtually all pollinator individuals occurring across the landscape mosaic could use the resources provided even in a single habitat patch. Additionally, increasing temporal landscape heterogeneity can have beneficial effect due to 'landscape complementation' for pollinators that need more than one habitat type during their life cycle (Fahrig *et al.*, 2011). However, from a conservation perspective it should be considered that some rare and highly-specialized pollinators might not benefit from increased resources in non-preferred habitats such as arable crops (Diekötter *et al.*, 2010). Finally, as evidenced by the rarefaction curve, it cannot be excluded that the previously discussed limitations of the pan trap method might have partially biased the results; further investigations using alternative pollinator sampling methods are needed to confirm our findings.

In conclusions, it is increasingly clear that detailed knowledge of species-habitat interactions is needed in order to efficiently manage functional biodiversity and enhance the associated ecosystem services at the landscape scale (Tscharntke *et al.*, 2005b). Our novel species-habitat network approach elucidated how different functional groups are impacted by alterations of landscape composition and configuration. Additionally, it proved that individual species can show a remarkable behavioral plasticity, changing their degree of habitat specialization depending on the landscape structure. A better understanding of the way landscape composition and configuration contribute in modifying community specialization could have far reaching consequences in both conservation and restoration ecology.

Chapter 4

Using species-habitat networks to inform agricultural landscape management for spiders

Nardi D, Lami F, Pantini P, Marini L

Abstract

Land-use intensification is a major threat to arthropods across agricultural landscapes. To mitigate these negative effects through appropriate landscape management, it is necessary to understand how entire species communities respond to land-use at the landscape scale. We performed a whole-landscape sampling of spiders in 300 habitat patches across 15 landscapes and built species-habitat networks to evaluate the impact of compositional and configurational simplification on network modularity and habitat specialization. Within each landscape mosaic, spiders showed a high degree of habitat selectivity, i.e. patches of the same habitat type tended to cluster into modules that rarely interacted with each other. Although spiders are expected to disperse between habitat patches more often when landscapes are fragmented, their high modularity and habitat selectivity were not influenced by edge density. However, modularity was the highest at intermediate cover of semi-natural habitats, probably due to the simultaneous presence of multiple habitats with sufficient area to support the associated specialist species. Despite the high habitat selectivity, perennial crops and meadows seemed to play a central role in connecting different habitat modules across the landscapes. On the contrary, forest and hedgerows hosted very distinct species communities that did not occur outside woody habitats. Encouraging the spill-over of spiders from semi-natural habitats to crops to enhance biological control might be more effective for the better-connected permanent crops, while for annual crops it would be probably more effective to improve local field quality for crop specialists or to introduce open semi-natural habitats such as meadows.

Introduction

Agricultural intensification has multiple components operating at different spatial scales, from local field management to landscape simplification (Gámez-Virués *et al.*, 2015). Since the second half of the 20th century, landscape simplification through the removal of natural and semi-natural habitats has caused severe biodiversity losses (Dainese *et al.*, 2015; Lichtenberg *et al.*, 2017), thereby compromising the delivery of key ecosystem services, such as pollination and natural pest control (Tscharntke et al. 2012). Spiders are amongst the most abundant and diverse invertebrate predators (Nyffeler & Birkhofer, 2017), greatly contributing to natural pest control in several agro-ecosystems (Birkhofer *et al.*, 2016, 2018b), and as such, they are a major focus for biodiversity conservation and ecosystem service enhancement efforts (Michalko *et al.*, 2019).

The field of landscape ecology has made significant inroads towards understanding spider responses to landscape processes, providing a solid evidence base for managing different habitats for spider conservation (Shackelford *et al.*, 2013). Most of these studies have investigated the effects of local quality of a focal habitat (either semi-natural or cropland) (Batáry *et al.*, 2008; Djoudi *et al.*, 2018) or the composition/configuration of the surrounding landscape (Schmidt *et al.*, 2005; Öberg *et al.*, 2007; Drapela *et al.*, 2008). A staggering amount of biodiversity studies focus on the effects of these variables on individual habitat types (Gallé *et al.*, 2019), but this research does not provide a full understanding of how community-level processes are affected by land-use at the scale of whole landscapes.

Capturing the complexity of these spatial interactions is challenging and can be only achieved if the entire landscape is sampled and species are observed in all potentially available habitats (Scherber *et al.*, 2019). Recently, it has been proposed to adapt bipartite network tools to landscape ecology (Marini *et al.*, 2019) to unveil the complexity of species-habitat associations at the landscape scale. Species-habitat interactions are suited to be displayed as the two types of nodes of a bipartite network, allowing the use of the large set of metrics developed for ecological interaction networks. In particular, network analyses can help reveal the full range of species habitat preferences (i.e. habitat specialization) across a landscape simplification gradient, providing pivotal information for the conservation of diverse and widespread groups such as spiders. On the one hand, community habitat specialization is expected to be high in undisturbed landscapes with large cover of semi-natural habitats. In this case, species-habitat networks should exhibit strong modularity and specialization, where patches belonging to the same habitat are tightly connected to each other but only weakly connected to patches belonging to different habitats. On the other hand, severe losses of semi-natural habitats are expected to reduce network modularity and specialization through species turnover, where specialists are progressively lost and replaced by more generalist species (Gámez-Virués *et al.*, 2015). Similarly, habitat fragmentation and increased configurational complexity can lead to an overall decrease in specialization by increasing edges between different habitats and thus the chances of spill-over between patches (Fahrig *et al.*, 2011). In the most severe scenarios of habitat loss and fragmentation, network modularity should be completely disrupted due to the dominance of super-generalists. These changes in community specialization can have important consequences for species diversity conservation and associated ecosystem services (Clavel *et al.*, 2011). Hence, understanding how spider species use different habitats and upscaling the effect of land-use change at the landscape scale are becoming urgent tasks in order to identify effective conservation strategies.

Here, we sampled spider communities using pit-fall traps across 15 landscapes spanning statistically independent gradients in landscape composition and configuration. First, we investigated the role of the main habitat types occurring across the landscapes in supporting spider diversity at the local scale using traditional diversity analyses. We hypothesised that semi-natural habitats should host higher diversity of spiders than crop habitats and that the latter should host more habitat generalists than the former. Second, we built species-habitat networks (Marini *et al.*, 2019) and evaluated the impact of compositional and configurational simplification on network modularity and specialization. We hypothesised a decrease in network modularity and specialization with the loss of semi-natural habitats -which should favour generalist species- and with habitat fragmentation, which is expected to promote the spill-over of individuals and species among habitats (Fahrig *et al.*, 2011). Third, to exemplify the application of the species-network approach to conservation issues, we identified landscape management strategies to enhance spider communities potentially contributing to pest control in crop habitats.

Materials and methods

Study area

The study took place in the Friuli plain, in north-east Italy (46°04′N; 13°14″E) (Appendix C Fig. C1). The area is dominated by crops (i.e. mostly cereals and vineyards) interspersed with different semi-natural elements (i.e. forests, hedgerows, and meadows). The region is characterized by a temperate climate, with a mean annual precipitation of c. 1300 mm and a mean annual temperature of 13°C.

Sampling design

We selected 15 different landscapes, representing independent gradients of semi-natural habitat cover (range: 4-60%) and edge density (range: 31-291 m ha^{-1}) (Pearson's correlation= 0.33, P=0.23) (see the landscape descriptors section for more details about the landscape metrics). Each landscape was a circular area of 1 km radius, selected based on a 2013 soil use map. We overlaid a grid (cell side length: 350 m) on each landscape, and selected a sampling point for each of 20 cells, for a total of 300 sampling points in the whole study area. The number of traps per habitat type was selected proportionally to the habitat cover in each landscape (Appendix C Fig. C2). A minimum of five semi-natural sites, however, were selected in all landscapes, to enable the comparison of the two macro-habitat categories (semi-natural and crop) even in very

intensively-cropped landscapes. The final location of each sampling point had to be adjusted at the beginning of field work to guarantee access. The scale of 1 km was selected to be large enough to have a c. 500 m buffer area also around the most peripheral traps (Batáry *et al.*, 2008, 2012).

Spider sampling and identification

A single pitfall trap was placed at each sampling site, with each trap consisting of a 0.5 L plastic cup (upper diameter of 10 cm, depth of 14 cm) buried flush with the soil surface and protected from rain by a plastic cover. Traps were activated with $\simeq$ 100 ml of 40% ethylene glycol for 4 weeks from May to June of 2017. The sampling period was chosen to catch the spring-summer species according to the local knowledge of spider phenology (based on PP's spider collection in the Museo di Scienze Naturali di Bergamo). Traps were emptied and immediately reactivated after the first two weeks, to avoid overfilling, resulting in two consecutive sampling rounds. Collected spiders were stored in 75% ethanol. Adult specimens were identified to the species level using morphological characters as indicated in the latest references available on the World Spider Catalog (World Spider Catalog, 2019). To first identify family and genus, we used the keys available on https://araneae.nmbe.ch/. For this study, we removed from the datasets all spider species known not to be ground-dwelling (Cardoso et al. 2011), as pitfall trapping is not an appropriate sampling method for those species. All specimens were stored in the collection of the Museo di Scienze Naturali di Bergamo (PP).

Limitations of the sampling design

A potential limitation of our trapping was the reduced spatial and temporal sampling effort per site. As such, the sampling captured the peak of activity of the spring-summer species, but might not be representative of the species more active in late summer and fall. The main reason to use only one pit-fall trap per site and to sample only spring-summer species was the need to replicate multiple species-habitat networks without collecting an excessively high (and thus not readily determinable) number of individuals. We expected that the large sampling effort at the landscape scale (n=20 traps) could compensate the use of single traps. The shape of the rarefactions curves seemed to support this prediction (see *Diversity analysis* section). To reduce the potential effects of micro-habitat variation on pit-fall catches (Sattler *et al.*, 2010), we located the trap in homogeneous vegetation representative of the selected habitat type. Although inherent differences in micro-habitat heterogeneity between habitat types existed, they were not expected to bias the results due to the large number of sampling sites (n=300 traps). Temperature is another factor that can affect activity-density estimates based on pit-fall traps

(Saska *et al.*, 2013). However, the comparable elevation and climate across the 15 landscapes and the simultaneous sampling of all sites should have reduced this potential bias. Finally, although some habitat types can present cooler temperatures than others (e.g. forests compared to arable crops), the species composition sharply changed between habitats making the outcomes of any potential correction method unpredictable when applied to different species assemblages.

Landscape descriptors

For each landscape, we manually digitized a vectorial habitat map based on satellite imagery (Google Earth 2015). We categorized all habitat patches according to the following classes: forest, meadow, hedgerow, annual crop, perennial crop, urban area and water body.

Landscape metrics were calculated using Fragstats 4.2 (Mcgarigal & Ene, 2013). For class-based metrics, we did not consider the "urban area" and "water body" classes, as they were scarce in the chosen landscapes and hostile to most spider species. We selected semi-natural habitat cover (%) as a composition metric and edge density of semi-natural habitat (ED) as a configuration metric, as they are widely employed proxies for landscape simplification (Holzschuh *et al.*, 2010; Chaplin-Kramer *et al.*, 2011; Martin *et al.*, 2016).

Diversity analyses

For each landscape, sampling effort was evaluated by calculating species rarefaction curves using the R package "vegan" (Oksanen *et al.*, 2019), based on 1000 randomizations. Using the same method, we also built rarefaction curves for each habitat type. The rarefaction curves showed that the sampling effort was comparable across the 15 landscapes (Appendix C Fig C3a), while the different habitats showed different slopes with meadows, hedgerows and perennial crops exhibiting the highest spatial turnover (Appendix C Fig. C3b). The different slopes did not bias the comparison between habitats based on alpha-diversity (average species richness per trap).

For each trap, we calculated activity-density, species richness (alpha-diversity) and evenness (E_{var} index) (Smith & Wilson, 1996; Tuomisto, 2012). In order to detect the differences between habitats, we fitted linear mixed-effects models with habitat type as a fixed effect and landscape ID as a random factor using the *nlme* package (Pinheiro *et al.*, 2018) in R 3.5.1 (R Core Team, 2016). Pairwise differences between habitats were further tested using a post-hoc Tukey test.

To visualize the variation in species composition across habitats we created an ordination plot based on a Multidimensional Scaling (MDS) and tested compositional

differences between habitats using analysis of similarities (ANOSIM) in the package *vegan* in R. We used Bray-Curtis distance for both analyses. The advantage of MDS is that it represents the ordering relationships amongst species assemblages where distance between objects in the ordination plots can be directly interpreted as dissimilarity values. In the ordination plot, 95% confidence ellipses based on bootstrap were drawn using the coord.ellipse function in the FactoMineR package for R (Lê *et al.*, 2008).

To test the effects of landscape composition and configuration on species diversity at the landscape scale, we pooled the traps per landscape, computed total spider activity-density, species richness (gamma-diversity) and evenness (E_{var} index) and fitted linear models with semi-natural habitat cover and edge density as explanatory variables. We also included the quadratic term of both variables to test for potential non-linear effects.

Species-habitat networks

For each landscape, we built a species-habitat network, with habitat patches and spider species acting as nodes, and species activity-density in each patch acting as links (Marini *et al.*, 2019). We focused on modularity, defined as the tendency to form modules in which species and habitats interact more strongly with each other than with the rest of the network (Olesen *et al.*, 2007). Once the modular structure is identified, it is possible to determine the role of each patch within the network and the potential interchange of species between modules across the entire landscape (Marini *et al.*, 2019). Modularity represents an efficient tool to identify sets of patches, which could be considered management units hosting similar species assemblages. In particular, the presence of modules composed of patches belonging to the same habitat type would indicate high habitat specialization. To calculate the modularity index Q for each landscape, we applied the DIRTLPAwb+ algorithm (Beckett, 2016). We checked for modularity significance by comparing the observed values with those obtained from 1000 null models (Dormann & Strauss, 2014) calculated with the Patefield algorithm (Patefield, 1981). Additionally, we computed the network-level specialization index H_2' (Blüthgen *et al.*, 2006). H_2' is an index that ranges from 0 to 1 and describes the level of "complementarity specialisation" of an entire bipartite network. The more selective the species in the network are, the higher is the value of H_2'. When all species behave as full generalists (random choice of habitats) the index tends to zero. Before computing the metrics described above, we removed from each network the singletons (i.e. species with only one individual per landscape). Then, we tested whether Q and H_2' depended on landscape composition and configuration by fitting a linear model with proportion of semi-natural habitats and edge density as explanatory

variables. We also included the quadratic term of both variables to test for potential non-linear effects.

Finally, we calculated the among-module connectivity (Guimerà & Amaral, 2005), also known as the participation coefficient, for each habitat patch. For a given network node, this index is close to 1 if the node is well connected to the rest of the network and its links are uniformly distributed among modules, while it is 0 if all of its links occur within its own module. If one specific habitat exhibits high participation coefficient this indicates that the patches of that habitat tend to host species that also occur in different modules, revealing a hub role of those patches. On the other hand, patches with values close to zero indicate that the patches do not share species outside their module (very high habitat specialization). All networks analyses were performed using the R package "bipartite" (Dormann *et al.*, 2009b). We tested whether the participation coefficient differed between habitat types using linear mixed-effects models, with habitat type as a fixed effect and landscape ID as a random factor.

Results

General results

A total of 7921 adult individuals (146 species, 27 families) of spiders were collected, of which 7469 were determined to species level (females of the genus *Trochosa* were not determined) or to sibling species groups (*Pardosa lugubris* gr. and *Dysdera ninnii* gr.) (Appendix C Table C1). Only 7002 records of ground-dwelling species were used for statistical analyses. The species most caught by pitfall traps were *Trochosa hispanica* Simon, *Pardosa hortensis* (Thorell), *Pardosa proxima* (C. L. Koch) and *Pardosa agrestis* (Westring). Lycosidae comprised about 77% of all individuals.

Diversity patterns

The average number of species per trap (alpha-diversity) was higher in perennial crops and open semi-natural habitats (i.e. meadows and hedgerows) than in annual crops and forests (Fig. 1a), while activity-density and evenness showed less variation between habitats (Table 1a, Fig. 1b - c).

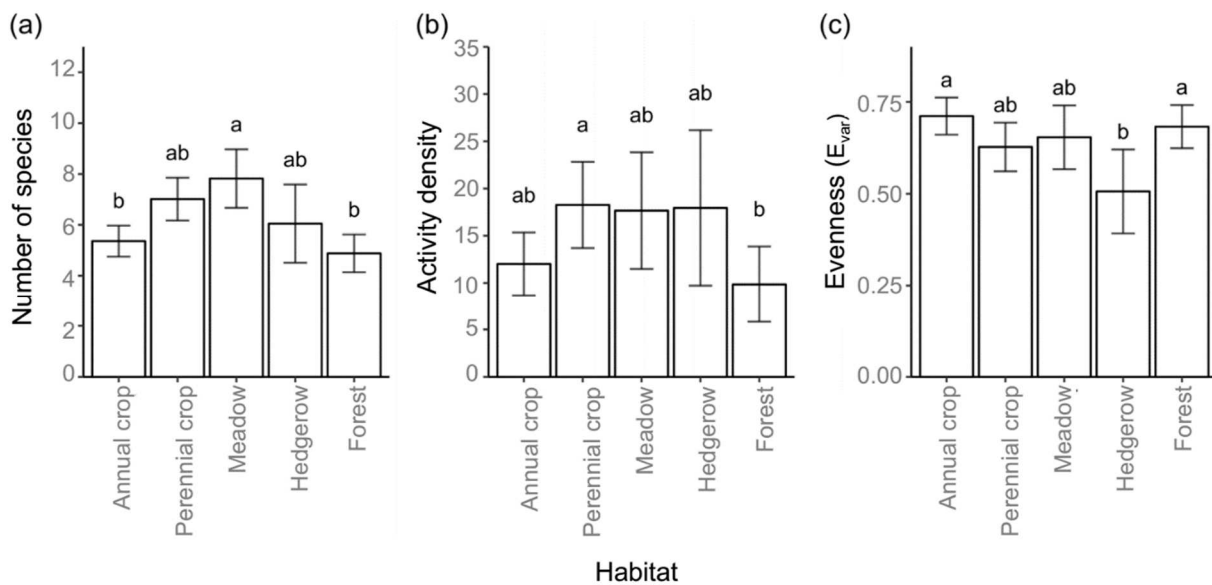**Table 1.** (a) Species richness, (b) activity-density and (c) evenness (Evar index) for each habitat type. Bars represent mean ± intervals of confidence (95%) from a the linear mixed-effects model. The differences were assessed using a post-hoc Tukey test (P<0.001).

Response variable	Explanatory	MS	df	F	P
a) Species richness	Habitat type	63.268	4, 275	7.97	<0.001
b) Activity density	Habitat type	739.59	4, 275	3.305	0.011
c) Evenness (E_{var})	Habitat type	0.16437	4, 275	3.986	0.004

Fig. 3. (a) Species richness, (b) activity-density and (c) evenness (Evar index) for each habitat type. Bars represent mean ± intervals of confidence (95%) from a the linear mixed-effects model. The differences were assessed using a post-hoc Tukey test (P<0.001).

The ANOSIM indicated that the different habitats tended to host different species assemblages (R-statistic=0.274, p= 0.001 based on 999 randomizations). In particular, hedgerow and forest patches hosted similar species assemblages, that were very distinct from those inhabiting arable crop patches (Fig. 2). Perennial crops and meadows tended to present an intermediate species composition between arable crops and woody habitats.
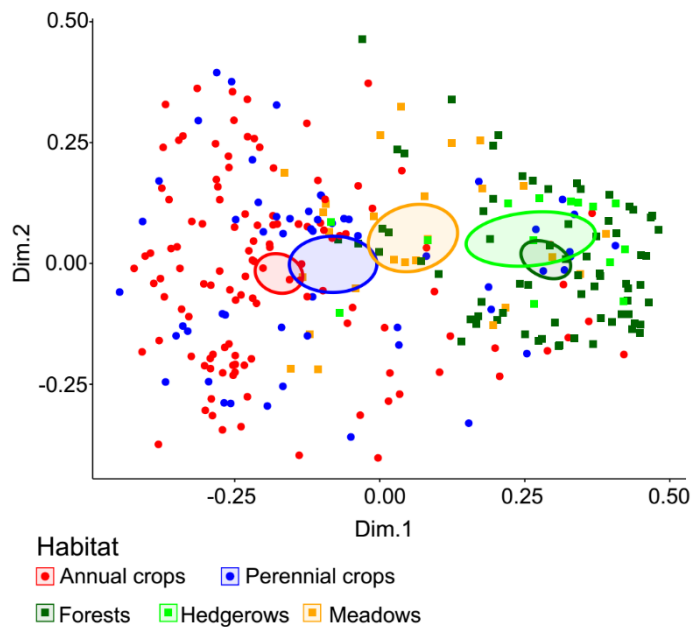
Fig. 2. Ordination plot based on MDS. Dots of different colours indicated habitat types while shaded areas represent confidence ellipses indicated (95%) created using the coord.ellipse function in the FactoMineR package for R (Lê *et al.*, 2008) interval of confidence (95%) around mean group. Habitat classification was superimposed after ordination. The distance between points is proportional to their community dissimilarity (Bray-Curtis distance).

Landscape-level species richness (gamma-diversity) showed a weak hump-shaped relationship with the cover of semi-natural habitats (Fig. 3a), while the number of individuals decreased and evenness increased with semi-natural habitat cover (Fig. 3b - c). There was no relationship between any diversity metric and edge density (Table 2).

Table 2. Results from the linear models testing the linear and quadratic effect of landscape composition (proportion of semi-natural habitat) and configuration (edge density) on species richness, activity density, evenness at the landscape level (n=15) and network modularity and specialization. Quadratic terms were removed if P>0.1.

| Response	Explanatory	Estimate	SE	t	p	R^2
a) Species richness	Semi-natural	0.663910	0.312949	2.121	0.055	0.273
	Semi-natural^2	-0.010297	0.005062	-2.034	0.065	
	Edge density	0.00445	0.02188	0.203	0.842	-
	Edge density^2	-	-	-	-	
b) Log(Activity density)	Semi-natural	-0.010551	0.004294	-2.457	0.029	0.317
	Semi-natural^2					
	Edge density	0.009079	0.016642	0.546	0.595	-
	Edge density^2	-	-	-	-	
c) Evenness (E_{var})	Semi-natural	0.002170	0.000804	2.699	0.018	0.36
	Semi-natural^2	-	-	-	-	
	Edge density	-0.000153	0.000212	-0.723	0.483	-
	Edge density^2	-	-	-	-	
d) Modularity (Q)	Semi-natural	0.003740	0.001670	2.249	0.044	0.306
	Semi-natural^2	-0.000062	0.000027	-2.293	0.041	
	Edge density	0.000151	0.000112	1.351	0.200	-
	Edge density^2	-	-	-	-	
e) Specialization (H_2')	Semi-natural	-0.000756	0.000844	-0.896	0.387	-
	Semi-natural^2	-	-	-	-	
	Edge density	0.000146	0.000183	0.798	0.439	-
	Edge density^2	-	-	-	-	
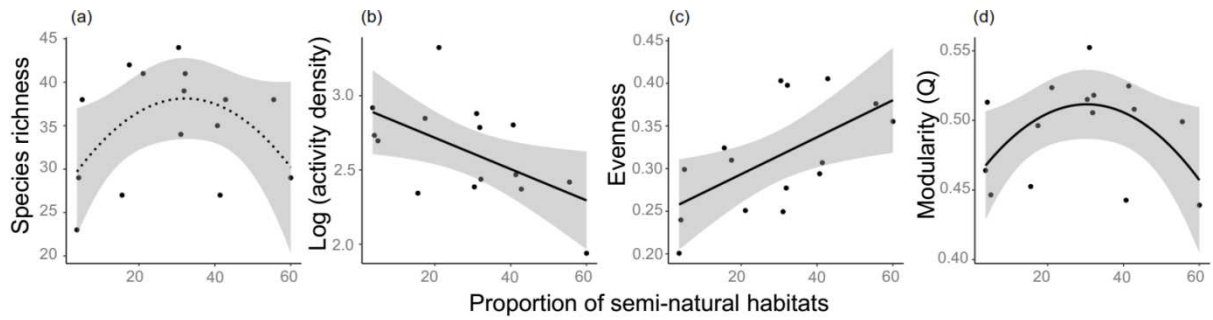
Fig. 3. Relationship between (a) species richness, (b) activity density, (c) evenness (Evar) and (d) modularity (Q) at the landscape scale (n=15) vs. cover of semi-natural habitats (P-values of linear and quadratic terms shown in Table 2). Solid lines represent model estimates and shaded areas intervals of confidence (95%).The dotted line in (a) indicate a marginal effect.

Species-habitat networks

The average value of modularity Q for the 15 networks was 0.49. All networks were significantly more modular than the null models (one-tail Z test, P < 0.001) (Appendix C Fig. C4). Modularity did not depend on edge density but it presented a hump-shaped relationship with the cover of semi-natural habitats (Fig. 3d). Average H_2' was 0.43 and did not depend on either semi-natural cover or edge density. We found a positive linear relationship between modularity and H_2' (P<0.001, R^2= 0.54). A qualitative analysis of the 15 species-habitat networks revealed that c. 50% of the modules were composed of patches belonging to the same habitat (e.g. Fig. 4k, m, o). Additionally, there were often several modules for a single habitat type within the same landscape mosaic.

We found differences in the participation coefficient between habitat types (mixed-effect model, χ^2=83.75, df=4,278, P<0.001). In particular, open habitats (i.e. annual crops, perennial crops and meadows) hosted a large number of species also occurring in other habitat types, while species found in forest patches tended to occur only within forest modules (Fig. 5). The modularity patterns and the participation coefficients reflected the general topology of the regional species-habitat network, with many forest or hedgerow species showing higher habitat fidelity, while the species pool interacting with perennial crops and meadows were found in both open and woody habitats also at the regional scale (Fig. 6).
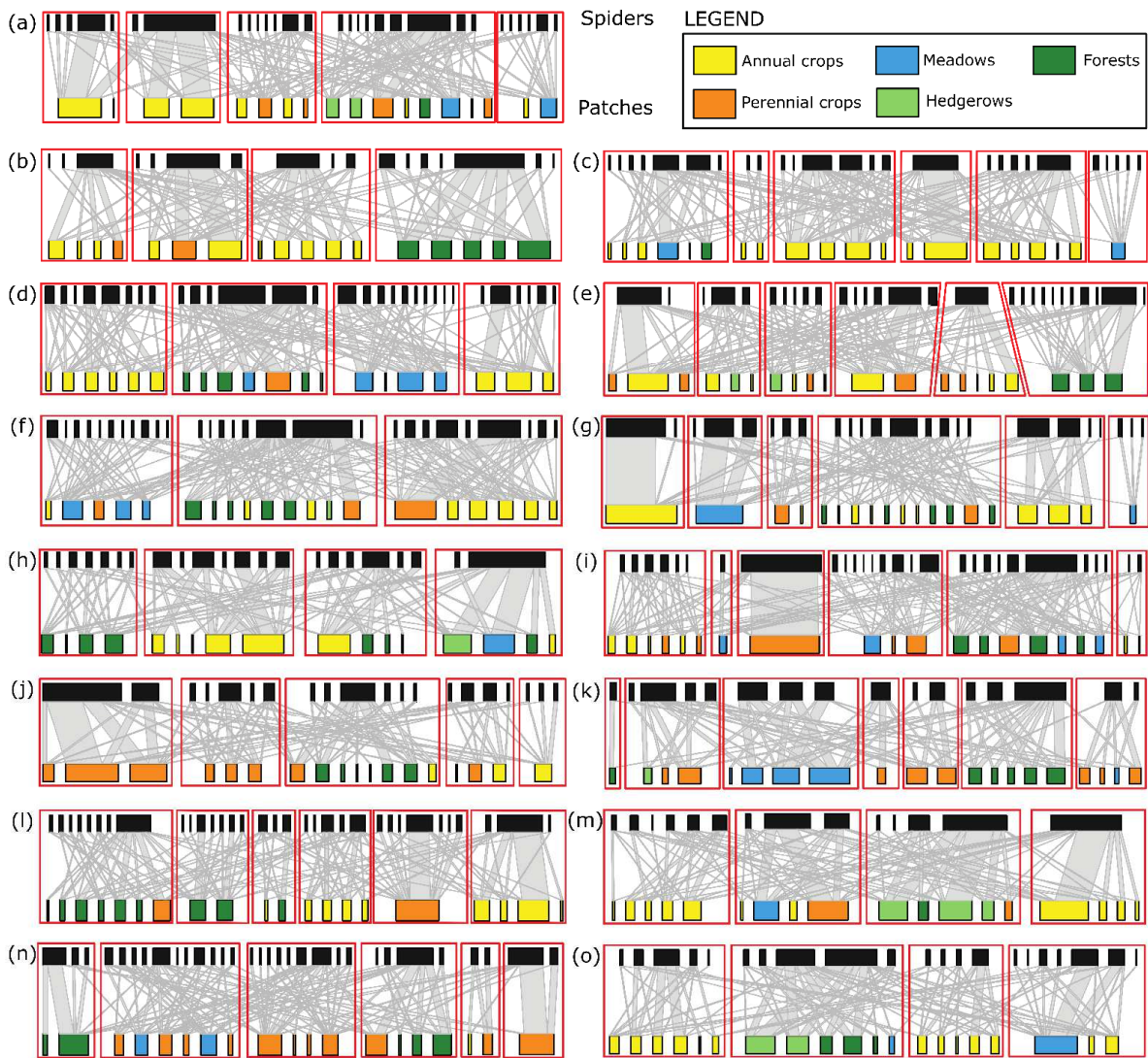
Fig. 3. Species-habitat networks of the 15 landscapes (a-o). The lower level represents habitat patches while the higher level represents spider species. The width of the links represents the number of individuals of each spider species in each patch. Different colours represent the five major habitat types (see legend). Red outline identifies the network modules.
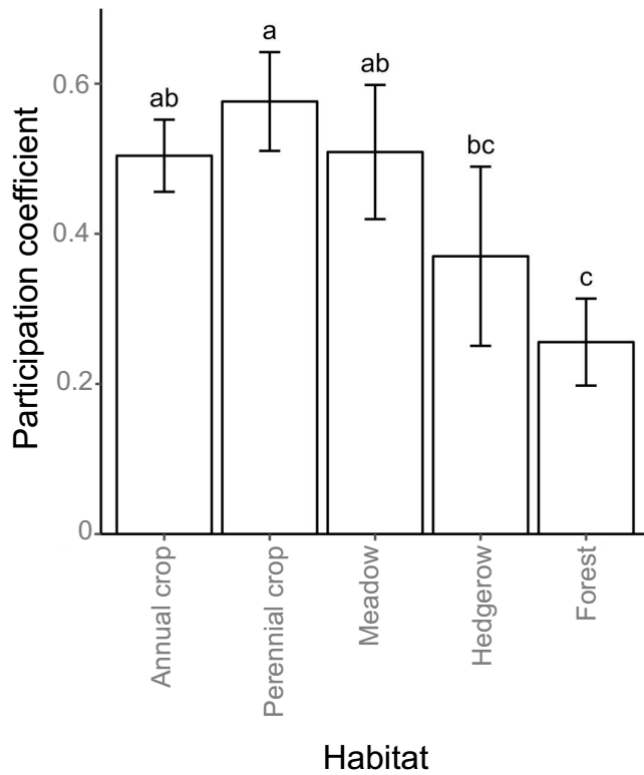
Fig. 3. Among-modules connectivity (i.e. participation coefficient) for the five habitat types. Bars represent means ± intervals of confidence (95%) from the linear-mixed effects model. The differences were assessed using a post-hoc Tukey test (P<0.001).
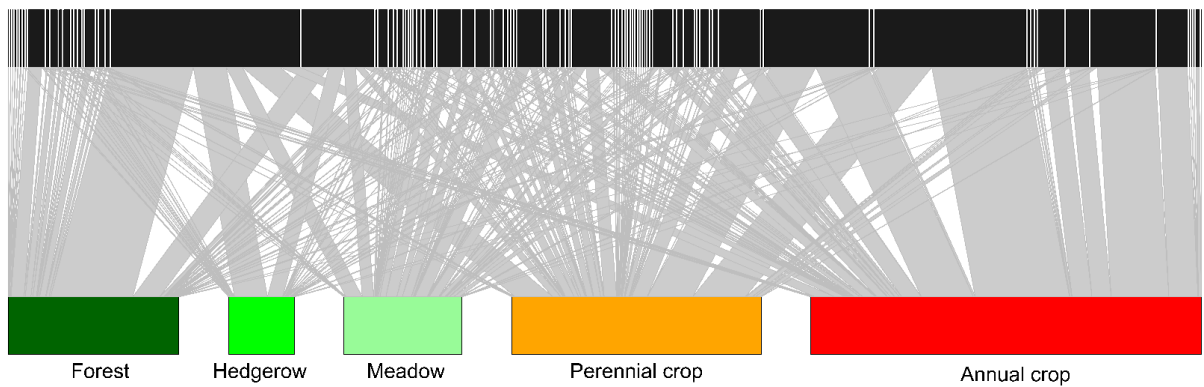

Fig. 3. Regional species-habitat network. The higher level represents spider species, and the lower level represents habitat types. The width of the links is proportional to the total number of individuals caught in each habitat type across the whole region.

Discussion

By using a species-habitat network approach, our study sheds light on the response of spider communities to land-use at the landscape scale. We found that spiders active in spring and summer tended to be highly specialized for different habitat types, showing high network modularity and habitat selectivity, mostly irrespective of any variation in landscape composition and configuration. Despite the high habitat selectivity, perennial crops and meadows seemed to play a central role in connecting different habitat network modules across the landscapes. On the contrary, forest and hedgerows hosted very distinct species communities that did not occur outside woody habitats. The application of the species-habitat network approach suggests the need to adopt different management strategies depending on the focal crop habitat.

Similarly to previous studies, traditional diversity analyses revealed that spider species richness was higher in semi-natural habitats (meadows and hedgerows) than in disturbed annual crops (Schmidt & Tscharntke, 2005; Mestre *et al.*, 2018; Rosas-Ramos *et al.*, 2018). Interestingly, perennial crops such as vineyards and olive groves supported a number of species similar to the aforementioned semi-natural habitats (Bruggisser *et al.*, 2010; Fischer *et al.*, 2013), while forest patches hosted the lowest activity-density and diversity of ground-dwelling spiders. Beside these well-known diversity patterns, our network approach revealed that habitat identity was a key factor in shaping spider assemblage composition across the landscapes. Network modularity was always higher than expected from the null models, indicating that many species tended to occur only in certain subsets of habitat patches within each landscape, with c. 50% of the modules across the 15 networks being composed of patches belonging to the same habitat type. Furthermore, modularity was associated with habitat selectivity (Lewinsohn *et al.*, 2006), which is coherent with previous knowledge about spider habitat preferences (Schmidt & Tscharntke, 2005). We only found a weak trend for a unimodal relationship between modularity and proportion of semi-natural habitats indicating that modularity was highest with intermediate cover of semi-natural habitats. This is probably due to the simultaneous presence of multiple habitats with sufficient area at the landscape scale to support the associated specialist species (Kadmon & Allouche, 2007). While generalist predators such as agrobiont spiders are expected to disperse between habitat patches more often when landscapes are fragmented (Fahrig, 2003; Horváth *et al.*, 2019), most spider species in the studied area appeared to be highly specialized for one or few habitat types irrespective of the

configurational complexity of the landscapes. These patterns, however, might change in different seasons due to large fluxes of resources across different habitats.

In spite of this general pattern of high selectivity, perennial crops and meadows seemed to act as dispersal facilitators or connectors of spider communities belonging to different habitat modules. Conventional management of perennial crops such as vineyards and olive groves has been shown not to be particularly detrimental to spider diversity (Isaia *et al.*, 2006; Bruggisser *et al.*, 2010), suggesting that they might host relatively species-rich communities of ground hunting spiders (Picchi *et al.*, 2016). In perennial crops, the simultaneous presence of inter-row herbaceous vegetation and woody elements is the likely reason for the hub role played by this habitat in connecting open and forest habitats. On the other hand, woody habitats (forests in particular), while contributing substantially to the regional diversity of spiders, appeared to be isolated from the rest of the habitat network as suggested by the low participation coefficient. Although previous studies found that forest spiders are able to move to open habitats to exploit resources at the ecotones (Pluess *et al.*, 2010; Lacasella *et al.*, 2015), our large-scale analysis revealed that woody habitats often hosted highly specialized species that are unlikely to occur outside the preferred habitat types (Sarthou *et al.*, 2014; Mestre *et al.*, 2018). Even very simple habitats such as hedgerows presented similar patterns to forests and hosted highly specialized species that were not able to colonize disturbed annual crop fields or grasslands (Gallé *et al.*, 2018b). Previous studies showed that, amongst spiders, large species with low to intermediate dispersal capabilities are the most impacted by land-use conversion from relatively undisturbed forests to arable fields (Birkhofer *et al.*, 2015).

Considering the 15 habitat networks, we found that total activity density declined and evenness increased with semi-natural habitat, while we observed a weak unimodal relationship between total species richness and cover of semi-natural habitats – a trend similar to modularity. The results support previous findings that spider diversity is maximum with high landscape heterogeneity while the dominance of one habitat type has a generally negative effect (Öberg *et al.*, 2007). The highest dominance and activity density of spiders in landscapes with little cover of semi-natural habitats are probably related to the dominance of a few abundant species that can thrive in disturbed crop fields (Schmidt *et al.*, 2005).

The lack of effect of edge density on both diversity and network metrics is probably related to the observed high degree of specialization of spiders that perceived hard boundaries between different habitats. This result is in agreement with a recent study investigating the effect of landscape configuration on spider functional diversity (Gallé *et al.*, 2019), although

high edge density of small-scale agricultural landscapes was found to be associated with higher densities of agrobiont spiders (Gallé *et al.*, 2018a).

Implications for conservation of spiders in agroecosystems

Given the importance of spiders as biological control agents in agroecosystems (Birkhofer *et al.*, 2018b; Michalko *et al.*, 2019), there is an increasing interest in their conservation in crop habitats. A full understanding of the way spiders use different habitats across the same landscape mosaics is pivotal for guiding their management. Spill-over of beneficial organisms from semi-natural habitats to agricultural fields is often considered an important process for pest control enhancement (Pluess *et al.*, 2010; Blitzer *et al.*, 2012). However, this might be challenging for ground-dwelling spiders active in spring and summer, due to their high degree of habitat selectivity and habitat network modularity. On the one hand, to enhance biological control delivered by spiders in annual crop fields, the proximity to forest patches or hedgerows might not necessarily be beneficial, as they would be mainly occupied by strict forest specialists. It follows that, to enhance ground-dwelling spiders assemblages in arable fields, a better strategy would be to manage the fields themselves in a way that makes them a more suitable environment for the resident open-habitat species (Fox *et al.*, 2016), or to introduce open semi-natural habitats such as meadows or flower strips to promote species spill-over (Happe et al., 2019; Schmidt-Entling and Döbeli, 2009; but see Havlova et al., 2017; Pluess et al., 2010). On the other hand, if the focal crop is perennial, i.e. vineyards or olive groves, both open and woody semi-natural habitats could potentially contribute to some degree to the spill-over of beneficial spiders. Our recommendations are further corroborated by recent data on spider overwintering preferences, which have been shown to be highly sensitive to vegetation type, with herbaceous and woody semi-natural habitats hosting very distinct species assemblages of ground hunting spiders (Sarthou *et al.*, 2014; Birkhofer *et al.*, 2018a; Mestre *et al.*, 2018).

Conclusions

Our whole-landscape sampling provided key ecological information that cannot be easily derived from studies based on the sampling of single habitats. One key advantage of the application of the framework is that the scale of the derived ecological information matches the scale of landscape management, embracing the full complexity of the spatial interactions between species and habitat patches across heterogeneous landscapes. Improved knowledge of species-habitat associations at the landscape scale might also help solving potential trade-offs when multiple conservation targets are involved.

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Chapter 5

Seed predation intensity and stability in agro-ecosystems: Role of predator diversity and soil disturbance

Lami F, Boscutti F, Masin R, Sigura M, Marini L

Abstract

Seed predation by arthropods can contribute in regulating population and community dynamics of weeds. While the role of insects, and especially ground beetles (Coleoptera: Carabidae) as seed predators in crop fields is well studied, the drivers of predation stability and the relationships between species diversity and predation are less understood. The aims of the study were: 1) to unveil the direct relationships between predator community diversity and seed predation intensity and stability, and 2) to test the effects of soil disturbance (conventional vs. conservation tillage) and distance from field margin on seed predator communities and predation. Seed predation was measured using seed cards, and predator communities were sampled using pitfall traps over two years. Granivorous ground beetles, ants and crickets were the most abundant seed predators in both conventional and conservation tillage fields. Abundant and diverse predator communities were beneficial to predation intensity and stability. However, in communities dominated by large predators, an increase in number of species was related to a partial suppression of seed predation. Soil disturbance *per se* did not influence the overall predator community composition and predation, but it modified their spatial patterns within the fields. At the margins of conventional tillage fields, predation was lower and patchier than at the margins of conservation tillage fields. However, predation increased more steeply towards the center of conventional tillage field. Our results could find applications in sustainable weed management through biological control, as well as in better understanding the role of functional diversity in regulating ecosystem services.

Introduction

Conservation agriculture (based on minimum soil disturbance, permanent soil plant cover and crop rotation) has often been proposed as an effective alternative to tillage worldwide (Holland, 2004). Fields managed under conservation agriculture have been proven to generally harbor higher biodiversity and to provide pivotal ecosystem services such as reduced soil erosion, higher fertility, and carbon sequestration (Tamburini *et al.*, 2016c). However, conservation tillage fields are also expected to be more prone to weed infestation (Chauhan *et al.*, 2012). Given that weeds are one of the most important biotic factors limiting yields worldwide in both conservation and conventional tillage systems (Oerke, 2006), and that herbicide use causes pollution and the evolution of resistant populations (Jasieniuk & De, 2013; Annett *et al.*, 2014), there is great interest in finding complementary, more sustainable strategies of weed control.

Seed predation has been shown to play an important role in regulating population and community dynamics of weeds (Hulme, 1998; Larios *et al.*, 2017). There is a wide variety of animals that act as seed predators including birds, rodents, arthropods and gastropods (O'Rourke et al., 2006). Ground beetles (Coleoptera: Carabidae), in particular, are among the most abundant and important invertebrate seed predators in agroecosystems (Honek, Martinkova, & Jarosik, 2003). While ecosystem services provided by insects are generally under-investigated and based on proxies rather than on the quantification of the service itself (Noriega *et al.*, 2017), the general role of ground beetles as seed predators in crop fields is relatively well studied (Petit *et al.*, 2014). The factors affecting predation stability across time and space, however, are less understood (Kolb *et al.*, 2007; Labruyere *et al.*, 2018). Soil invertebrates, including ground beetle seed predators (Shearin *et al.*, 2007; Blubaugh & Kaplan, 2015) can suffer direct mortality from the mechanical actions of tillage practices or indirect effects through habitat modification, exposure to predators and reduced prey availability (Holland & Luff, 2000; Hance, 2002; Holland, 2004). Additionally, it is known that different ground beetle species can present clumped spatial distributions even within the same field (Thomas *et al.*, 2001; Holland *et al.*, 2005), with potential repercussions on the spatial stability of ecosystem services linked to these insects, including seed predation. As maintaining homogeneous, high intensity levels of predation of seeds is highly desirable in weed control, a deeper understanding of how soil disturbance influences predation stability is needed.

While most studies on the subject focused on seed predation (Kulkarni *et al.*, 2015), there is still a lack of understanding about the relationship between predation intensity and stability and carabid community features such as abundance, richness and functional diversity (Saska *et al.*, 2008; Trichard *et al.*, 2014). Trophic composition of the predator assemblage can play an important role in determining the shape of the relationship between predator diversity and function (Finke & Denno, 2005a; Charalabidis *et al.*, 2019). High functional complementarity in natural enemy communities is expected to be linked with higher and more stable consumption of the lower trophic levels (Peralta *et al.*, 2014). However, increasing predator diversity can also increase the probability to include intra-guild predator species with potential negative feedbacks on functioning (Arim & Marquet, 2004). For instance, it has been shown that ground beetles might alter their feeding behaviour in response to the risk of intra-guild predation, or to the distribution of alternative preys (Petit *et al.*, 2018). Alongside species diversity, functional diversity has become an increasingly important lens to interpret ecological phenomena in the past decades (Petchey & Gaston, 2006). Functional diversity is deeply linked with the concept of species trait, i.e. any feature of an organism that can influence either its

fitness (response trait) or its effect on the surrounding environment (effect trait) (Violle *et al.*, 2007). It has been shown that morphological effect traits of arthropod consumers can significantly influence their impact on lower trophic levels (Deraison *et al.*, 2015). It is, thus, likely that morphological traits of seed predators, such as body size, are important in modifying weed suppression. Identifying the role of key functional traits will help deciphering the link between predator communities and functioning.

Here, using a paired design, we contrasted conventional vs. conservation tillage systems to isolate the role of soil disturbance on seed predation. The main aims are the following: 1) To assess the influence of seed predator community structure (activity density, species richness and community-weighted body size) on predation intensity and stability, and 2) To test how soil disturbance (conventional vs. conservation tillage) and distance from field margin influence seed predator community features, and how the same variables influence predation intensity and stability of eight weed species. We hypothesized that high predation intensity and stability should be related to carabid communities characterized by higher activity density, species richness and dominated by large-bodied species. Additionally, we expected for conventional tillage systems to present lower predator diversity and abundance and, consequently, lower predation intensity and stability due to the higher negative impact of soil disturbance (Baraibar et al., 2009; Cromar et al., 1999; Menalled et al., 2007; Petit et al., 2017).

Materials and Methods

Study sites

The study was carried out across 16 field pairs in three geographical areas of the Udine province, NE Italy (Appendix D Table D1). The study area is an agricultural lowland (c. 615 km^2) with temperate climate (mean annual precipitation of c. 1300 mm; mean annual temperature of 13°C). Three sampling rounds were performed. Eight pairs (1A – 8A) were sampled in September 2017 (first round), while the other eight (1B – 8B, roughly in the same areas) were sampled in June 2018 (second round) and August 2018 (third round). Sampling periods were chosen to coincide with ground beetle breeding seasons and period of seed dissemination of weeds, which in temperate areas (including Italy) are generally in spring and autumn (Bousquet, 2010; Talarico *et al.*, 2016; Bell *et al.*, 2017), and to cover different developmental stages of the crop (Supplementary Material Table D2).

Within each field pair, one field was managed under conventional tillage and one under conservation tillage. Conservation soil management included all techniques characterized by non-inversion of soil for at least 5 to a maximum of 20 years (Appendix D Table D1). On the other hand, under conventional tillage the seedbed was prepared by a deep primary tillage with inversion of the surface layer of soil. We had to change field pairs after the first sampling round to match crop identity within pair. A variety of crops was grown in pairs 1A – 8A, including soybean, maize, alfalfa and sorghum (as a cover crop), with crop species being consistent within each pair except for one (Appendix D Table D1). Soybean was the only crop species in pairs 1B – 8B. Although crop identity might affect predator communities and activity, the effect was consistent within pair and did not influence the comparison between conservation and conventional tillage. Ploughing depths were 40 cm for summer crops (maize, soybean) and 30 cm for barley, respectively. Ploughing was immediately followed by one or two tills for seedbed preparation. Mowing was the only cropping operation for alfalfa. In the study area, the typical crop rotation for conservation tillage fields was wheat/barley-soybean-maize-cover crop (e.g. *Sorghum* sp. and *Vicia* sp.), while in conventional tillage the main rotation was maize-soybean.

In most pairs, distance between fields was less than 400 m. As landscape structure can have important effects on ground beetles (Labruyere *et al.*, 2016), we quantified basic landscape composition metrics within a 750 m radius from each field – a scale at which landscape features were shown to have the strongest effects on ground beetles in the studied area (Tamburini *et al.*, 2016a). However, since we focused our analysis on local management and landscape composition was kept similar within each pair during site selection (paired t-test: p= 0.19 for urban cover, p= 0.92 for semi-natural cover), we did not test any landscape metrics in our models.

Seed predation

Seed predation was assessed using seed cards (Westerman *et al.*, 2003), consisting of 11 x 6 cm rectangles of sandpaper (P80 grain) with seeds glued with repositionable glue (Ripo Spray Ferrario). Seeds of eight common weed species were selected for the experiment, representing a variety of families, seed shapes and sizes. Under natural conditions, the seeds of these species are released in late spring/early summer or at the beginning of autumn (Table 1), coinciding with the studied period. Thirty seeds of each species (240 in total) were glued on each seed card, with the spatial arrangement of the species on the card being random. With this method, all species could be placed in the exact same micro-sites, thus being more easily comparable. To transfer cards on field, they were individually wrapped in transparent plastic bags. Seeds

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that detached during the transfer were counted and taken into account for the final analysis. The selected seed density per card can be considered relatively high based on literature. However, while seed predation by rodents is known to be influenced by seed density and aggregation over small areas, we did not expect for this factor to significantly affect predation intensity by ground beetles and other invertebrates (Marino *et al.*, 2005; Baraibar *et al.*, 2012).

Table 1. Family, seed shape,1000 seeds weight and germination and dissemination period for the eight weed species used in the experiment.

Species	Family	Shape	1000 seeds weight	Germination period	Dissemination period
Amaranthus hybridus L.	Amaranthaceae	Lenticular	0.34 g	Summer	Summer - early Autumn
Echinochloa crus-galli (L.) P. Beauv.	Poaceae	Ovoid	2.15 g	Summer	Summer - early Autumn
Eleusine indica (L.) Gaertn.	Poaceae	Trigonal	0.46 g	Summer	Summer - early Autumn
Oenothera biennis L.	Onagraceae	Prismatic	0.45 g	Indifferent	Late Summer - Autumn
Papaver rhoeas L.	Papaveraceae	Reniform	0.14 g	Winter	Late Spring - Summer
Persicaria maculosa Gray	Polygonaceae	Lenticular	2.35 g	Spring	Summer – early Autumn
Taraxacum sect. Taraxacum F.H. Wigg.	Asteraceae	Fusiform	0.45 g	Indifferent	Summer
Verbena officinalis L.	Verbenaceae	Cylindrical	0.25 g	Indifferent	Summer – early Autumn

Four transects (4 m from each other) were placed in each field, starting from a field margin consisting of a semi-natural habitat (herbaceous plants, hedgerows or small woods – see Appendix D Table D1). Along each transect, seed cards were placed at 1 m, 3 m, 8 m and 20 m from the margin (1 seed card per position, 16 seed cards per field – see Appendix D Fig. D1). In a few very narrow fields (6 out of 32), the last 1 or 2 positions in the 2 outermost transects were excluded, as a distance of at least 8 or 20 m from a margin could not be guaranteed. Cards were fixed to the ground with nails, with a plastic cover and a metal net cage (mesh size: 1 cm) to protect them from rain and small vertebrate interference, respectively. During each of the three sampling rounds, cards were exposed for 3 days.

For each round, position and weed species, we quantified predation intensity as the ratio between the number of disappeared seeds and the total number of glued seeds (Abbott, 1925; O'Rourke *et al.*, 2006). Beside predation intensity, we calculated two measures of predation

stability using the coefficient of variation (CV). First, we calculated an "among-species CV" using the predation of the eight weed species for each seed card. This metric quantified the variability in predation between different weed species, and it follows the formula:

$$among\text{-}species\ CV = \frac{\sigma_{sp}}{\mu_{sp}}$$

where σ_{sp} and μ_{sp} are the standard deviation and the mean of predation among seed species on a single seed card, respectively. Second, we quantified a "spatial CV", between the seed cards at the same distance from margin. For each position, we computed the CV of total predation (all species pooled) based on the four seed cards located at the same distance from the margin, irrespective of the weed species. The formula was:

$$spatial\ CV = \frac{\sigma_{pos}}{\mu_{pos}}$$

where σ_{pos} and μ_{pos} are the standard deviation and the mean of predation among seed cards at the same distance from field margin, respectively. This metric quantified the spatial variability in predation within field areas at the same distance from the margin. We did not employ any temporal stability metric since we had a maximum of only two sampling rounds on the same field.

To exclude potential effects of wind and other factors in removing seeds from the cards, during the first sampling round (September 2017), control seed cards were also employed. Control seed cards were placed near the seed cards of one transect per field in half of the field pairs (Appendix D Table D1). For control seed cards, the net cage was completely enveloped in tulle to prevent arthropod access. Since mean seed disappearance in the control seed cards was very low (average: 3.44%, SE = 0.30), and was not related to any of our treatments (both soil disturbance and distance), we did not include control seed cards in the following rounds.

Insect sampling

Ground-dwelling arthropods active during the experiment were sampled using pitfall traps. Each trap consisted of a 0.5 l plastic cup (10 cm in diameter), activated with 150 – 200 ml of ethylene glycol 40%. In September 2017, traps were placed along one transect in each field, located between the two central seed card transects. In June and August 2018, traps were placed along three transects (4 m apart from each other, alternating with the seed cards transects). In each transect, four traps were placed at distances from margin corresponding to the seed card positions, for a total of 12 traps per field (Appendix D Fig. D1). During all sampling rounds,

traps were active for the 3 days of exposure of the seed cards. All data were pooled per position by averaging the species abundance. Based on previous samplings and literature (Tamburini *et al.*, 2016a), we expected for ground beetle activity density in the area to be very high, and thus we assumed that traps would not significantly impact the number of active beetles and have an effect on predation. Moreover, this potential negative effect on predation was equal across soil management systems and positions, and did not affect the relative differences between them.

Arthropods collected in the traps were stored in ethanol 70%, and individuals for each main seed eating group (ground beetles, ants and crickets) were counted. Ground beetles were identified to species level (or, in some cases, morphospecies). For granivorous species, information on body size (the mean body length) was collected from literature (Honek *et al.*, 2007; Tamburini *et al.*, 2016a). For crickets, two similarly-sized morphospecies were found, and their average body size recorded. For ants, we calculated the mean size among the most commonly-found morphospecies. For body size, we calculated a community-weighted mean in each position using species activity density as weight and including all seed predator groups.

Data analysis

Effect of predator community structure on seed predation

We first used linear mixed-effects models to test the effect of predator community features on predation intensity, spatial CV and among-species CV irrespective of local management and position in the field. In spite of insect mobility, we could not exclude *a priori* the possibility of seed predators differentially occupying different areas of the fields (Thomas *et al.*, 2001; Holland *et al.*, 2005). We thus considered as likely predators for each seed card only the arthropods caught in the nearest pitfall traps. For that reason, and given that different sampling rounds had to be comparable in spite of the different number of traps per position, we calculated weighted body size, mean predator activity density and mean species richness between all the traps at the same distance from margin in each field. These community metrics and their interactions were used as explanatory variables. Seed species was also included as an explanatory variable for predation intensity and spatial CV. Predation intensity and among-species CV were calculated as means between all traps of each within-field position. We verified the absence of multicollinearity between explanatory variables using Variance Inflation Factors. All VIFs were around 1, indicating very low collinearity. Geographical area, pair ID, field ID and position ID were included as nested random factors. We included only predominantly granivorous ground beetles (i.e. tribes Harpalini and Zabrini) based on literature (Pilon *et al.*, 2013; Homburg *et al.*, 2014), as models including all ground beetle species had

lower goodness-of-fit according to the Akaike Information Criterion (AIC). Analyses were carried out using packages "nlme" and "car" in R 3.5.0 (Pinheiro *et al.*, 2011; Fox *et al.*, 2012).

Effect of soil disturbance and distance from margin on predator communities

To test the direct effects of soil disturbance on predator activity density, species richness and weighted body size, we fitted linear mixed-effects models. For reasons stated in 2.4.1, we used weighted body size, mean predator activity density and mean species richness calculated between all the traps at the same distance from margin in each field as response variables. We then included soil disturbance, distance from margin and their interaction as fixed effects. Geographical area, pair ID, field ID and trap position ID were used as nested random factors.

We also calculated the mean captures per trap in each field for each seed predator species, and used the results to visualize the variation in species composition between the two soil management systems. We created an ordination plot based on a Multidimensional Scaling (MDS) and tested compositional differences between soil management systems using analysis of similarities (ANOSIM) in the package vegan in R. We used Bray-Curtis distance in both MDS and ANOSIM.

Effect of soil disturbance, distance from margin and seed species on seed predation

We used similar linear mixed-effects models to test the effects of soil disturbance, distance from margin, their interaction and weed seed species on predation intensity, spatial CV and among-species CV. Geographical area, pair ID, field ID, transect ID and within-transect position ID were used as nested random factors (transect ID was not included for spatial CV models, as spatial CV was calculated between transects).

Results

A total of 6168 ground beetles were collected, 1451 of which belonging to 10 species and three morphospecies of Harpalini and Zabrini (predominantly granivorous) (Supplementary Materials Table D3). Among these, 828 were collected in conservation tillage fields and 623 in conventional tillage fields. The most abundant granivorous species was *Pseudoophonus rufipes* (DeGeer) with 1096 individuals, while the most abundant ground beetle overall was the generalist predator *Pterostichus melas* (Creutzer) with 2170 individuals. Additionally, 1437 ants and 492 crickets were collected, of which 609 ants and 159 crickets in conservation tillage fields and 828 ants and 333 crickets in conventional tillage fields.

Effects of predator community structure on predation

We found significant or near-significant three-way interactions between seed predator activity density, species richness, and weighted-community body size on predation intensity and stability (Table 2). In species-poor communities, increases in the activity density of large predators led to higher levels of predation compared to small predators. In species-rich communities, conversely, increases in the activity density of small predators led to higher predation intensity than increases in the activity density of large predators (Fig. 1a). Spatial and among-species CV decreased with predator activity density in species-rich communities of small predators, while in species-rich communities of large predators this tendency was less marked (for spatial CV) or non-existent (for among-species CV) (Fig. 1b - c). In species-poor communities, spatial and among-species CV tended to become higher with activity density for small predators, and to decrease with activity density for large ones.

Table 2. Results of the linear mixed effects models testing the effects of the explanatory variables on predation features (predation intensity, spatial coefficient of variation and among-species coefficient of variation) and predator community features (predator activity density, species richness and weighted body size). Distance from the margin, predator activity density and predator species richness were log-transformed when used as explanatory variables.

Explanatory variables	DFs	F test	p
Effect of predator community structure and seed species on predation			
a) Predation intensity (model 1)			
Predator activity density	1, 1209	103.99	<0.0001
Predator richness	1, 1209	8.32	0.0040
Body size	1, 1209	8.11	0.0045
Seed species	7, 1209	74.63	<.0001
Predator activity density x Predator richness	1, 1209	1.94	0.1638
Predator activity density x Body size	1, 1209	3.92	0.0481
Predator richness x Body size	1, 1209	26.62	<.0001
Predator activity density x Predator richness x Body size	1, 1209	3.76	0.0528
b) Spatial CV (model 2)			
Predator activity density	1, 1065	46.52	<0.0001
Predator richness	1, 1065	3.76	0.0527
Body size	1, 1065	1.61	0.2047
Seed species	7, 1065	7.65	<0.0001
Predator activity density x Predator richness	1, 1065	0.75	0.3857
Predator activity density x Body size	1, 1065	3.84	0.0503
Predator richness x Body size	1, 1065	7.11	0.0078
Predator activity density x Predator richness x Body size	1, 1065	5.12	0.0238
c) Among species CV (model 3)			
Predator activity density	1, 47	8.11	0.0065
Predator richness	1, 47	0.22	0.6400
Body size	1, 47	1.11	0.2982
Predator activity density x Predator richness	1, 47	0.37	0.5441

Predator activity density x Body size	1, 47	0.06	0.8061
Predator richness x Body size	1, 47	4.86	0.0325
Predator activity density x Predator richness x Body size	1, 47	4.04	0.0502

Effect of soil disturbance and position on predator community structure

d) Predator activity density (model 4)

Distance from margin	1, 90	0.29	0.5910
Soil disturbance	1, 15	0.18	0.6802
Soil disturbance x Distance from margin	1, 90	0.02	0.8954

e) Predator species richness (model 5)

Distance from margin	1, 90	0.19	0.6583
Soil disturbance	1, 15	0.22	0.6425
Soil disturbance x Distance from margin	1, 90	3.14	0.0799

f) Weighted body size (model 6)

Distance from margin	1, 79	0.55	0.4596
Soil disturbance	1, 15	1.11	0.3098
Soil disturbance x Distance from margin	1, 79	3.14	0.0804

Effect of soil disturbance, position and seed species on predation

g) Predation intensity (model 7)

Distance from margin	1, 354	31.17	<0.0001
Soil disturbance	1, 15	0.03	0.8737
Seed species	7, 4986	137.29	<0.0001
Soil disturbance x Distance from margin	1, 354	4.45	0.0356

h) Spatial CV (model 8)

Distance from margin	1, 84	10.20	0.0020
Soil disturbance	1, 15	0.02	0.8835
Seed species	7, 1143	7.85	<0.0001
Soil disturbance x Distance from margin	1, 84	3.78	0.0552

i) Among species CV (model 9)

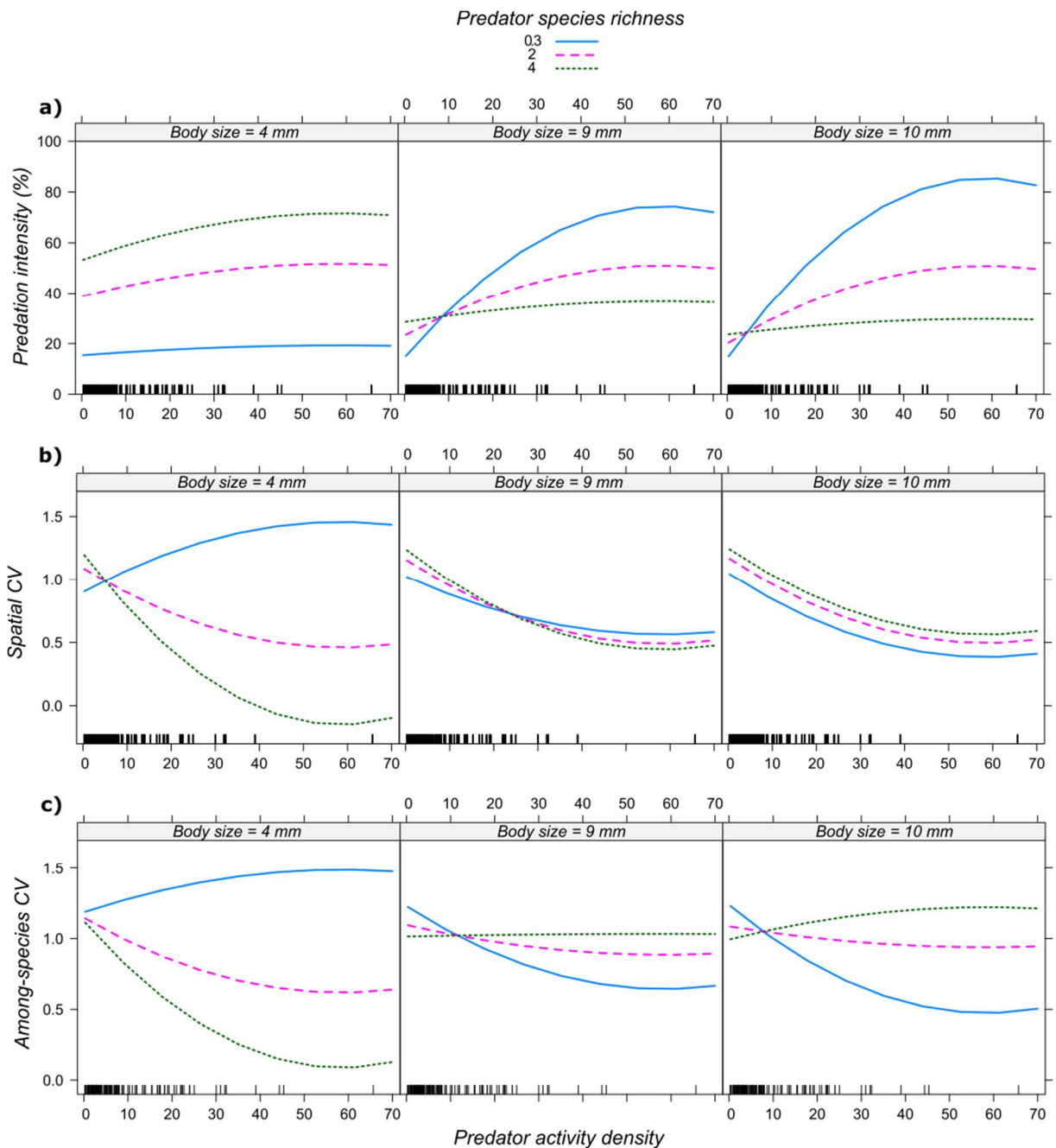|			
Distance from margin	1, 354	13.94	0.0002
Soil disturbance	1, 15	0.02	0.8991
Soil disturbance x Distance from margin	1, 354	0.01	0.9266

Fig. 1. Influence of predator activity density, species richness and mean weighted body size on predation intensity (a), spatial CV (b) and among-species CV (c). Both activity density and species richness were log-transformed. Thresholds were selected automatically by the "effect" function (effects package in R) to help visualizing the interaction between two continuous variables. The reported values of body size are equally spaced across the full range of the predictor.

Direct effects of soil disturbance and distance from margin on predator communities

No significant differences in predator community composition between conservation and conventional tillage treatments were observed (Table 2, Supplementary Materials Table D3, Fig. D2). However, there was a near-significant interaction between soil disturbance and distance from the margin on predator diversity and weighted body size. In conservation tillage

fields, species richness increased (Fig. 2b) and weighted body size slightly decreased (Fig. 2c) near the center compared to the margins of the field. The opposite was found for conventional tillage fields.
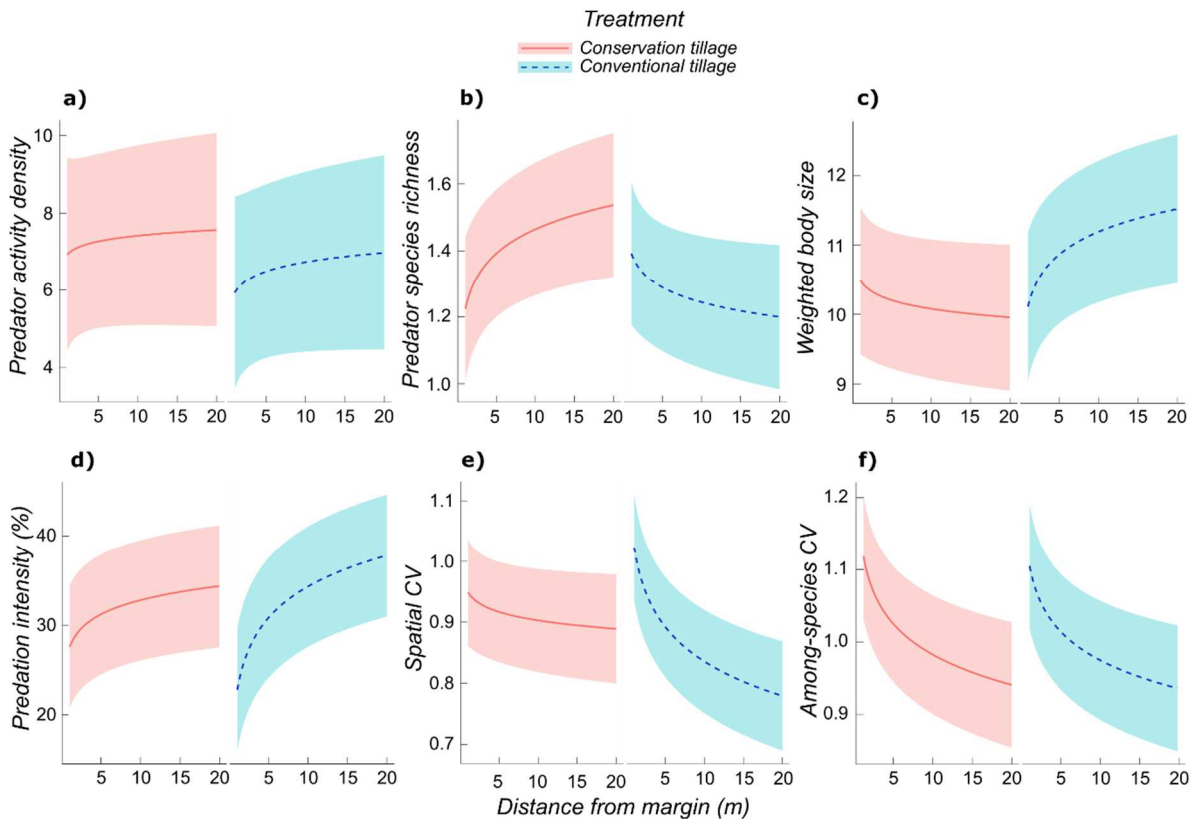

Fig. 2. Influence of distance from margin on predator community features (a – c) and seed predation (d – f) in the conventional and conservation tillage treatments. The fitted lines indicate model predictions and the shaded areas the intervals of confidence (95%).

Effects of soil disturbance, distance from margin and seed species on predation

Seed species had a significant effect on predation (Table 2), with some species being preferred over others. Specifically, *Taraxacum sect. Taraxacum* F.H. Wigg. and *Oenothera biennis* L. were the two most intensely and homogeneously consumed species (Fig. 3). Average seed predation was 33.1% (SE= 1.1) and 37.1 % (SE= 1.28) for conservation and conventional tillage treatments, respectively. The main effect of soil disturbance was not significant (Table 2), but there were significant or near-significant interactions between soil disturbance and distance from the margin. Predation intensity (Fig. 2d) and spatial CV (Fig. 2e) in conservation tillage fields were more uniform across the field, while in conventional tillage fields predation was lower and spatial CV higher at margins, rising (in the case of predation) or decreasing (in the case of spatial CV) much more steeply when approaching the center of the field. The interaction was not significant for among-species CV (Fig. 2f). Distance from field margin showed

80

significant effects on all variables, with predation becoming generally more intense and CV lowering towards the center of the field.
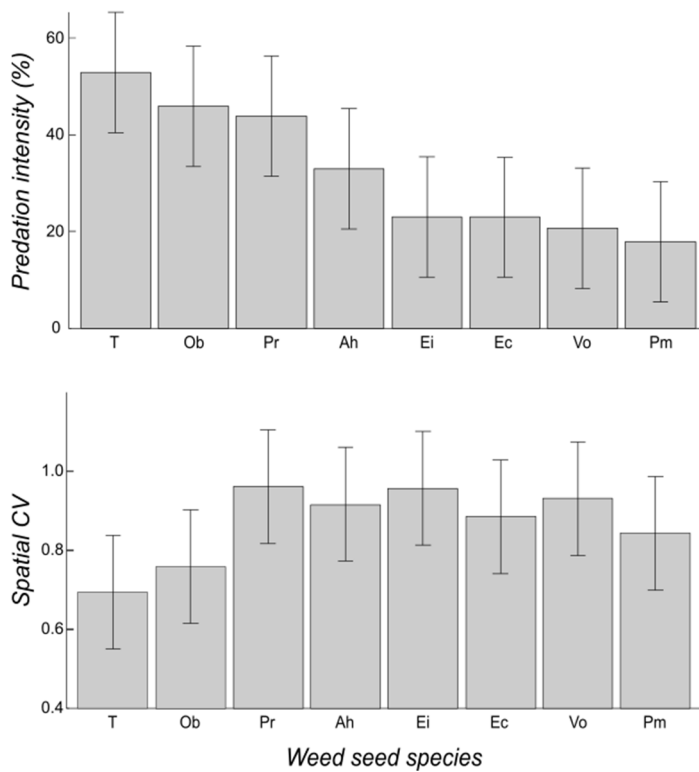

Fig. 3. Differences in predation intensity (a) and spatial CV (b) of the eight weed species. Species abbreviations: Ah = *Amaranthus hybridus*; Ec = *Echinochloa crus-galli*; Ei = *Eleusine indica*; Ob = *Oenothera biennis*; Pr = *Papaver rhoeas*; Pm = *Persicaria maculosa*; T = *Taraxacum sect. Taraxacum*; Vo = *Verbena officinalis*.

Discussion

The present study sheds light on the influence of soil disturbance and predator community structure on seed predation intensity and spatial stability. The results confirmed that ground beetles, ants and crickets are active seed predators in agroecosystems (Risch & Carroll, 1986; Carmona *et al.*, 1999; Honek *et al.*, 2003; Gallandt *et al.*, 2005; O'Rourke *et al.*, 2006; Baraibar *et al.*, 2009; Kulkarni *et al.*, 2016). Abundant and diverse predator communities were beneficial to predation intensity and stability, but considering communities dominated by large predators, an increase in number of species was related to a partial suppression of seed predation. Soil disturbance *per se* did not influence the overall predator community composition or the level of predation, but it modified their spatial patterns within the fields.

Direct effects of predator community structure on predation

In species-poor communities, an increase in the activity density of large predators resulted in higher predation intensity and stability compared to an increase in the activity density of smaller predators. Large predators are expected to consume more seeds per capita than smaller ones (Honek *et al.*, 2003; Saska *et al.*, 2010). However, in species-rich communities the trend was opposite, i.e. increases in activity density of small predators led to higher and more stable predation rates compared to increases in the activity density of large predators. A possible explanation for this pattern might be intra-guild predation (Charalabidis *et al.*, 2019). An increase in the diversity of predators may be considered a desirable factor to enhance prey suppression for services such as biocontrol (Cardinale *et al.*, 2003; Snyder *et al.*, 2006; Straub & Snyder, 2008), including weed seed biocontrol (Jonason *et al.*, 2013). However, when predator species can also prey on each other, crowding may lead to less efficient predation of lower trophic levels (Rosenheim *et al.*, 1993; Finke & Denno, 2005b; Vance-Chalcraft *et al.*, 2007). Usually intra-guild predation occurs when larger species can consume smaller ones (Woodward & Hildrew, 2002). Hence, an increase in the amount of large predator species might increase the chance of intra-guild predation, which might partially disrupt seed predation. An increase in the amount of small species, on the other hand, would not increase the risk of intra-guild predation, while it should increase species niche complementarity (Thomas *et al.*, 2001; Holland *et al.*, 2005). Highly diverse communities of small species should increase the chance of a higher number of seed species being consumed more uniformly across space, leading to an overall higher predation intensity.

Effects of soil disturbance, distance from margin and seed species

In many studies, conservation tillage was found to have positive effects on predator communities and seed predation (Cromar *et al.*, 1999; Menalled *et al.*, 2007; Baraibar *et al.*, 2009; Petit *et al.*, 2017), although there are also exceptions (Cardina *et al.*, 1996; Trichard *et al.*, 2014; Quinn *et al.*, 2016). In our case, no main effect of soil disturbance on overall community composition or predation levels was detected. However, the observed spatial patterns of seed predator functional and taxonomic diversity differed among conventional and conservation tillage fields. Previous studies confirmed that seed predation is usually weaker near field margins and become more intense towards the field center (Saska *et al.*, 2008; Trichard *et al.*, 2014). Additionally, predation at field margins was more spatially heterogeneous and uneven among weed species, while it became more homogeneous towards the field center. In conservation tillage fields, this can be mostly related to an increase in species

richness, paired with a relatively smaller body size, from the margins to the center. In conventional tillage fields, similar but stronger trends can be mostly related to the opposite phenomenon – an increase in body size paired with a relatively lower species richness from the margin to the center. It appears that weighted body size might have had a larger impact than species richness, leading to a more noticeable difference between margins and center in conventional if compared to conservation tillage. However, seed predation intensity in margins and conservation fields might have been underestimated, as weed seeds tends to be more abundant in margins than in the field center (Wilson & Aebischer, 1995) and in conservation than in conventional fields (Cardina *et al.*, 2002). This might lead to predator satiation and thus confounding effects on predation intensity estimation (Cromar *et al.*, 1999). Finally, as reported by many other studies (White *et al.*, 2007; Honek *et al.*, 2011; Petit *et al.*, 2014; Youngerman *et al.*, 2019), seed predators showed a preference for certain seed species compared to others. This indicates that biological weed control by arthropods might be particularly useful against certain weeds, such as the genera *Taraxacum* and *Oenothera*. However, we cannot exclude that with the unavailability of these preferred taxa, the same predator community might also increase the consumption of the other, less preferred species.

Conclusions

With weed problems constantly worsening because of herbicide-induced resistance (Green, 2014) and the effects of climate change (Peters *et al.*, 2014), a correct management of seed predators may represent a powerful asset for improving sustainable weed control (Petit et al., 2018). It is widely accepted that biodiversity can play a key role in efficiently maintaining ecosystem services (Balvanera *et al.*, 2006; Isaacs *et al.*, 2009) including seed predation (Gaines & Gratton, 2010). Our study confirms that larger, richer predator communities are linked to more intense and stable seed predation. However, the role played by predator body size, likely through intra-guild predation, should not be underestimated, and a deeper knowledge of the ecology and community composition of a given area is required to correctly predict possible interference effects of intra-guild predation on biological weed control. We have also shown that the interaction between soil disturbance and distance from field margin may have important practical implications by influencing the spatial patterns of predator taxonomic and functional diversity, and consequently of seed predation. Ecosystem services that depend on distance from margin, such as biological control (Holland *et al.*, 2008) are expected to be influenced by field size and shape (Bengtsson, 2015). For that reason, the efficacy of one soil management system over another in promoting weed seed predation might depend on the perimeter/area ratio of

each field. Further investigations on the possible role of weed seed density, predator satiation and other factors in shaping these patterns are however needed.

Chapter 6

General conclusions
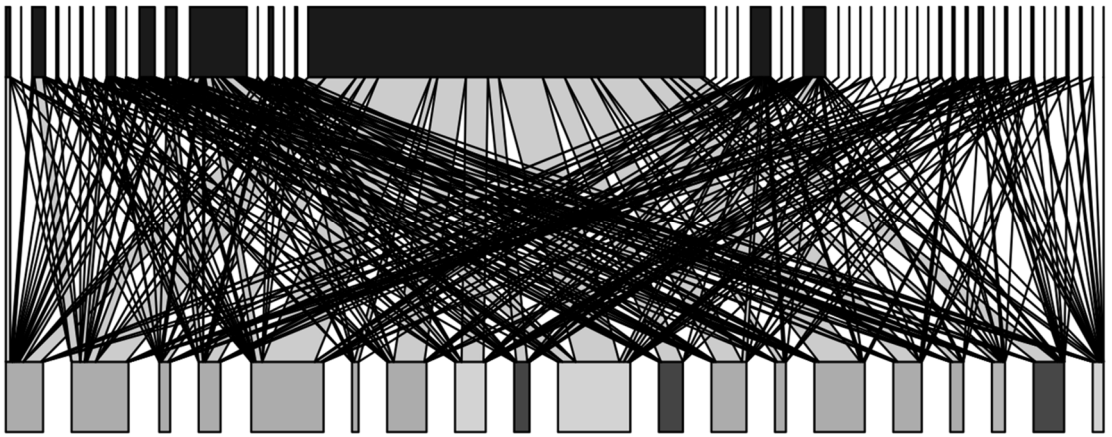
This study aimed at better understanding the effect of landscape simplification and local factors on species communities of functionally important arthropods. Landscape-level management actions are increasingly considered necessary to enhance functional biodiversity at different spatial scales. To achieve this result, we need to gain a deeper understanding of the interactions between entire biological communities and the multiple habitats forming a landscape. In spite of the advancements made possible by traditional landscape ecology approaches, however, this task remains extremely challenging.

Chapter 2 introduces the species-habitat network concept, which is based on pre-existing analytical techniques and tools normally employed in the study of mutualistic interactions. This novel framework allows to model the interactions between multiple species and habitat types as a bipartite network. Network topology and the level of habitat specialization (at the level of individual species or as an emergent propriety of the entire network) can then be described by a series of well tested, easily interpretable metrics. This approach is focused on habitat use – a central functional aspect of the community-landscape system - and can thus potentially detect the effects of anthropic impacts even when community composition remains relatively unchanged. Possible applications of the method include habitat prioritization for conservation, enhancement of ecosystem services in agricultural ecosystems and detection and mitigation of the effects of land use change, invasive species and other potentially damaging factors. In Chapters 3 and 4, we explored some of these subjects pertaining to functionally important arthropods.

When studying habitat use and planning biodiversity management actions, a critical information is the degree of habitat specialization of the focal species communities. Habitat specialization is a key feature for biodiversity management, as specialist species are the most vulnerable to landscape alterations (Henle *et al.*, 2004). Additionally, from the point of view of ecosystem services and disservices, knowing the level of habitat specialization of beneficial or harmful organisms can help to predict how likely they are to spill over from natural habitats to crops (Tscharntke *et al.*, 2005b). By using the species-habitat network approach, we showed that landscape simplification can have important effects on the specialization of low-mobility arthropods (Chapter 3). Namely, habitat specialization was reduced by semi-natural habitat loss for predatory ground beetles and by increasing patch density for sap-feeding herbivores. As expected, beta-diversity analyses suggested that these changes were in part mediated by changes in community composition (with generalist species replacing specialists). However, the network approach revealed that behavioral plasticity also played an important role, with

individual species adapting to lower-quality landscapes by becoming more generalist. Pollinators, on the other hand, were unaffected by landscape changes at the studied scale. This fact is likely explained by their higher mobility, which allows them to opportunistically exploit a wide range of resources scattered across the landscape. The differential responses of different arthropod guilds to landscape changes and the ability of insect species to change their level of habitat specialization should be taken into account in landscape-level agroecosystem management.

Another important question in landscape-level management is which habitats are the most important in influencing the behavior and distribution of a species community. We investigated this subject by focusing on ground-dwelling spiders as a case study (Chapter 4). Using the species-habitat network approach, we confirmed that these spiders show a very strong degree of habitat specialization, forming highly modular networks that are not significantly influenced by landscape changes. However, some habitats (namely permanent crops and meadows) seemed to act as connectors or sources of more generalist species, especially if compared to forest habitats. These habitats should thus become a primary focus of management actions aimed at spiders in agroecosystems, especially if the main goal is to enhance the biocontrol service they provide.

In addition to the landscape context, many local-level factors can influence functional biodiversity and the related ecosystem services. In Chapter 5, we focused on a critical arthropod-related ecosystem service, weed seed predation. Our data showed that the functional composition of the predator assemblage plays an important role in regulating seed predation. Abundant and diverse predator communities were overall beneficial to predation intensity and stability, but an increase in number of large species lead to a partial suppression of seed predation, likely due to intra-guild predation. Additionally, we showed that soil disturbance (conventional vs. conservation tillage) influences predation intensity and stability depending on distance from field margin. The overall level of predation was similar in the two management systems, but predation was more homogeneous across conservation tillage fields, while it was lower near the margins and higher near the center of conventional tillage fields. This is likely a consequence of the differential distribution of seed predators in the two types of field, and could have important implications in the choice of management system depending on the size and other features of the field.

In conclusion, this thesis successfully employs a novel approach to answer some pressing questions about the way arthropods (and biodiversity in general) interact with the

landscape mosaics, how they are influenced by landscape simplification and which landscape-level strategies could be adopted in conservation and ecosystem services enhancement. The versatility of the species-habitat network allowed us to elucidate landscape-biodiversity interactions at multiple levels, devising a variety of management indications. From a species-centric point of view, we showed that the specialization level of arthropod guilds reacts differently to landscape simplification depending on their functional traits, suggesting that management strategies should change according to the focal group. We also demonstrated that network-level alterations depend both on changes in community composition and, more unexpectedly, on individual species behavioral changes. While the first process is universally recognized as important, behavioral plasticity has often been ignored. From a more habitat-centric point of view, our method was able to pinpoint the different roles of each habitat in the network (i. e. which habitats were more or less connected to the rest of the network), highlighting the most vulnerable ones and the most important for the stability of the system – all of which is pivotal for conservation prioritization. This framework has the potential to address a variety of other pressing issues in ecology and conservation in the future. These include the previously scarcely-explored question of how species-habitat interactions change through time because of the species natural life cycle within the year (Rasmussen *et al.*, 2013) or because of large-scale environmental transformations across multiple years (Olesen *et al.*, 2011). Another possible field of application of the method is the direct management of ecosystem services, which might benefit from focusing on functional rather than taxonomic biodiversity, and thus from using groups based on functional traits as nodes rather than species (de Bello *et al.*, 2010). In all cases, a careful choice of the sampling methods is necessary to ensure a correct representation of species diversity across all of the habitat or patches of the dataset.

Additionally, we highlighted local factors influencing arthropod-mediated ecosystem services in some of the studied landscapes. Arthropod community features were pivotal in influencing seed predation both directly and indirectly (through intra-guild predation). Similarly, soil management practices had significant and complex effects on seed predators and consequently on weed seed predation, changing its intensity, stability and spatial distribution within the field. This underlines the importance of taking into account multiple factors and their possible interactions (at both the local and the landscape scale) to have a more realistic and complete understanding of agroecosystem functioning and to efficiently manage functional biodiversity.

Appendix

Appendix A (Chapter 2)

A worked example of the species-habitat network concept using R

All code and data for creating the practical example included in the supplementary material is available via the Zenodo Repository at https://doi.org/10.5281/zenodo.2525376.

To show how to technically implement the species-habitat network framework, we use data reported in Hill & Bartomeus (2016), which can be found in an updated version at https://github.com/ibartomeus/hab-sp_ntw/blob/master/data/powerlines3.csv. The sampling was not originally conceived to apply this framework and therefore it should not be considered an optimal design for this purpose. The nature of the data is, however, suitable to technically exemplify how to compute some of the available metrics using simple examples that can be more easily visualized and interpreted by the users.

In the study, surveys were carried out in multiple habitats across 10 landscapes of 2 x 2 km. The habitat types were:

a) Corridors

b) Forest

c) Forest/grassland boundary

d) Non-flowering crop boundary

e) Semi-natural grassland

f) Maintained roadside

g) Maintained drain

Within each habitat type, a 50 x 3 m transect with the highest number of flowering plant species was selected. Bumblebee species abundance was recorded for 15 minutes. Each study plot was surveyed twice between 9th July 2014 and 25th August 2014.

We start by loading and formatting the data:

```
#load libraries
library(reshape)
library(vegan)
library(bipartite)
#next we read and review the data
d <-read.csv("data/powerlines3.csv", h =TRUE)
head(d)
str(d)
# check for any inconsistencies
```

```
levels(d$Gen_sp)
# remove unidentified species.
d <-subset(d, Gen_sp != "Bombus_spp")
levels(d$Site)
#due to issues with Swedish letters, they are renamed
levels(d$Site)[1] <- "Angeby"
levels(d$Site)[4] <- "Gavsta"
levels(d$Site)[7] <- "Kottgrind"
levels(d$Site)[8] <- "Laby_Norra"
levels(d$Site)[9] <- "Laby_Sodra"
#each of the two sampling rounds are pooled for this example
str(d)
d2 <-cast(d, formula = Site +Plot +Habitat +Gen_sp  ~. , fun.aggregate = length)
head(d2)
#rename using same nomenclature as in the paper
colnames(d2) <-c("Site","Patch","Habitat","Gen_sp","Abundance" )
```

Species-habitat network visualization

To start with this exercise we can work with a single network.

```
#subset one site
site1 <-subset(d2, Site == "Angeby")
#create the network in matrix format
ntw1 <-cast(site1, Patch ~Gen_sp, fun.aggregate ="sum", value ="Abundance")
#we can remove the first column with rownames
ntw1_  <-ntw1[,-1]
ntw1 <-as.matrix(ntw1_)
colnames(ntw1) <-gsub(pattern ="Bombus_", replacement ="B. ",
x =colnames(ntw1_), ignore.case = T)
#create a patch dataframe to store its properties.
patch <-unique(site1[, c("Patch", "Habitat")])
patch$color <-c("gold", "green", "gold", "darkgreen",
"grey", "green", "darkgreen",
"darkgreen", "lightgreen")
rownames(ntw1) <-patch$Patch
#create a vector of bees
bees <-cast(site1, Gen_sp ~., fun.aggregate = sum, value ="Abundance")
colnames(bees)[2] <- "abundance"
bees$labs <-colnames(ntw1)
```

To plot the network, we can use the *bipartite* package:

```
#prepare legend
legend <-unique(patch[,c("Habitat", "color")])
par(xpd = T) #allow plotting outside the plot
plotweb(ntw1, col.low =as.character(patch$color)) # plot the bipartite network (Figure A1)
legend(x=0, y=0.25, as.character(legend$Habitat), pch=21,
col="#777777", pt.bg=as.character(legend$color),
pt.cex=1, cex=.6, bty="n", ncol=2)
```
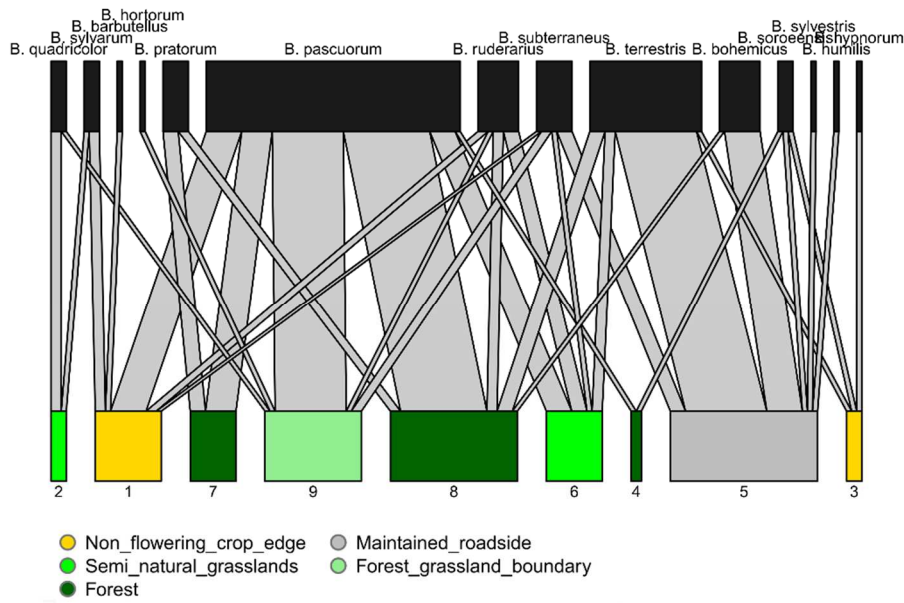
Fig. A1. Visualization of a species-habitat network built using 9 habitat patches as a bipartite network where nodes are species and habitat patches.

visweb(ntw1, prednames = T, preynames = T, labsize =0.6) *# plot the bipartite network as a matrix (Figure A2)*
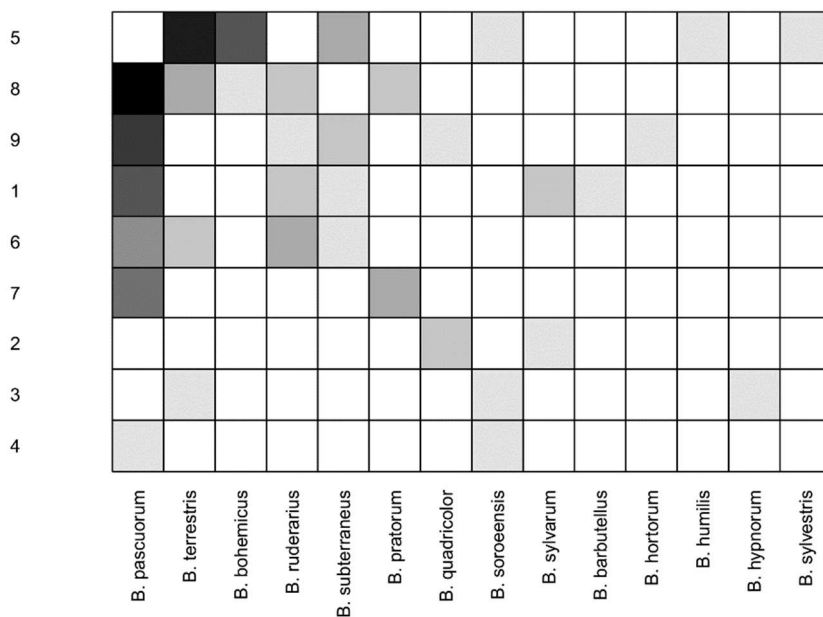

Fig. A2. Visualization of a species-habitat network built using 9 habitat patches as a matrix species by habitat patches.

By inspecting the network, we can see that *Bombus pascuorum* is the most abundant (large box) and highly connected (6 links), especially to semi-natural habitats (in green). We may now explore other visualization options by using the *igraph* package.

```
#alternative visualization tools:
library(igraph)
#prepare data for igraph
links <-site1[,c("Gen_sp", "Patch", "Abundance")]
colnames(links)[3] <- "weight"
node1 <-unique(site1[,c("Patch", "Habitat")])
colnames(node1) <-c("node", "attribute")
node1$type <- "habitat"
node2 <-data.frame(node =unique(site1[,c("Gen_sp")]),
attribute =NA,
type ="species")
nodes <-rbind(node1, node2)
#create igraph object
net <-graph_from_data_frame(d=links,
vertices=nodes, directed=F)
# generate colors for each habitat type:
clrs <-data.frame(nod =V(net)$attribute,
cols =c(patch$color, rep("blue", 14)))
V(net)$color <-as.character(clrs$cols)
# compute node degrees (#links) and use that to set node size:
deg <-degree(net, mode="all")
V(net)$size <-deg*3
# setting them to NA will render no labels:
V(net)$label <-as.character(nodes$id)
# set edge width based on weight:
E(net)$width <-E(net)$weight/3
#change arrow size and edge color:
E(net)$arrow.size <-.2 #but note no arrows in unidirected graphs like this
E(net)$edge.color <- "gray80"
#prepare colors
cl <-unique(clrs)
cl$nod <-as.character(cl$nod)
cl$nod[which(is.na(cl$nod))] <- "Bombus"
plot(net, vertex.label =NA) #force vertex label NA to make visualization clearer (Figure A3).
legend(x=-1.5, y=-1.1, cl$nod, pch=21,
col="#777777", pt.bg=as.character(cl$cols),
pt.cex=2, cex=.8, bty="n", ncol=2)
```
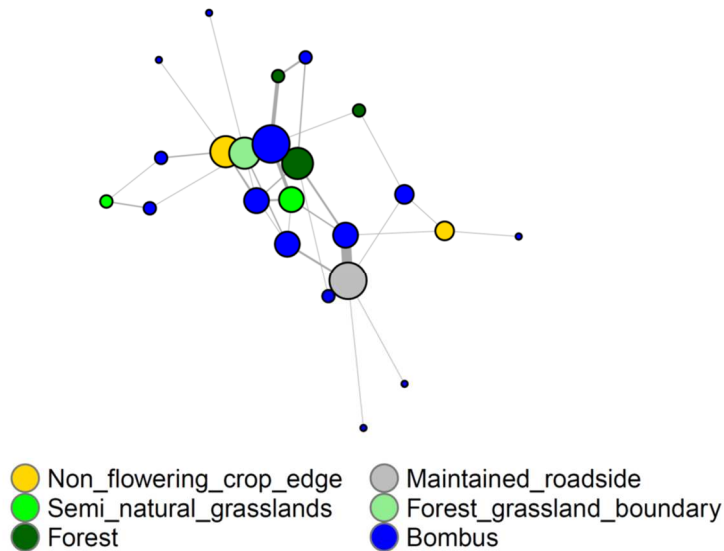
Fig. A3. Visualization of a species-habitat network built using 9 habitat patches as a web.

Here, we can see that the four larger habitat nodes are highly connected. Interestingly, these belong to four different habitat types.

Yet another option is the package *visNetwork,* which generates interactive plots that may be better for visualizing and exploring this kind of graphs. Note that the interactive plots cannot be embedded in this document.

```r
library('visNetwork')
colnames(nodes)[1] <- "id"
nodes$shape <- "dot"
nodes$shadow <-TRUE# Nodes will drop shadow
nodes$attribute <-as.character(nodes$attribute)
nodes$attribute[10:23] <-as.character(nodes$id[10:23])
nodes$title <-nodes$attribute # Text on click
nodes$label <-nodes$type # Node label
nodes$size <-deg*3# Node size
nodes$borderWidth <-2# Node border width

nodes$color.background <-clrs$cols
nodes$color.border <- "black"
nodes$color.highlight.background <- "orange"
nodes$color.highlight.border <- "darkred"
links$width <-links$weight # line width
links$color <- "gray"# line color
#links$arrows <- "middle" # arrows: 'from', 'to', or 'middle'
links$smooth <-TRUE# should the edges be curved?
links$shadow <-FALSE# edge shadow
colnames(links)[1:2] <-c("from", "to")
visNetwork(nodes, links)
```

Next, we can calculate a few network parameters.

Single network structure

To quantify network *nestedness*, we will calculate the weighted NODF, one of the most popular and robust nestedness metrics (Almeida-Neto *et al.*, 2008; Almeida-Neto & Ulrich, 2011), but other options are also available.

```
obs <-networklevel(web = ntw1, index ="weighted NODF")

## weighted NODF
##      20.8399
```

To know if the network is more nested than expected by chance, we need to compare this value with a null model using the Patefield algorithm (Figure A4):

```
nm <-nullmodel(web = ntw1, N=1000, method="r2d")
null <-unlist(sapply(nm, networklevel, index="weighted NODF"))
plot(density(null), xlim=c(min(obs, min(null)), max(obs, max(null))),
main="comparison of observed with null model Patefield")#plot the comparison (Figure A4)
abline(v=obs, col="red", lwd=2)
```
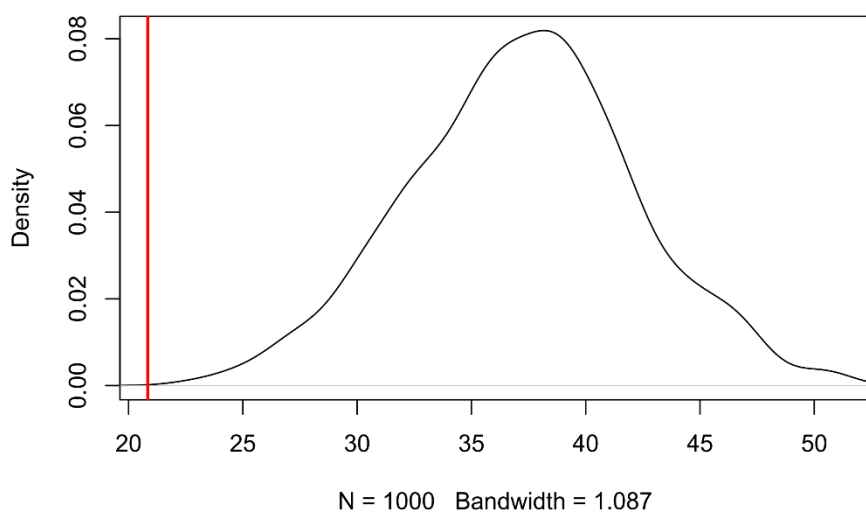

Fig. A4. Comparison of the observed NODF (red line) with the null model using the Patefield algorithm (black line).

```
praw <-sum(null>obs) /length(null)
```

Here, we can see that this network is less nested than expected by chance (p value < 0.001). This suggests that these species do not use habitats in a nested way (i.e. species-rich habitats do not host species found in species poor habitats) and we should check for other network structural features. To gain further insights on the structure of species habitats networks, we can use another important structural metric: *modularity*. In this example, we will calculate a quantitative version of the metric (Dormann & Strauss, 2014).

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```
res <-computeModules(ntw1)
plotModuleWeb(res, displayAlabels = T) #plot modules (Figure A5)
```
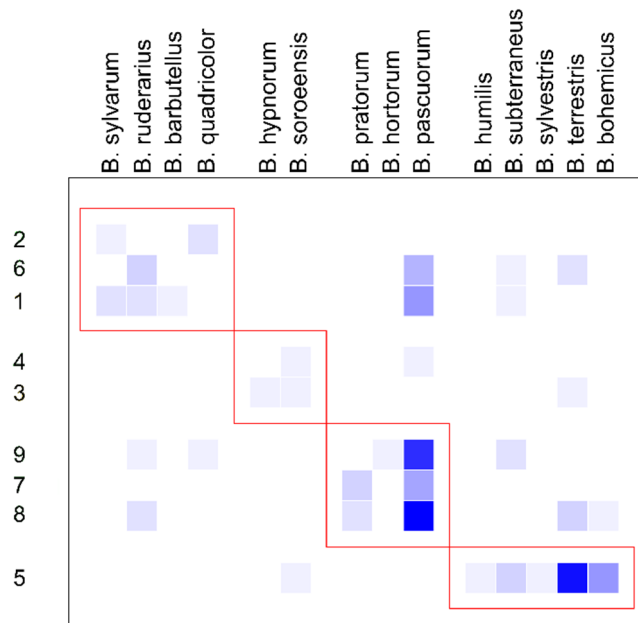

Fig. A5. Visualization of the division in modules (red outline) of the selected network with the species abundance (blue shading).

```
#listModuleInformation(res)
#printoutModuleInformation(res)
```

We can identify four modules. To see if modularity is higher than expected by chance we can compare the observed modularity with a null model.

```
mod <- computeModules(ntw1)
modules.nulls <- sapply(nm, computeModules)
like.nulls <- sapply(modules.nulls, function(x) x@likelihood)
praw <- sum(like.nulls>mod@likelihood) / length(like.nulls)
praw
```

The network is more modular than expected by chance (p-value < 0.001). This confirms that each habitat tends to harbour a quite unique assemblage of species, with limited exchange between habitat patches. For the purpose of this worked example, we now focus on the description of these modules. We can see that patches 7, 8 and 9 (forest areas) form a dense module with common bumblebee species. Patches 1, 2 and 6 (grasslands and open habitats) host rarer bumblebees. The other modules are very small. It is interesting to note that the only roadside patch has its own module.

We can also see the among-module (c) and within-module (z) connectivity of different patches. Interestingly, patch 6, 8 and 9 tend to act as connectors among modules. Patch 9 is the interface

between forest and grassland boundaries. Note that z cannot be computed for modules composed by a single patch, and hence patch 5 is not plotted.

```
#we can calculate 2 values for each node
cz <-czvalues(res, weighted =TRUE, level ="lower")
#c : among-module connectivity
#z : within-module connectivity
#Olesen et al. (2007) give critical c and z values of 0.62 and 2.6, respectively. According to their mode
l, species exceeding these values can be deemed connectors or hubs of a network.
plot(cz[[1]], cz[[2]], pch=16, xlab="c", ylab="z",
cex=0.8, las=1, col = patch$col)
text(cz[[1]], cz[[2]], names(cz[[1]]), pos=4, cex=0.7) # z c plot (Figure A6)
```


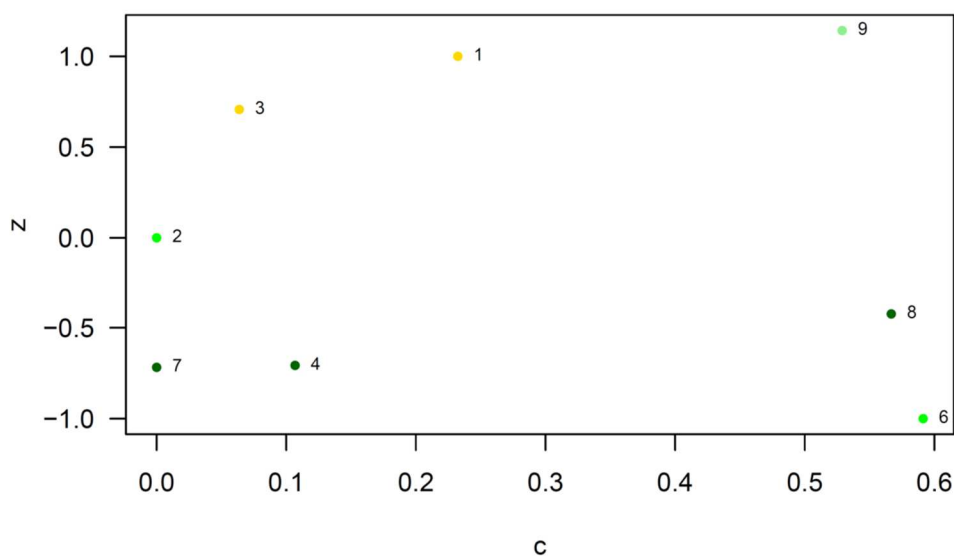**Fig. A6.** Plot of within-module (z) versus among-modules (c) connectivity in the selected network.

```
#we can check congruence between runs with function metaComputeModules
#res2 <- metaComputeModules(as.matrix(ntw1))
```

The next priority is to identify which habitat patches to prioritize in a conservation action. For this we can calculate the strength (Bascompte *et al.*, 2006) of each patch.

```
#we transpose the matrix to calculate it for the lower level.
patch$strength <-bipartite::strength(t(ntw1), type="Bascompte")
patch
```

```
##      Patch  Habitat                       color       strength
## 1    1      Non_flowering_crop_edge       gold        2.1995238
## 6    2      Semi_natural_grasslands       green       1.0000000
## 8    3      Non_flowering_crop_edge       gold        1.3787879
## 11   4      Forest                        darkgreen   0.3533333
## 13   5      Maintained_roadside           grey        4.3641775
## 19   6      Semi_natural_grasslands       green       0.7087662
## 23   7      Forest                        darkgreen   0.7200000
## 25   8      Forest                        darkgreen   1.2513636
## 30   9      Forest_grassland_boundary     lightgreen  2.0240476
```

Interestingly, the roadside habitat has the highest strength. This is because it sustains both common and rare species. However, we may want to correct for the fact that this habitat is only represented once in the dataset. Not surprisingly forests tend to rank lower, as they host a moderate number of common species.

We can see now how patches influence each other (Muller *et al.*, 1999):

```
inf <-PAC(ntw1)
```

```
##      1            2            3            4            5            6
## 1    0.30432234   0.05128205   0.000000000   0.010769231   0.03296703   0.12252747
## 2    0.22222222   0.55555556   0.000000000   0.000000000   0.00000000   0.00000000
## 3    0.00000000   0.00000000   0.459595960   0.111111111   0.35353535   0.03030303
## 4    0.07000000   0.00000000   0.166666667   0.176666667   0.16666667   0.05000000
## 5    0.01477833   0.00000000   0.036572623   0.011494253   0.73725556   0.06493506
## 6    0.14480519   0.00000000   0.008264463   0.009090909   0.17119244   0.17724321
## 7    0.09333333   0.00000000   0.000000000   0.013333333   0.00000000   0.06666667
## 8    0.11520000   0.00000000   0.005454545   0.013600000   0.12227273   0.10890909
## 9    0.13135338   0.03508772   0.000000000   0.014736842   0.04511278   0.10845865
##      7            8            9
## 1    0.06461538   0.22153846   0.19197802
## 2    0.00000000   0.00000000   0.22222222
## 3    0.00000000   0.04545455   0.00000000
## 4    0.06000000   0.17000000   0.14000000
## 5    0.00000000   0.10540752   0.02955665
## 6    0.05454545   0.24752066   0.18733766
## 7    0.28000000   0.36000000   0.18666667
## 8    0.12960000   0.30456364   0.20040000
## 9    0.08842105   0.26368421   0.31314536
```

We can read the values in this matrix as the influence mediated by shared pollinators between each pair of habitat patches. Influence is low overall (mean = 0.111) but some patches influence each other via shared pollinators (e.g. 8->7 influence is 0.36, but note this is not reciprocal, as 7->8 influence is moderate: 0.1296)

Additionally, we can identify the most selective bumblebees (Blüthgen et al., 2007). For this we must aggregate the data at the habitat level.

```
d3 <-cast(d, formula = Site +Habitat +Gen_sp  ~. , fun.aggregate = length)
colnames(d3) <-c("Site","Habitat","Gen_sp","Abundance" )
site1b <-subset(d3, Site == "Angeby")
#create the network in matrix format
ntw1b <-cast(site1b, Habitat ~Gen_sp, fun.aggregate ="sum", value ="Abundance")
#we can remove the first column with rownames
ntw1b <-ntw1b[,-1]
# visualize the network with bipartite
#plotweb(ntw1b)
#and calculate d'
#here low.abun can be used if we know patch attributes like area.
bees$d <-specieslevel(web = ntw1b, index ="d", level ="higher")
bees
```

```
##       Gen_sp              abundance    labs            d
## 1     Bombus_barbutellus  1            B. barbutellus  0.22629439
## 2     Bombus_bohemicus    8            B. bohemicus    0.36040676
## 3     Bombus_hortorum     1            B. hortorum     0.17833866
## 4     Bombus_humilis      1            B. humilis      0.06033821
## 5     Bombus_hypnorum     1            B. hypnorum     0.22629439
## 6     Bombus_pascuorum    50           B. pascuorum    0.39456717
## 7     Bombus_pratorum     5            B. pratorum     0.35516628
## 8     Bombus_quadricolor  3            B. quadricolor  0.30913755
## 9     Bombus_ruderarius   8            B. ruderarius   0.17267753
## 10    Bombus_soroeensis   3            B. soroeensis   0.01736694
## 11    Bombus_subterraneus 7            B. subterraneus 0.14189519
## 12    Bombus_sylvarum     3            B. sylvarum     0.31301000
## 13    Bombus_sylvestris   1            B. sylvestris   0.06033821
## 14    Bombus_terrestris   22           B. terrestris   0.34582083
```

Species such as *B. terrestris* or *B. pascuorum* have high values of d' (highly unselective), while *B. humilis* or *B. soroeensis* are highly selective.

A simple analysis using multiple networks

At the regional level we have sampled 10 networks. We can determine which network is more nested and if the nestedness pattern correlates with the amount of semi-natural habitats or species richness. Additionally, we can determine whether nestedness is positively correlated to robustness in species-habitat networks (Memmott *et al.*, 2004).

For each of the 10 networks, we can calculate nestedness as well as other parameters such as species richness, robustness and number of semi-natural patches. Remember that to compare nestedness values, we need to standardize them. We suggest to follow the method of Song et al. (2017).

```r
source("toolbox.R") #load code developed by Song et al. (2017) and available in his paper.
# loop through all sites
#first we create empty objects to store the data
sites <-unique(d2$Site)
ntwks<-list()
nested <-c()
NODF <-c()
st_NODF<-c()
rob_rand<-c()
rob_real<-c()
rich <-c()
seminat<-c()
for(i in 1:length(sites)){
sitex<-subset(d2, Site ==sites[i])
#create the network in matrix format
ntwx<-cast(sitex, Patch ~Gen_sp, fun.aggregate ="sum",
value ="Abundance")
#we can remove the first column with rownames
ntwx<-ntwx[,-1]
#visualize it with bipartite
#plotweb(ntwx)
  ntwks[[i]] <-ntwx
#calculate nestedness
  nested[i] <-networklevel(web = ntwx, index ="weighted NODF")
  rob_rand[i] <-robustness(second.extinct(web = ntwx, nrep =50, participant ="lower", method ="ran
dom"))
  NODF[i] <-nestedness_NODF(as.matrix(ntwx))
  st_NODF[i] <-comb_nest(web = ntwx, NODF = NODF[i], max_NODF =max_nest(ntwx))
#create a realistic extinction sequence
  ext_seq <-unique(sitex[,c("Patch", "Habitat")])
#quick way to order habitats
levels(ext_seq$Habitat) <-c("gCorridor", "bForest",
"cForest_grassland_boundary",
"fMaintained_drain",
"eMaintained_roadside",
"dNon_flowering_crop_edge",
"aSemi_natural_grasslands")
  ext_seq$Patch <-order(as.character(ext_seq$Habitat))
  rob_real[i] <-robustness(second.extinct(web = ntwx, participant ="lower", method ="external", ext.
row = ext_seq$Patch )) #grasslands first, forest, etc...
  rich[i] <-ncol(ntwx)
  seminat[i] <-length(subset(ext_seq, Habitat %in%
c("aSemi_natural_grasslands",
"bForest"))$Patch)
}
sites_measures <-data.frame(sites, nested, NODF, st_NODF, rob_rand, rob_real, rich, seminat)
```

Now we can address several ecological questions across the 10 networks.

1. *Is nestedness correlated with the amount of semi-natural habitats?*


```r
plot(sites_measures$st_NODF ~sites_measures$seminat) #plot nestedness vs. seminatural habitat am
ount
abline(lm(sites_measures$st_NODF ~sites_measures$seminat)) #plot regression line (Figure A7)
```
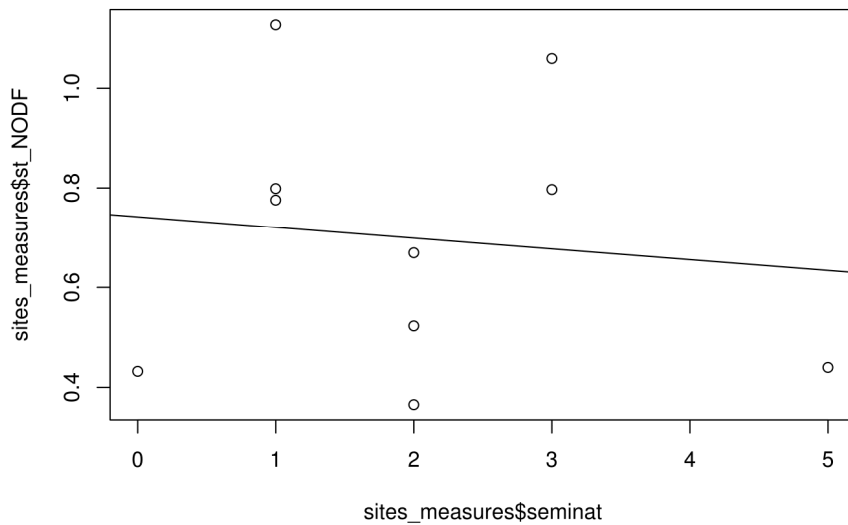
Fig. A7. Plot of nestedness versus semi-natural habitat amount in 10 networks.

A simple visual inspection tells us that there is a very weak trend for sites with more semi-natural habitat patches (forests and grasslands) to be less nested. We would need better information on the proportion of semi-natural habitats in the landscape to run more accurate statistical tests.

2. *Is nestedness related to species richness?*

scatter.smooth(sites_measures$st_NODF ~sites_measures$rich) *#plot nestedness vs. species richness (Figure A8)*
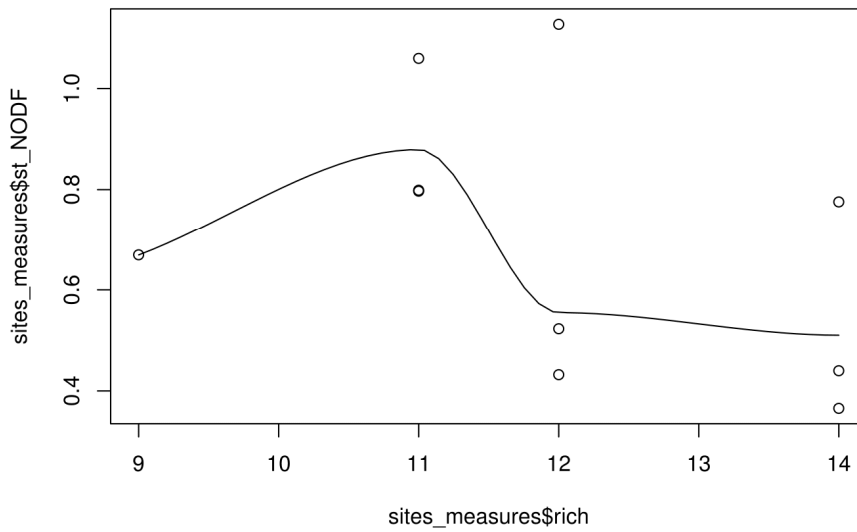
Fig. A8. Plot of nestedness versus species richness in the 10 networks.

In this case, the plot suggests that nestedness is not related to bumblebee richness levels.

3. *Are more nested sites also more robust to* in silico *patch removal?*

scatter.smooth(sites_measures$st_NODF ~sites_measures$rob_rand) *#plot nestedness vs. robustness when patches are removed in a random order (Figure A9)*
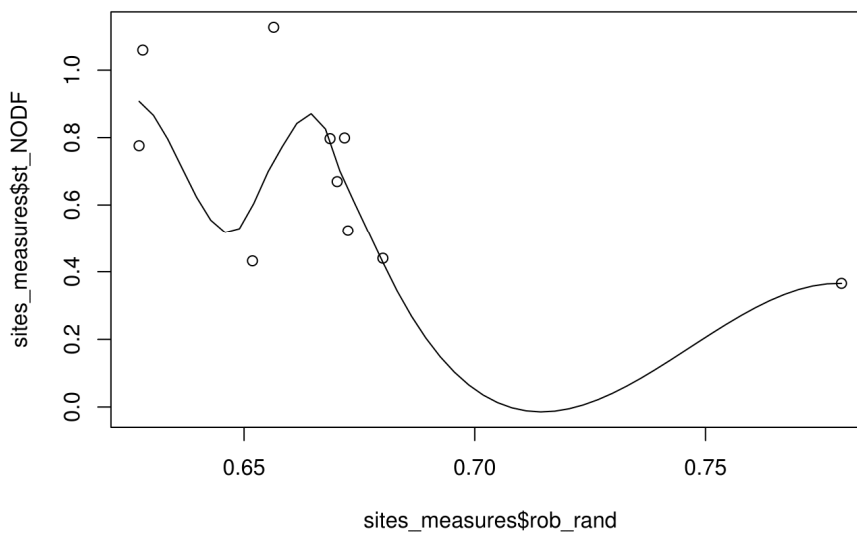
Fig. A9. Plot of nestedness versus robustness when removing habitat patches in a random order.

scatter.smooth(sites_measures$neste ~sites_measures$rob_real) *#plot nestedness vs. robustness when semi-natural patches are removed first (Figure A10)*
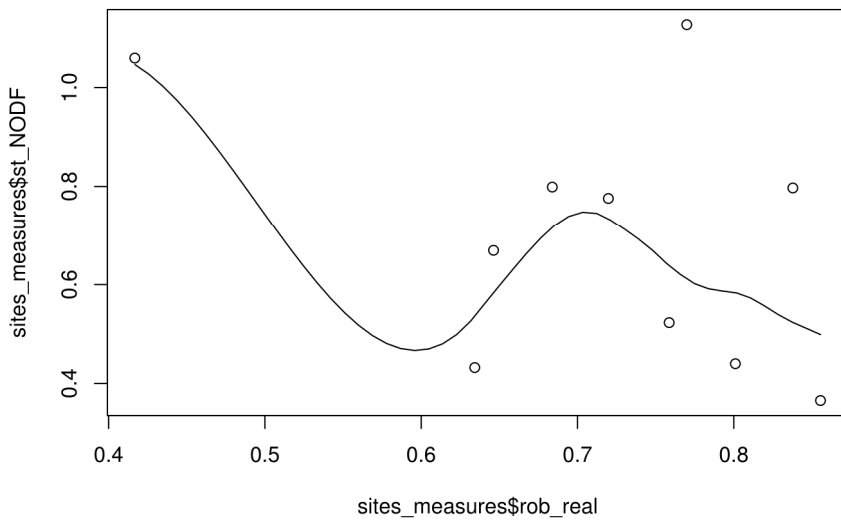
Fig. A10. Plot of nestedness versus robustness when removing semi-natural habitat patches first.

In this example, robustness is not clearly related with nestedness either when removals are random or when semi-natural patches are removed first.

What have we learned?

We have shown how to apply network tools to analyse species-habitat networks. This is just a technical example to show in practice how to use available packages in R and it is not meant as an ideal application of the framework.

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Appendix B (Chapter 3)

Table B1. z-scores of network-level metrics (Dormann & Strauss, 2014) for all the three groups. Almost all values are significant ($z < -2$ or $z > 2$).

|	Site	$H_2{'}$	Modularity	NODF
Predators	pred1	81.85526	45.66559	-11.15891
	pred2	18.27387	17.66045	-7.17488
	pred3	33.38658	32.26045	-6.76951
	pred4	41.28643	36.85626	-10.66419
	pred5	22.50096	21.59949	-4.92517
	pred6	93.34424	75.65438	-9.61001
	pred7	26.61507	26.10903	-5.31013
	pred8	27.04642	21.46804	-5.40744
	pred9	41.26921	37.99273	-8.98810
	pred10	43.00337	30.88094	-7.99094
	pred11	52.64062	37.16081	-9.11378
	pred12	43.09161	41.63446	-11.51292
	pred13	14.73183	13.26648	-5.42607
	pred14	77.00479	34.21268	-6.41233
	pred15	38.67073	34.44949	-7.67467
Herbivores	herb1	75.09392	49.71530	-13.00962
	herb2	66.16059	36.02815	-8.87715
	herb3	80.00163	41.68170	-10.58165
	herb4	64.62467	36.95740	-12.23584
	herb5	37.26408	23.77481	-8.88570
	herb6	45.43400	37.30342	-9.89910
	herb7	67.25677	32.85310	-7.27709
	herb8	36.41106	26.15022	-6.07129
	herb9	88.16739	58.74894	-8.43807
	herb10	44.27896	35.07843	-9.04343
Pollinators	poll1	18.33453	16.69370	-6.23842
	poll2	11.55269	9.20800	-3.77052
	poll3	5.97168	7.46975	-1.77378
	poll4	6.33276	4.95096	-2.04942
	poll5	10.83897	10.26037	-4.03225
	poll6	10.39475	9.61060	-4.12920
	poll7	17.51772	14.09833	-5.44714
	poll8	4.80992	4.01543	-2.88298
	poll9	17.96264	13.37802	-5.22541
	poll10	25.00941	18.22123	-7.19341
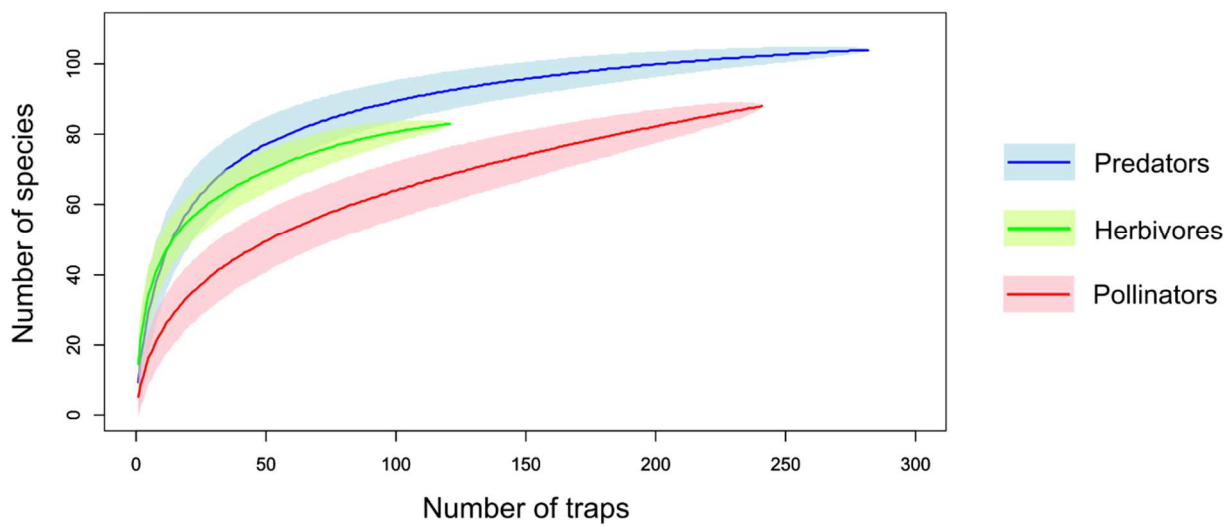
Fig. B1 Accumulation curves for the three studied groups based on 1000 randomizations. The different sampling effort is due to different number of traps.

Appendix C (Chapter 4)

Table C1 List of the spider species with their total activity density in the five habitat types. Nomenclature is according to the World Spider Catalog (World Spider Catalog, 2019).

Species	Annual crops	Perennial crops	Forest	Hedgerow	Meadow
Agelenidae	**6**	**7**	**58**	**4**	**2**
Agelena labyrinthica (Clerck, 1757)	2	1		1	
Eratigena fuesslini (Pavesi, 1873)			2		
Histopona torpida (C. L. Koch, 1837)	3	1	51		2
Tegenaria hasperi Chyzer, 1897		5	2	2	
Tegenaria silvestris L. Koch, 1872	1		3	1	
Amaurobidae			**4**		
Amaurobius jugorum L. Koch, 1868			4		
Anyphaenidae			**2**		
Anyphaena accentuata (Walckenaer, 1802)			2		
Araneidae		**1**	**1**		**2**
Cercidia prominens (Westring, 1851)		1			2
Hypsosinga sanguinea (C. L. Koch, 1844)			1		
Atypidae	**2**		**22**	**2**	**2**
Atypus piceus (Sulzer, 1776)	2		22	2	2
Clubionidae		**1**	**6**	**2**	
Clubiona lutescens Westring, 1851			1	1	
Clubiona phragmitis C. L. Koch, 1843			2		
Clubiona terrestris Westring, 1851		1	3	1	
Dictynidae	**2**	**3**			
Argenna patula (Simon, 1874)	1				
Argenna subnigra (O. P.-Cambridge, 1861)	1	3			
Dysderidae	**6**	**8**	**75**	**10**	**1**
Dasumia canestrinii (L. Koch, 1876)	4		39	2	1
Dysdera adriatica Kulczyński, 1897	1		9	5	
Dysdera lantosquensis Simon, 1882	1		15	1	
Dysdera microdonta Gasparo, 2014			5		
Dysdera ninnii Canestrini, 1868		5	2	2	
Dysdera ninnii-group (females)		3	5		
Gnaphosidae	**84**	**130**	**64**	**13**	**54**
Callilepis schuszteri (Herman, 1879)		1			
Civizelotes gracilis (Canestrini, 1868)		6			
Drassodes lapidosus (Walckenaer, 1802)	3	5	2		4
Drassodes pubescens (Thorell, 1856)	1	2			4
Drassyllus praeficus (L. Koch, 1866)	3	3	4		7
Drassyllus pumilus (C. L. Koch, 1839)	22	30	6	2	
Drassyllus pusillus (C. L. Koch, 1833)	8	1			2

Species					
Drassyllus villicus (Thorell, 1875)	5		2	3	1
Gnaphosa lucifuga (Walckenaer, 1802)	5	7	1	1	
Haplodrassus dalmatensis (L. Koch, 1866)	1	4			1
Haplodrassus kulczynskii Lohmander, 1942					1
Haplodrassus signifer (C. L. Koch, 1839)	1				2
Micaria pulicaria (Sundevall, 1831)	18	7		1	5
Nomisia exornata (C. L. Koch, 1839)		8			
Phaeocedus braccatus (L. Koch, 1866)	1	4	1		
Trachyzelotes adriaticus (Caporiacco, 1951)	2	1			
Trachyzelotes mutabilis (Simon, 1878)		1			
Trachyzelotes pedestris (C. L. Koch, 1837)	5	17	31	3	7
Zelotes apricorum (L. Koch, 1876)			1	2	
Zelotes atrocaeruleus (Simon, 1878)	2	28	13		12
Zelotes exiguus (Müller & Schenkel, 1895)	5	2	3		2
Zelotes hermani (Chyzer, 1897)	1	1			1
Zelotes latreillei (Simon, 1878)					1
Zelotes tenuis (L. Koch, 1866)	1	2		1	4
Linyphiidae	**85**	**31**	**27**	**2**	**16**
Agyneta fuscipalpa (C. L. Koch, 1836)			1		
Agyneta mollis (O. P.-Cambridge, 1871)					1
Agyneta rurestris (C. L. Koch, 1836)	8	2			2
Ceratinella brevis (Wider, 1834)					2
Cnephalocotes obscurus (Blackwall, 1834)					1
Cresmatoneta mutinensis (Canestrini, 1868)		1			
Diplostyla concolor (Wider, 1834)	1	6	3	2	
Erigone autumnalis Emerton, 1882	2	2			1
Erigone dentipalpis (Wider, 1834)	35	2	1		
Erigonoplus globipes (L. Koch, 1872)		1			
Mermessus trilobatus (Emerton, 1882)	2	1	2		
Microlinyphia pusilla (Sundevall, 1830)	1				
Neriene clathrata (Sundevall, 1830)	1				
Oedothorax apicatus (Blackwall, 1850)	27	12	1		3
Oedothorax retusus (Westring, 1851)					5
Ostearius melanopygius (O. P.-Cambridge, 1879)	1				
Tenuiphantes flavipes (Blackwall, 1854)	1		5		1
Tenuiphantes tenuis (Blackwall, 1852)	6	4	2		
Trichoncus affinis Kulczyński, 1894			3		
Troglohyphantes poleneci Wiehle, 1964			2		
Walckenaeria atrotibialis (O. P.-Cambridge, 1878)			6		
Walckenaeria obtusa Blackwall, 1836			1		
Liocranidae	**2**		**18**	**1**	**3**
Agroeca brunnea (Blackwall, 1833)			1		
Agroeca cuprea Menge, 1873			6	1	1
Liocranoeca striata (Kulczyński, 1882)	2		11		2

Lycosidae	2236	1342	1427	463	586
Alopecosa albofasciata (Brullé, 1832)		1	2		
Alopecosa pulverulenta (Clerck, 1757)	12	14	8	3	47
Arctosa figurata (Simon, 1876)		4			2
Arctosa leopardus (Sundevall, 1833)	32	1	6		20
Arctosa lutetiana (Simon, 1876)		5	27	11	1
Arctosa maculata (Hahn, 1822)	2		1		1
Arctosa personata (L. Koch, 1872)	3				2
Aulonia albimana (Walckenaer, 1805)	5	43	12	3	77
Hogna radiata (Latreille, 1817)	3	29	10		39
Pardosa agrestis (Westring, 1861)	331	41	85	3	3
Pardosa amentata (Clerck, 1757)	23				
Pardosa cribrata Simon, 1876	135	23	2		
Pardosa hortensis (Thorell, 1872)	481	249	192	13	6
Pardosa lugubris-group	80	64	201	111	60
Pardosa prativaga (L. Koch, 1870)	11		5		2
Pardosa proxima (C. L. Koch, 1847)	376	341	27		34
Pardosa vittata (Keyserling, 1863)	72	15	3	10	39
Pirata piraticus (Clerck, 1757)	1				
Piratula hygrophila (Thorell, 1872)			1		
Piratula latitans (Blackwall, 1841)	5				45
Piratula uliginosa (Thorell, 1856)			4		
Trochosa hispanica Simon, 1870	162	287	593	230	84
Trochosa robusta (Simon, 1876)	2	3			3
Trochosa ruricola (De Geer, 1778)	83	91	30	19	70
Trochosa sp. (females)	109	87	148	59	49
Xerolycosa miniata (C. L. Koch, 1834)	143	39	13		1
Xerolycosa nemoralis (Westring, 1861)	165	5	57	1	1
Mimetidae			**1**		
Ero furcata (Villers, 1789)			1		
Miturgidae	**11**	**1**	**40**	**7**	**1**
Zora spinimana (Sundevall, 1833)	11	1	40	7	1
Nesticidae	**1**				
Eidmannella pallida (Emerton, 1875)	1				
Oxyopidae		**1**			
Oxyopes lineatus Latreille, 1806		1			
Philodromidae	**23**	**6**	**2**	**2**	**4**
Philodromus pinetorum Muster, 2009	1				
Philodromus rufus Walckenaer, 1826			1		
Thanatus atratus Simon, 1875	22	5	1	2	4
Tibellus macellus Simon, 1875		1			
Phrurolithidae	**22**	**52**	**11**	**4**	**3**
Phrurolithus festivus (C. L. Koch, 1835)	17	51	9	3	3
Phrurolithus minimus C. L. Koch, 1839	5	1	2	1	

Pisauridae	**2**	**4**	**7**	**2**	**4**
Dolomedes fimbriatus (Clerck, 1757)	1		4	2	2
Pisaura mirabilis (Clerck, 1757)	1	4	3		2
Salticidae	**13**	**21**	**7**	**6**	**6**
Attulus penicillatus (Simon, 1875)		3			
Attulus saltator (O. P.-Cambridge, 1868)	1				
Chalcoscirtus infimus (Simon, 1868)		1			
Euophrys frontalis (Walckenaer, 1802)	4	2	6	5	4
Heliophanus cupreus (Walckenaer, 1802)		3	1		
Leptorchestes berolinensis (C. L. Koch, 1846)					1
Myrmarachne formicaria (De Geer, 1778)	1	4		1	
Phlegra fasciata (Hahn, 1826)	1	2			1
Pseudeuophrys erratica (Walckenaer, 1826)		1			
Salticus zebraneus (C. L. Koch, 1837)	1				
Sibianor tantulus (Simon, 1868)	5	4			
Talavera aequipes (O. P.-Cambridge, 1871)		1			
Segetriidae			**1**		
Segestria bavarica C. L. Koch, 1843			1		
Sparassidae	**1**		**3**	**1**	
Micrommata virescens (Clerck, 1757)	1		3	1	
Tetragnathidae	**39**	**37**	**21**	**5**	**81**
Pachygnatha degeeri Sundevall, 1830	39	37	16	2	80
Pachygnatha listeri Sundevall, 1830			5	3	1
Theridiidae	**16**	**42**	**106**	**10**	**33**
Asagena italica (Knoflach, 1996)	3	19	1		22
Asagena phalerata (Panzer, 1801)	6	13	2	2	7
Crustulina guttata (Wider, 1834)			1		
Enoplognatha thoracica (Hahn, 1833)		2	4		
Episinus truncatus Latreille, 1809		1	6		
Euryopis flavomaculata (C. L. Koch, 1836)	6	5	89	8	4
Robertus mediterraneus Eskov, 1987			2		
Robertus neglectus (O. P.-Cambridge, 1871)		1			
Steatoda albomaculata (De Geer, 1778)		1			
Trichoncus affinis Kulczyński, 1894	1		1		
Thomisidae	**157**	**130**	**39**	**2**	**30**
Cozyptila blackwalli (Simon, 1875)			3	1	
Ozyptila praticola (C. L. Koch, 1837)	1	9	22		
Ozyptila simplex (O. P.-Cambridge, 1862)	1				1
Xysticus acerbus Thorell, 1872		1			
Xysticus bifasciatus C. L. Koch, 1837		1	4		8
Xysticus kochi Thorell, 1872	155	119	7	1	19
Xysticus lineatus (Westring, 1851)					2
Xysticus luctator L. Koch, 1870			3		
Titanoecidae	**2**	**21**	**1**		**2**

Nurscia albomaculata (Lucas, 1846)	1				
Titanoeca tristis L. Koch, 1872	1	21	1		2
Zodariidae	**4**	**29**	**15**	**11**	**5**
Zodarion hamatum Wiehle, 1964	3	6	9	10	2
Zodarion italicum (Canestrini, 1868)	1		5	1	
Zodarion rubidum Simon, 1914		23	1		3
TOTAL	**2714**	**1867**	**1958**	**547**	**835**
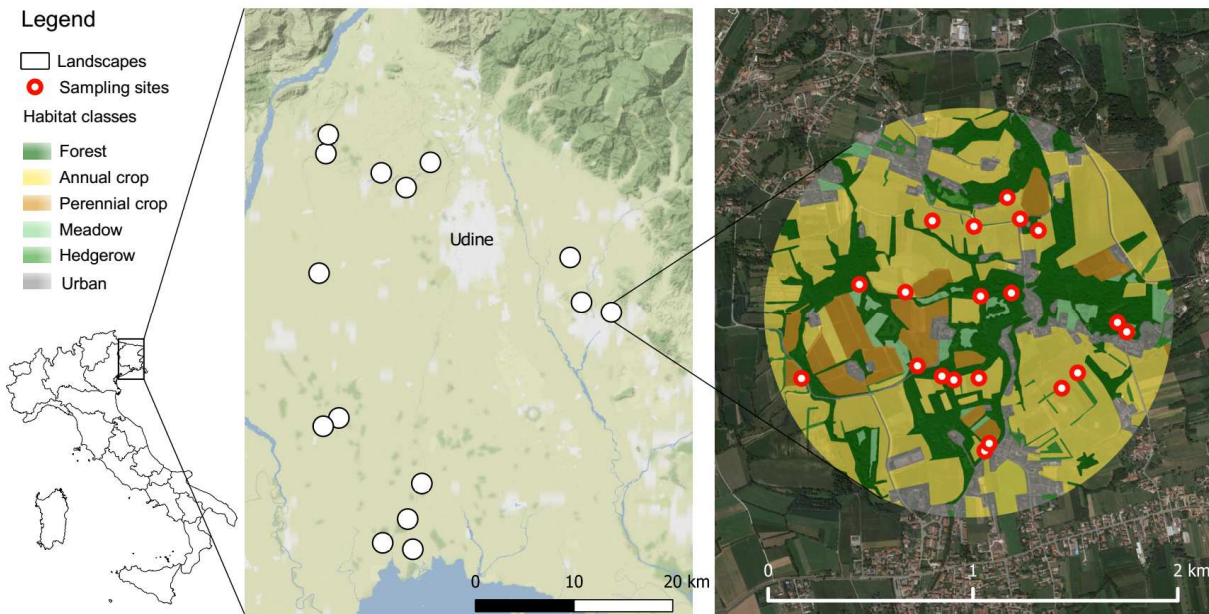
Fig. C2 Geographical location of the 15 landscapes in Friuli (NE Italy). Each landscape consisted of a circular area of 2 km diameter, with 20 sampling points reflecting the main habitat types and their relative abundance.
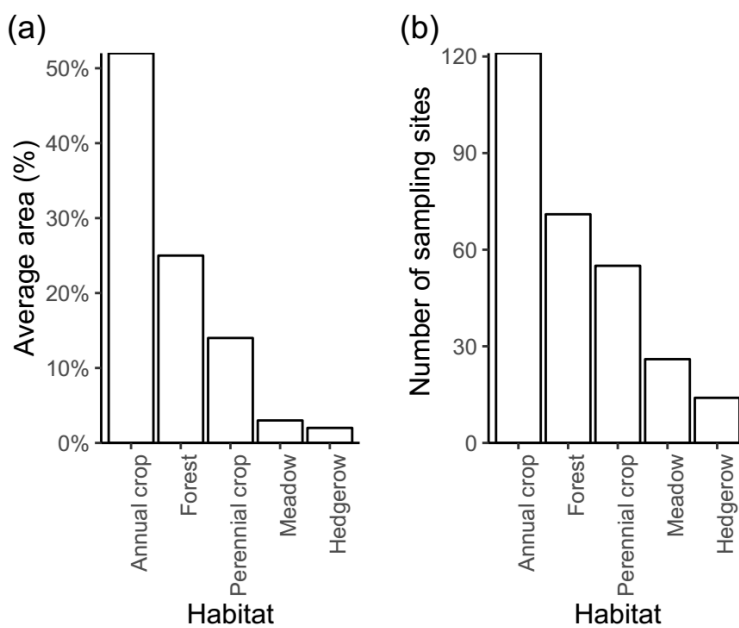
Fig. C2 (a) The average area of each habitat (%) across the 15 landscapes and (b) the total number of traps per habitat.
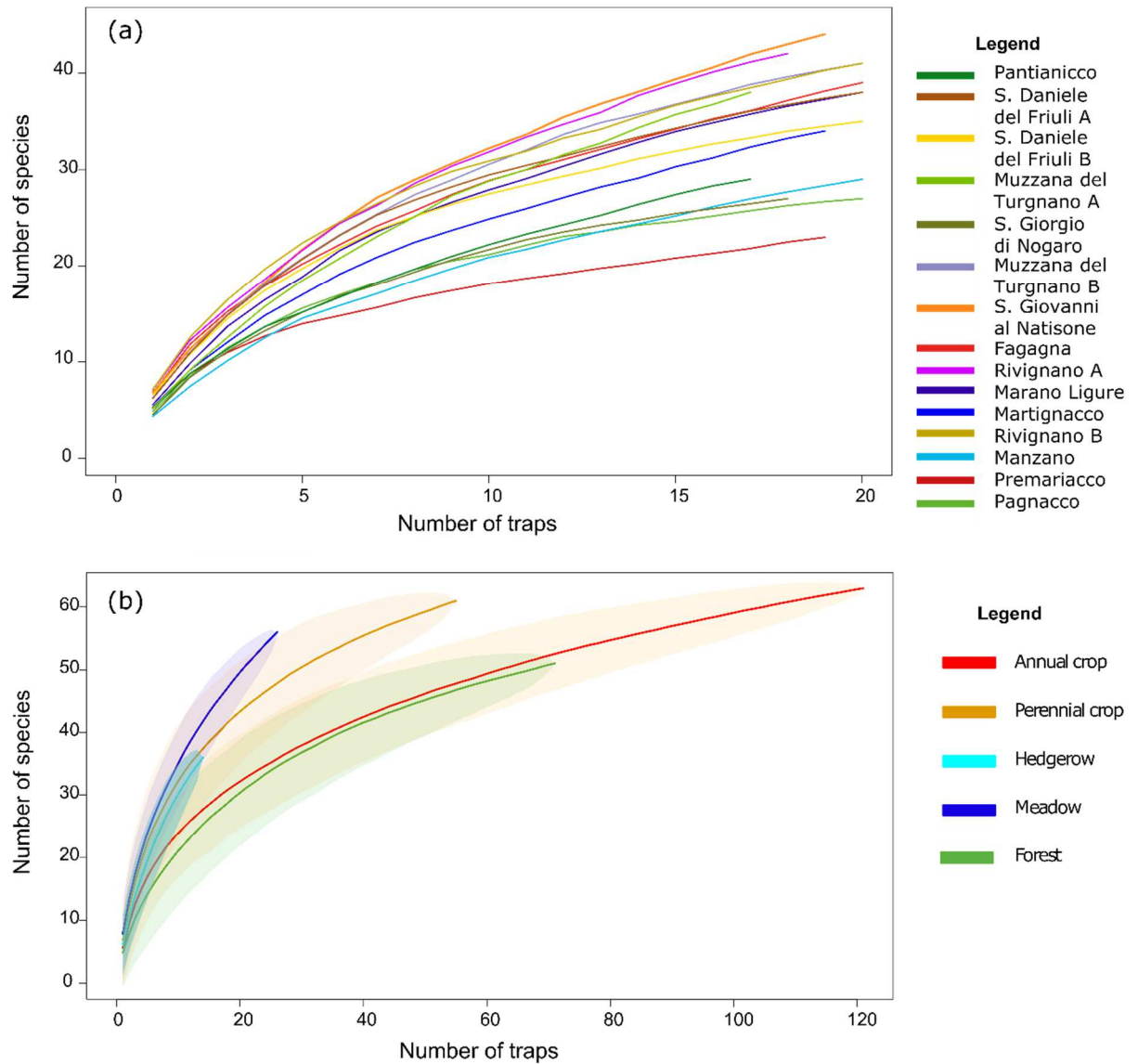
Fig. C3: Accumulation curves for (a) each landscape and (b) each habitat type (n=15) based on 1000 randomizations. The different sampling effort is due to different number of traps. Nevertheless, forest and annual crop seem to have similar accumulation curves.
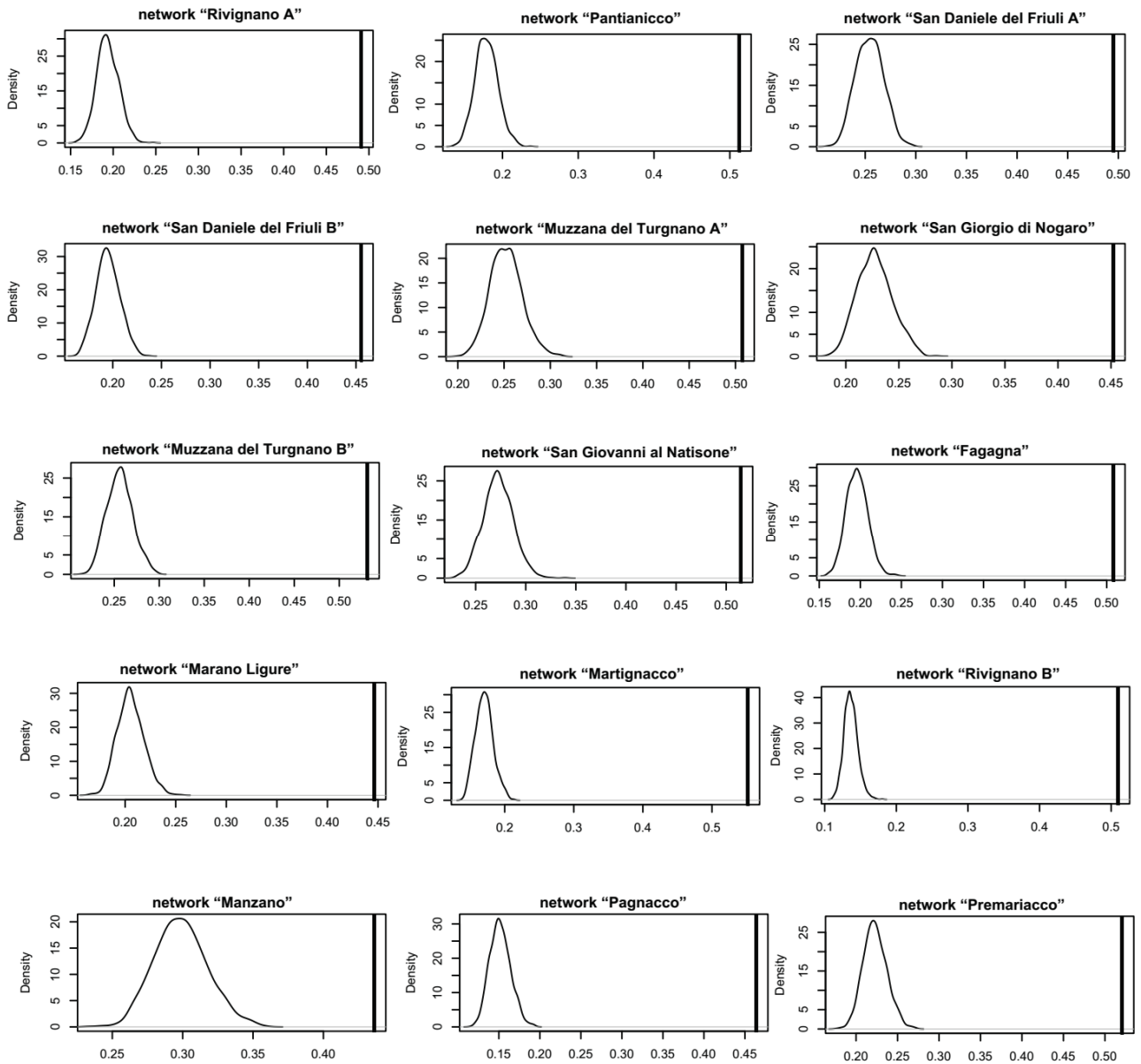
Fig. C4 Comparison between expected modularity based on 1000 null models (density curve) and the observed modularity value (solid vertical line) in the 15 species-habitat networks. All observed values were larger than the expected ones.

Table D1. Features of the fields used during the experiment.

Pair	Field management	Distance between fields in a couple (m)	Coordinates (WGS 84)	Geographical area	Sampling period	Crop	Margin	Control	Years No till	Urban cover 750 m (%)	Seminatural 750 m (%)
1A	Conventional	2500 m	45°53'14.01"N, 13°01'41.15"E	Rivignano (UD)	Sept 2017	Soybean	Grass	No	-	6,50%	17,90%
1A	Conservation		45°51'52.61"N, 13°01'51.82"E	Rivignano (UD)	Sept 2017	Soybean	Grass	No	15	2,30%	2,30%
2A	Conventional	2700 m	45°51'49.74"N, 13°01'44.61"E	Rivignano (UD)	Sept. 2017	Sorghum cover	Grass	No	-	2,30%	2,30%
2A	Conservation		45°53'16.75"N, 13°01'46.75"E	Rivignano (UD)	Sept 2017	Sorghum cover	Grass	No	15	6,50%	17,90%
3A	Conventional	200 m	45°52'09.43"N, 13°02'01.59"E	Rivignano (UD)	Sept 2017	Soybean	Grass/hedg.	Yes	-	33,10%	0,10%
3A	Conservation		45°52'16.06"N, 13°02'01.08"E	Rivignano (UD)	Sept 2017	Soybean	Grass/hedg.	Yes	20	44,20%	0,10%
4A	Conventional	1100 m	46°09'21.65"N, 12°57'36.06"E	Aonedis (UD)	Sept 2017	Soybean	Wood	Yes	-	1,10%	13,50%
4A	Conservation		46°08'49.46"N, 12°57'56.19"E	Aonedis (UD)	Sept 2017	Barley (mown)	Wood	Yes	5	8,90%	6,70%
5A	Conventional	100 m	46°02'35.28"N, 13°22'40.50"E	Orsaria (UD)	Sept 2017	Alfalfa	Grass	Yes	-	33,90%	1,00%
5A	Conservation		46°02'38.32"N, 13°22'43.04"E	Orsaria (UD)	Sept 2017	Alfalfa	Grass	Yes	10	35,30%	2,10%
6A	Conventional	320 m	46°02'38.06"N, 13°22'16.20"E	Orsaria (UD)	Sept 2017	Maize	Grass/hedg.	No	-	8,70%	0,80%
6A	Conservation		46°02'44.27"N, 13°22'04.08"E	Orsaria (UD)	Sept 2017	Maize	Grass	No	10	1,00%	0,70%
7A	Conventional	500 m	46°02'17.33"N, 13°20'55.57"E	Orsaria (UD)	Sept 2017	Soybean	Grass	Yes	-	1,00%	0,00%
7A	Conservation		46°02'10.86"N, 13°20'34.61"E	Orsaria (UD)	Sept 2017	Soybean	Grass	Yes	10	1,00%	0,00%
8A	Conventional	960 m	46°02'02.13"N, 13°22'03.29"E	Orsaria (UD)	Sept 2017	Soybean	Grass	No	-	2,70%	0,00%
8A	Conservation		46°01'36.27"N, 13°21'37.88"E	Orsaria (UD)	Sept 2017	Soybean	Grass	No	10	0,70%	2,00%
1B	Conventional	160 m	45°52'14.89"N, 13°01'45.60"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Grass/hedg.	No	-	24,00%	0,00%
1B	Conservation		45°52'17.28"N, 13°01'44.51"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Hedgerow	No	15	32,50%	0,00%
2B	Conventional	100 m	45°51'41.27"N, 13°03'09.59"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Grass	No	-	23,00%	1,30%
2B	Conservation		45°51'38.98"N, 13°03'13.22"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Grass	No	18	23,00%	1,30%
3B	Conventional	200 m	45°53'12.72"N, 13°02'25.08"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Grass	No	-	21,70%	8,70%
3B	Conservation		45°53'07.35"N, 13°02'33.14"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Poplar	No	18	29,40%	8,90%
4B	Conventional	80 m	45°52'15.27"N, 13°02'57.16"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Hedgerow	No	-	40,60%	0,00%
4B	Conservation		45°52'18.07"N, 13°02'54.87"E	Rivignano (UD)	Jun-Aug 2018	Soybean	Grass	No	14	40,60%	0,00%
5B	Conventional	0 m	46°02'53.51"N, 13°22'36.91"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	-	12,90%	2,20%
5B	Conservation		46°02'54.32"N, 13°22'37.16"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Hedgerow	No	12	12,90%	2,20%
6B	Conventional	400 m	46°02'46.22"N, 13°21'42.26"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Wood	No	-	0,00%	2,00%
6B	Conservation		46°02'43.77"N, 13°21'55.54"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	12	0,00%	1,60%
7B	Conventional	900 m	46°02'15.24"N, 13°21'40.67"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	-	1,10%	1,50%
7B	Conservation		46°02'36.97"N, 13°21'09.03"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	12	1,40%	2,40%
8B	Conventional	80 m	46°01'41.98"N, 13°21'42.06"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	-	0,80%	2,30%
8B	Conservation		46°01'39.93"N, 13°21'36.74"E	Orsaria (UD)	Jun-Aug 2018	Soybean	Grass	No	12	0,80%	3,00%

Table D2. Sowing/harvesting periods and phenological stages of the crops included in the experiment. Phenological stages follow the nomenclature of the BBCH-scale (Meier, 2001).

	General information		Principal growth stage during samplings		
Crop	Sowing period	Harvesting period	September 2017	June 2018	August 2018
Alfalfa	NA	May, June, August, September	Principal growth stage 3 - Stem elongation	NA	NA
Barley	November	June	NA (mown)	NA	NA
Maize	April	October	Principal growth stage 8 - Ripening of fruits and seeds	NA	NA
Sorghum cover	August	March	Principal growth stage 3 - Stem elongation	NA	NA
Soybean	May/June	October/November	Principal growth stage 8 - Ripening of fruits and seeds	Principal growth stage 1: Leaf development (Main shoot)	Principal growth stage 6: Flowering (Main shoot)

Table D3. Total number of individuals and frequency of granivorous ground beetles, ants and crickets.

|	Number of individuals		Frequency	
Species	Conventional	Conservation	Conventional	Conservation
Amara sp.	8	3	6.32%	3.23%
Anisodactylus signatus (Panzer)	1	2	1.05%	2.15%
Diachromus germanus (L.)	0	3	0.00%	2.15%
Harpalinae sp.	2	10	2.11%	6.45%
Harpalus affinis (Schrank)	3	12	3.16%	9.68%
Harpalus dimidiatus (P. Rossi)	2	2	2.11%	2.15%
Harpalus distinguendus (Duftschmid)	72	32	30.53%	19.35%
Harpalus oblitus Dejean	0	1	0.00%	1.08%
Harpalus rubripes Duftschmid	0	1	0.00%	1.08%
Harpalus sp.	1	2	1.05%	2.15%
Ophonus azureus (Fabricius)	1	5	1.05%	5.38%
Pseudoophonus griseus (Panzer)	94	98	29.47%	26.88%
Pseudoophonus rufipes (De Geer)	439	657	63.16%	65.59%
Ants	828	609	51.58%	65.59%
Crickets	333	159	63.16%	59.14%
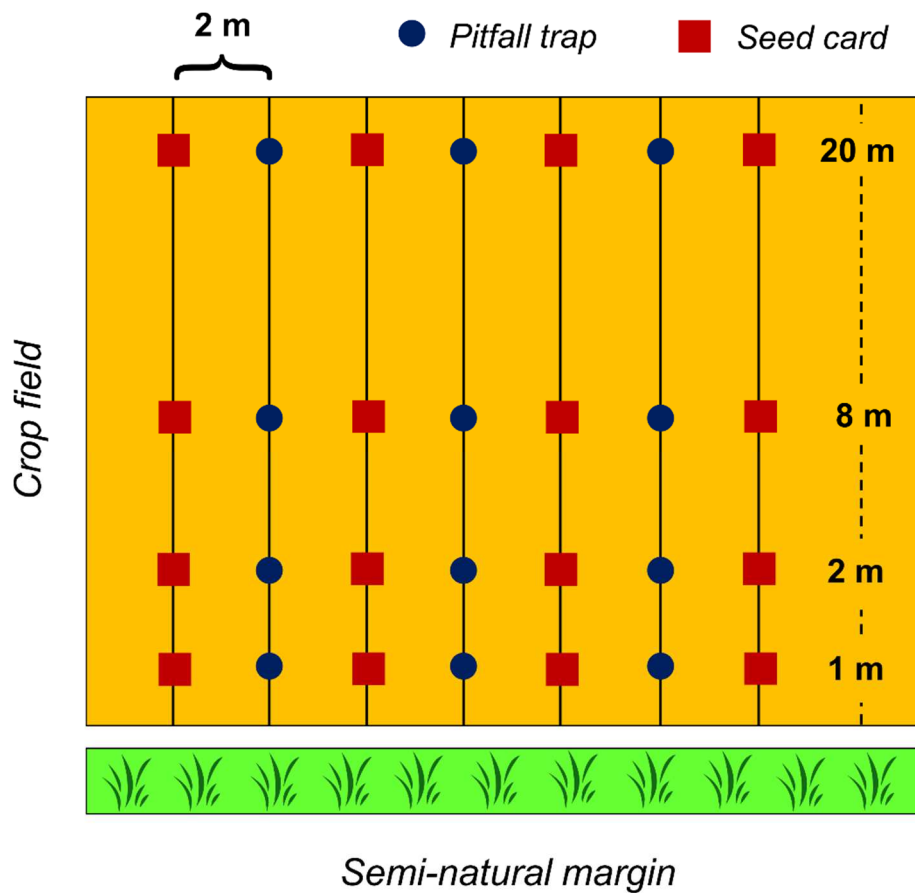
Fig. D1. Sampling design for each field. During the first sampling round (September 2017) the only active pitfall trap transect was the central one.
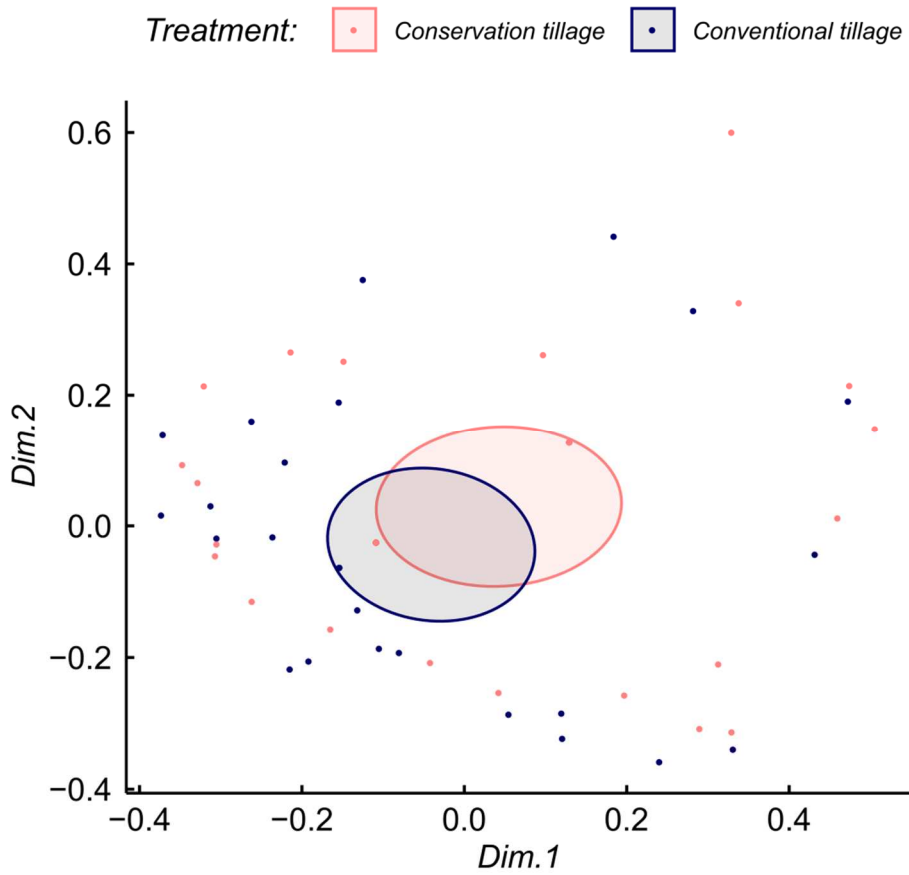
Fig. D2. Ordination plot based on Multidimensional Scaling (MDS) comparing species composition between conservation and conventional tillage. Soil disturbance classification was overlapped. Each dot is a field. Ellipses indicate 95% intervals of confidence. The ANOSIM indicated no difference in species composition between conservation and conventional tillage. We used Bray-Curtis distance in both MDS and ANOSIM.

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