Plant-pollinator networks in fragmented calcareous grasslands

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“There is still a window of time. Nature can win if we give her a chance.”

Dr. Jane Goodall

Contents

Summary

Understanding the dynamics of species interactions under the threats of habitat loss and fragmentation can be key to develop measures preventing further degradation of natural and agricultural systems. Agroecological knowledge and state of the art technologies can help to conciliate the often-discrepant objectives of biodiversity conservation and agricultural production. Specifically, information on the characteristics of plant-pollinator networks in agroecosystems can unveil the most efficient strategies to preserve ecosystem functionality and pollination services provision.

In **chapter 1**, I focused on the contributions of new technology to the objective of turning agricultural landscapes increasingly compatible with biodiversity. I reviewed the applications of unmanned aerial vehicles (UAVs) in ecology and precision agriculture. I 1) identified existing applications, 2) discussed limitations and advantages of the current technology, 3) highlighted knowledge gaps and 4) proposed new applications.

In **chapter 2**, I studied the characteristics of a plant-pollinator metanetwork of calcareous grasslands embedded in an agricultural matrix. I characterized and discussed the structural properties of the network that determine its stability and resilience to perturbations. Furthermore, I identified the traits of the most central nodes in the network. I found that the metanetwork was significantly more modular and less connected than expected by chance. This reflects the existence of many fragment-unique interactions and is an indication of poor metanetwork stability. I also demonstrated that habitat size and the diversity of land cover types in the surroundings of a grassland fragment are significant predictors of site centrality. Thus, these features can help to identify the most important fragments for metanetwork cohesiveness. Additionally, I found that the centrality of interactions depends on the pollinator size, species identity and also on the plant’s habitat specialization.

In **chapter 3**, I compared plant-pollinator networks constructed with flower visitation data to networks constructed with pollen transport data. The level of specialization of pollen transport networks was higher than that of visitation networks, as half of the interactions in the visitation networks did not occur in the pollen transport networks. This highlights the fact that visitation does not necessarily imply pollen transport, and I discussed its implications for the conservation of pollination. Considering that high specialization is known to be associated with low stability in

mutualistic networks, this result has important implications for conservation. According to these findings, traditional studies on plant-pollinator networks, based on visitation data, would overestimate the stability of pollination networks. Additionally, I identified that almost a third of the total number of interactions found are difficult to spot given their low frequency, occurring only in the pollen transport networks. Finally, I found positive effects of landscape diversity on the total number and proportion of single-fragment interactions for pollen transport, but not for visitation networks.

In conclusion, the protection of large and small calcareous grasslands as well as the enhancement of landscape heterogeneity was found to be essential for the maintenance of the plant-pollinator metanetwork. Furthermore, the importance of interactions among habitat specialist plants and large-bodied generalist pollinators appeared to be fundamental to connect the plant-pollinator metanetwork. Nonetheless, small solitary bees and the habitat specialist butterfly *Polyommatus coridon* also played a central role for the plant-pollinator networks in calcareous grasslands. By identifying the most central plants, pollinators and interactions at the metacommunity level, the information reported in this work can inform tailored management measures to protect them. Among others, I suggest considering plant species’ roles in the metanetwork when applying conservation measures, such as flower strips, and landscape coordination among farmers to increase crop diversification. Moreover, I showed the great potential of UAVs to contribute to such conservation measures and to biodiversity management in agricultural landscapes. UAVs can assist in diverse tasks such as quantifying encroachment of calcareous grasslands and plant diversity monitoring. Additionally, they can contribute to farmer´s cropland management and agri-environmental schemes surveillance by governmental agencies.

Introduction

The 2020-2030 decade is critical to the fight against climate change and environmental degradation, as many no-return ecosystem limits are predicted to be reached (Dakos et al., 2019; Ge et al., 2019a). Avoiding environmental collapse is fundamental to protect all types of life on Earth including humankind (Breyer et al., 2017) and can only be achieved by operating within the planetary biophysical boundaries (Rockström et al., 2009). The solutions to this challenges are certainly multidimensional and interdisciplinary, encompassing complex questions in the fields of philosophy, economy and ecology, among many others (Reid and Mooney, 2016).

This thesis aims to contribute to the solution of one of the main challenges on the ecological side of the problem: reconciling agricultural production and biological conservation (Egli et al., 2018). How do ecological networks respond to the pressures of habitat fragmentation in agricultural landscapes? Can we design agricultural landscapes that cannot just conserve biodiversity but also benefit from it?

The development of novel approaches and technologies is fundamental, as we cannot expect to solve new problems using old methods. Developments from one discipline can sometimes be applied to answer questions in a different scientific area. Unmanned aerial vehicles, for example, were initially developed for war and surveillance purposes (Newcome, 2004). However, in the last 15 years they have had an exponential adoption in conservation science and precision agriculture (Fig. 1, Librán-Embid et al., 2020). Network theory, on the other hand, was initially developed in the context of social sciences in the 1930s (Borgatti et al., 2009), but was quickly adopted by ecologists years later to study food webs and it has greatly developed afterwards (Bascompte, 2007).

Figure 1. Unamnned aerial vehicle (octocopter) used for the assessment of the flower diversity of calcareous grasslands. © Maxim Bogdanowitsch.

The recent fast advance in technology and especially computer science has allowed to handle large amounts of ecological data (Allan et al., 2018). Furthermore, ecologists have benefited from the concomitant development of statistical methods, such as mixed models. These were developed theoretically around three decades ago (Wolfinger and O'connell, 1993), but were only implemented in open source software more recently (Bates et al., 2006; Juricek, 2003). As a consequence of both phenomena, the complexity of the hypotheses that can currently be tested in ecology through statistical modelling could not be even imagined 15 years ago.

It is fairly clear today that the battle of conservation science to protect biodiversity exclusively in huge nature reserves will be lost in the middle term because of human pressure and illegal activities (Allan et al., 2017; Pringle, 2017). These conservation efforts need to continue as far as possible to protect many vulnerable and rare species that cannot survive in disturbed areas and are reservoirs of genetic and functional diversity (Allison et al., 1998; Bruner et al., 2001). Agricultural expansion and intensification have contributed to ecosystems degradation, but agriculture is an unavoidable companion of humanity and it is the main source of food and other goods (Duncan and Duncan, 1996; Laurance et al., 2014).

Agriculture and biodiversity do not need to be mutually exclusive (Chappell and LaValle, 2011). In fact, an increasing number of studies are focusing on, not just reducing the impacts of agricultural activities on natural and semi-natural habitats, but rather designing multifunctional biodiversity-friendly agricultural landscapes (Grass et al., 2019; Tscharntke et al., 2005). In these, landscape composition and configuration are taken into account in order to support biodiversity and agricultural activities by increasing the provision of ecosystem services such as pollination and biological control of agricultural pests (Grass et al., 2019; Tscharntke et al., 2005). If we can design these landscapes, pressure on natural reserves will decrease and food production will increase, helping humankind and all other types of life on Earth.

Such an ambitious objective can only be reached by embracing the complexity of the interactions among species and their environment. The effects of habitat fragmentation on ecological networks, for example, cannot be understood by analyzing single species or single interactions, simply because of the existence of emergent properties associated to increasing levels of complexity (Ponge, 2005). Because of the existence of emergent properties, biological systems tend to be more complex than physic systems. The performance of a car, for example, can be predicted by understanding the properties of its single components (i.e. its wheels, windows, etc) but the behavior of ecological networks cannot be predicted by understanding how single species act in isolation from the others.

In this context, the concept of ecological metaneworks (Fig. 2) gains special importance as it permits to link interactions between species with the habitat fragments where they occur (Emer et al., 2018; Hagen et al., 2012). This strategy is especially useful in agricultural landscapes, which are usually composed by complex mosaics of crops and fragments of natural or semi-natural habitats (Bennett et al., 2006). By using metanetworks, species interactions and habitat fragments can be studied as an integral dynamic unit and biodiversity conservation in multifunctional agricultural landscapes can be better achieved.

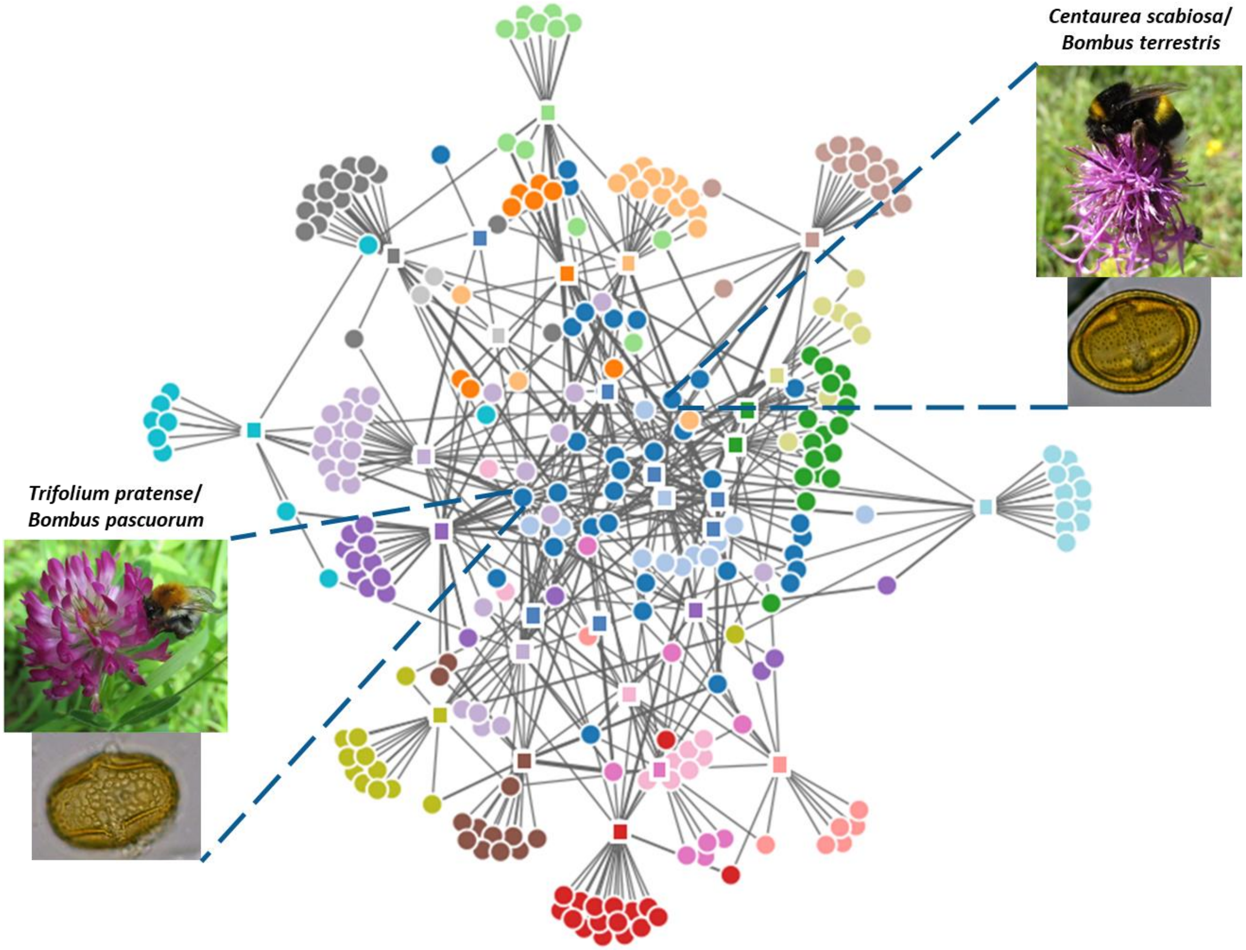

Figure 2. Pollen transport metanetwork structure among calcareous grassland fragments and unique pairwise plant-flower visitor interactions (n = 29 and n = 263, respectively). Circles indicate pairwise plant- flower visitor interactions and squares represent sites. Interactions occurring in at least two sites form links between sites. Thickness of links (gray lines) is proportional to interaction abundance. Colors represent metanetwork modules based on the Walktrap community-finding algorithm (igraph package). This algorithm indicates the presence of sub-graphs that constitute a distinctive community. Nodes with greater centrality occur in the central positions of the graph based on the gravitational force on degree (Bannister et al., 2013).

Study region

My study region comprises 285 sharply delimited semi-natural calcareous grasslands around the city of Göttingen (Germany) that differ in size, spatial connectivity, management and successional stage (Krauss et al., 2003b). These grasslands are embedded in an agricultural matrix mainly composed of arable land (42%) and managed European beech (*Fagus sylvatica*) forests (37%) (Krauss et al., 2003a). I conducted my study on 29 calcareous grassland fragments during the spring and summer of 2017 and 2018 (April-September). These fragments were selected in a previous study (Krauss et al. 2003a) along independent (i.e. non-correlated) gradients of habitat area and spatial connectivity.

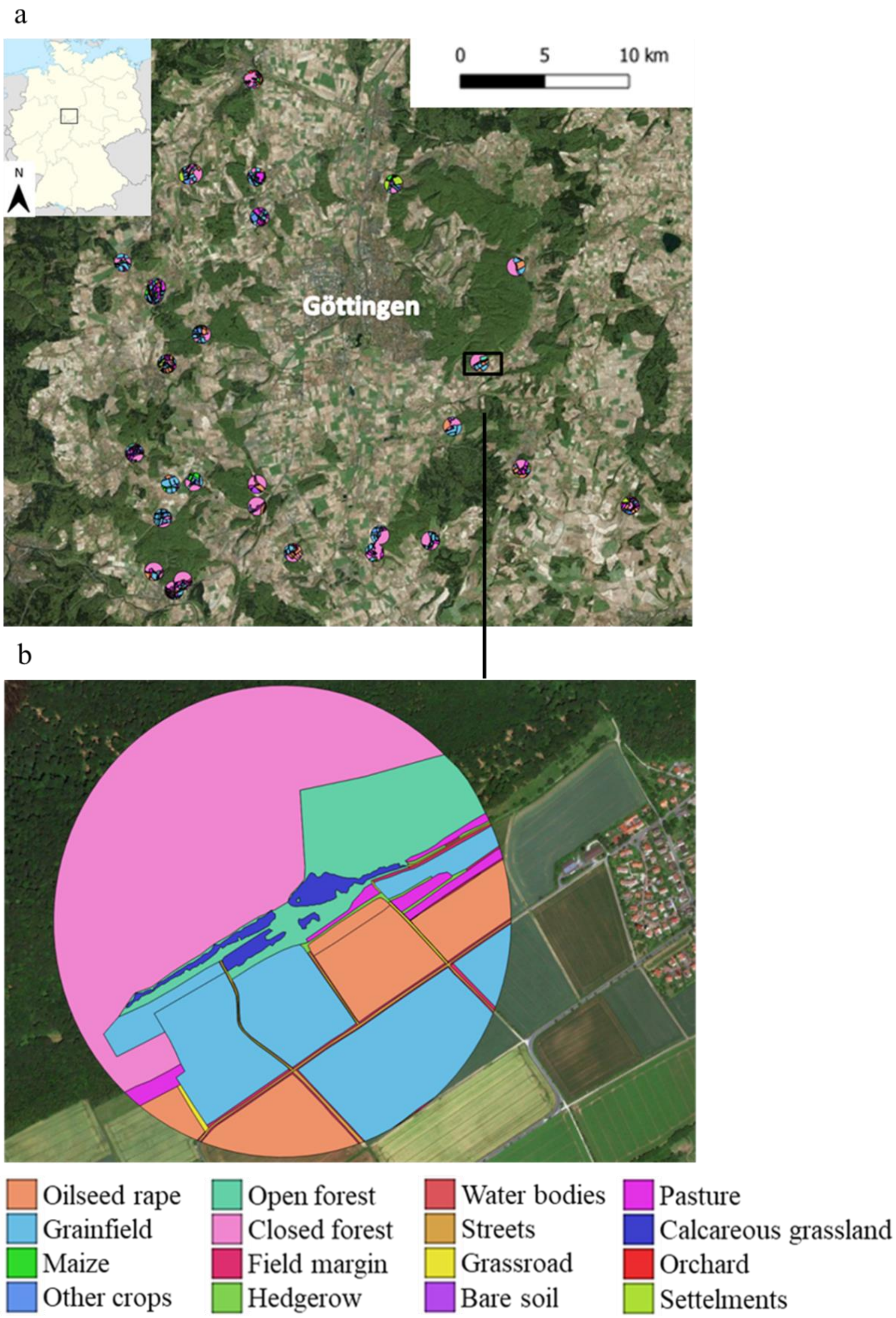

Figure 3. Study region in the surroundings of the city of Göttingen, Germany. a) The 29 studied calcareous grassland fragments with 500 m buffer of mapped cover types. b) Magnification of one fragment showing the land cover mapping in more detail.

Study system

I studied the interactions established by bees (Hymenoptera: Apiformes), butterflies (Lepidoptera: Papilionoidea) and burnet moths (Lepidoptera: Zygaenidae) with flowering herbaceous plants in calcareous grasslands (Fig. 4). These taxa are the most active and abundant diurnal flower visitors in calcareous grasslands and are considered fundamental for the reproductive success of native plants (Steffan-Dewenter and Tscharntke, 2002).

Figure 4. Examples of some common interactions in the studied calcareous grasslands. From top left to bottom right: *Polyommatus coridon* in *Lotus corniculatus*, *Bombus pascuorum* in *Trifolium pratense*, *Bombus pascuorum* in *Gymnadenia conopsea*, *Melanargia galathea* in *Knautia arvensis*, *Bombus terrestris* in *Centaurea scabiosa*, *Zygaena carniolica* in *Centaurea scabiosa*, *Maniola jurtina* in *Centaurea scabiosa*, *Aphantopus hyperantus* in *Valeriana officinalis*, *Melanargia galathea* in *Centaurea scabiosa*, *Polyommatus coridon* in *Clinopodium vulgare* (last two pictures) © Guillermo Gallardo Quilacán and Cristina Ganuza.

Objectives

In this thesis my objectives are twofold:

1) My first objective was to thoroughly review unmanned aerial vehicles (UAVs) applications in terrestrial ecology and agriculture, to identify research gaps and to highlight potential new UAV applications in ecology coming from developments in agricultural research and viceversa. These objectives were conceived under the overarching objective of contributing to the development of biodiversity-friendly agricultural landscapes, which we consider a major worldwide objective in the years to come. Objective one was met in chapter one of this thesis and was recently published in *Science of the Total Environment* under the title 'Unmanned aerial vehicles for biodiversity-friendly agricultural landscapes – A systematic review' (doi: 10.1016/j.scitotenv.2020.139204)

2) My second objective was to study the charachteristics of plant-pollinator interaction networks across a habitat fragmentation gradient. The importance of pollination systems, their structure and resilience under land use and climate change is a fundamental challenge given the importance of pollination for agricultural production and for the integrity of all natural and semi-natural habitats and the ecosystem services they provide. We used a novel approach to network theory, the concept of metanetwork, which allowed us to identify the most central plants, pollinators, interactions and habitat fragments to the system. This innovative approach can significantly help to adjust conservation efforts and strategies to the most important components of ecological networks and therefore to increase efficiency and accelerate results of conservation science. I met objective number two in chapters 2 and 3 of this thesis.

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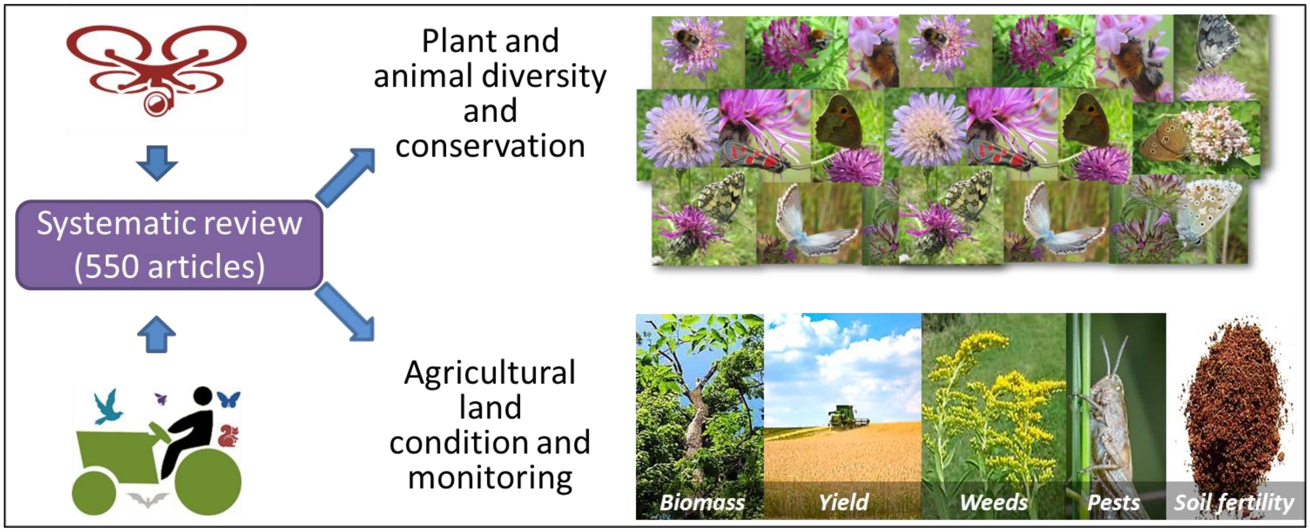
Chapter 1

Unmanned aerial vehicles for biodiversity-friendly agricultural landscapes - A systematic review



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Abstract

The development of biodiversity-friendly agricultural landscapes is of major importance to meet the sustainable development challenges of our time. The emergence of unmanned aerial vehicles (UAVs), i.e. drones, has opened a new set of research and management opportunities to achieve this goal. On the one hand, this review summarizes UAV applications in agricultural landscapes, focusing on biodiversity conservation and agricultural land monitoring, based on a systematic review of the literature that resulted in 550 studies. Additionally, the review proposes how to integrate UAV research in these fields and point to new potential applications that may contribute to biodiversity-friendly agricultural landscapes. UAV´s imagery can be used to identify and monitor plants, floral resources and animals, facilitating the detection of quality habitats with high prediction power. Through vegetation indices derived from their sensors, UAVs can estimate biomass, monitor crop plant health and stress, detect pest or pathogen infestations, monitor soil fertility and target patches of high weed or invasive plant pressure, allowing precise management practices and reduced agrochemical input. Thereby, UAVs are helping to design biodiversity-friendly agricultural landscapes and to mitigate yield-biodiversity trade-offs. In conclusion, UAV applications have become a major means of biodiversity conservation and biodiversity-friendly management in agriculture, while latest developments, such as the miniaturization and decreasing costs of hyperspectral sensors, promise many new applications for the future.

Key Words: Unmanned aerial systems (UAS), UAV, Drones, Smart farming, Yield-biodiversity trade-offs, Vegetation monitoring, Precision agriculture.

1 Introduction

Agricultural land covers 34% of the world land area and approximately half of the habitable land on Earth (WWF, 2016). To meet growing food demands, agricultural production systems are increasingly including novel techniques that rely on remote sensing and intelligent machines. Unmanned aerial vehicles (UAV), agribots and their sensors allow small-scale treatment of crop plants and farm animals with high accuracy (Walter et al., 2017; Zhang and Kovacs, 2012). Together with GPS guidance, this technology can increase yield (Saavoss et al., 2016; Zhao et al., 2013), reduce agrochemical inputs (Bongiovanni and Lowenberg-Deboer, 2004), fuel and time spent on crop management (Bora et al., 2012). Its application promises more sustainable agriculture to meet present and future demands for food and other agricultural products without compromising sustainability (Bongiovanni and Lowenberg-Deboer, 2004; Tilman et al., 2002).

In addition to food provision, agricultural landscapes are also key for biodiversity conservation, given that natural habitats are increasingly scarce (Rockström et al., 2009; Steffen et al., 2015). In fact, agricultural landscapes in tropical and temperate regions are often composed by a complex mosaic of different land covers, including cropland (usually dominant) and fragments of natural and semi-natural habitats. These different land cover types interact with each other (e.g. by species spillover) and management strategies should, therefore, consider them as dynamic interacting units (Grass et al., 2019). In agroecosystems, biodiversity at the local (i.e. field) scale is driven by colonization from the surroundings and, therefore, relies on source (natural and semi-natural) habitats in the proximities of cropland (Tscharntke et al., 2005). Protection of species that provide ecosystem services, such as pollination and biological pest control (Tscharntke et al., 2007), is crucial for sustained high yield, particularly given the high dependency of crops on animal pollination (Garibaldi et al., 2013; Klein et al., 2007; Kremen et al., 2007; Ollerton et al., 2011) and the magnitude of crop losses to pests (Deutsch et al., 2018; Oerke, 2006; Savary et al., 2019). Cropland management has also an important influence on the ability of species to use and cross agricultural land, and consequently, on their population dynamics and survival in agricultural landscapes (Batáry et al., 2015; Boesing et al., 2018; Magioli et al., 2016; Tomé et al., 2015). However, biodiversity and ecosystem services conservation have usually been seen as an obstacle to high yield achievement in the short term (Paul et al., 2020). Cutting-edge technology brings new possibilities to overcome this challenge and may contribute to high yield and biological conservation alike.

Unmanned aerial vehicles (UAVs) have experienced an exponential growth in the last 10 years, in terms of number of scientific publications (Fig. S1) and also regarding diversification of types and applications (Pajares, 2015). Fast technological advances and decreasing costs have made UAVs central for precision agriculture and smart farming, but also for a wide spectrum of research fields. This is partly due to their flexibility to transport many different kinds of sensors, their cost-effectiveness and their suitability to work at different scales (up to 1500ha) and in remote areas (Gago et al., 2015; Rango et al., 2006; Watts et al., 2010). In fact, UAV-based imagery outperforms other imaging acquisition technologies, such as satellites and manned aerial systems, in terms of increased temporal and spatial resolution, higher flexibility and reduced costs, especially when used for small (<5ha) to medium (5-50ha) spatial scale objectives (Cruzan et al., 2016; Matese et al., 2015; Pádua et al., 2017; Wich and Koh, 2018). Therefore, UAVs are starting to be implemented by NGOs, state organizations, researchers and practitioners around the world.

Although UAVs capabilities are well known in ecology, precision agriculture and conservation science, this review focuses on the, so far little developed, contributions of UAVs to biodiversity-friendly agricultural landscapes. Classical definitions of the agroecosystem are usually restricted to the field scale (Wezel et al., 2009). However, considering the already mentioned importance of surrounding habitats for biodiversity and associated ecosystem services, and the capability of UAVs to work beyond the limits of the strict agricultural land, we consider that the concept should be broadened. We understand by biodiversity-friendly agricultural landscapes those that integrate local (e.g. cropland diversification, flower strips, hedgerows, set asides and reduced agrochemical input) and landscape (e.g. natural habitat protection, heterogeneous landscape structure) measures to benefit biodiversity (Landis et al., 2000; Tscharntke et al., 2012). The interdependence between land use types in the agricultural landscape determines that sustainable development goals (e.g. zero hunger) will only be achieved by concealing food production and biodiversity conservation under the same joint effort (Kremen and Merenlender, 2018; Rosa-Schleich et al., 2019). Therefore, the objectives of this systematic review are 1) to summarize current applications of UAVs in ecology, precision agriculture and conservation science and 2) to identify potential applications towards the development of biodiversity-friendly agriculture at local and landscape scales.

2 Methods

A bibliographic search was conducted in Scopus and Web of Science on October 1st, 2019. Our search terms comprised the words *unmanned*, *RPAS* (Remotely Piloted Aircraft Systems) and either *conservation, ecology, biodiversity, richness* or *agriculture*. The word *unmanned* was used to capture studies on unmanned aerial vehicles (UAVs), unmanned aerial systems (UASs), unmanned aircraft systems (UASs) and unmanned aircraft vehicles (UAVs). We did not use the term *drone*, which usually occurs in addition to the most frequent term *unmanned*, to avoid retrieving articles regarding the ecology of male honeybees. As we were only interested in terrestrial landscapes, studies including the words *maritime, ocean and sea* were excluded. The exact search words used and other details can be found in the supporting information. To be included in the review, studies were required to: 1) Refer to or use unmanned aerial vehicles and no other type of ground or aquatic systems. 2) Focus on UAVs applications and not on technical properties (e.g. no studies focusing on endurance, manoeuvrability, etc.).

1946 articles were obtained as a result of the Scopus (1143) and Web of Science (803) searches. After excluding duplicates and unsuitable studies 529 articles were kept. We further added 21 additional publications that were found to be suitable for our review but did not appear on the original search totalizing 550 articles.

3 UAVs applications

Land cover mapping and classification has experienced a breakthrough with the advent of UAVs. UAVs can get very high spatial (<1cm/px) and temporal resolution images at relatively low cost when compared to manned airborne or satellite systems (Dufour et al., 2013; Lim et al., 2018; Ruwaimana et al., 2018; Whitehead and Hugenholtz, 2014). Classification has gone from differentiation among conspicuous land cover classes such as bare ground on rangelands (Breckenridge et al., 2012) to high resolution 3D maps of forests (Baena et al., 2017; Dandois and Ellis, 2013), and finally, to detailed land-use classifications of habitat types and land-cover classes (Ahmed et al., 2017; Strong et al., 2017). Plant and soil monitoring have also significantly improved since UAV imaging appeared. Particularly, monitoring of natural and semi-natural habitats in the context of restoration efforts (Malenovský et al., 2017; Reif and Theel, 2017; Zahawi et al., 2015) and recovery monitoring after fire events (Silva et al., 2014).

In the context of precision agriculture, cropland monitoring is rapidly evolving from traditional local assessments based on visual analysis to cutting-edge non-destructive methods based on optical remote sensing. Diagnostic information can be derived from the images and indices taken from on-board sensors; including biomass, disease, water stress and lodging; and is later used for crop management, yield forecasting, and environmental protection (Zhang and Kovacs, 2012). Constant and high resolution monitoring can precisely inform where and when applications are needed throughout the growing period of a crop, a former unfeasible task at farm scale given logistic and economic constrains. Farmers are therefore increasingly demanding flexible and high resolution systems (< 20cm/px; Bareth et al., 2015) to monitor crops on fine scale. Manned aerial imagery lacks flexibility and cannot provide data of enough temporal resolution for this task at affordable costs for most farmers. On the side of satellites, even the best current commercial ones are not able to provide data of enough spatial resolution (31cm/px, WorldView4) for precise crop monitoring at the farm scale. Centimetre and sub-centimetre imagery resolution, as the one provided by UAVs, contributes to a more accurate assessment of structural and biochemical plant traits (Jay et al., 2019). Thus, UAVs are helping to maximize efficiency in the applications of fertilizers, herbicides and insecticides (Gebbers and Adamchuk, 2010), and concomitantly, to minimize their impacts on the environment. Therefore, UAVs represent one of the most suitable available systems for crop monitoring objectives at farm scale.

In the following, topics of interest focusing on current and possible future applications of UAVs for the development of biodiversity-friendly agricultural landscapes are discussed (Table 1). Within each section, areas of interest related to UAV research are identified and related implications, relevance and knowledge gaps are discussed in further detail under the section "Perspectives on future research".

Table 1. Overview table of UAV applications, giving a description of the application and a few major references.

UAV application	Description	Major references
3.1 Biodiversity conservation *a. Plant diversity*	Identification and monitoring of single plant species and plant species richness estimation.	(Getzin et al., 2012; Ahmed et al., 2017; Malenovský et al., 2017; Capolupo et al., 2015; Knoth et al., 2013; Cruzan et al., 2016; Silva et al., 2014; Michez et al., 2016)
b. Animal diversity	Identification and monitoring of animal populations and communities as well as habitat quality, based on vegetation properties.	(Mulero-Pázmány et al., 2014; Chrétien et al., 2016; Hodgson et al., 2016; Weissensteiner et al., 2015; Goebel et al., 2015 Habel et al., 2016; Forbey et al., 2017)
3.2 Agricultural land monitoring *a. Plant height and biomass* b. *Yield and nutrient status* *c. Pest and pathogen damage*	Plant traits estimation for yield and carbon stock calculation. Early and precise physiological stress detection caused by pests, pathogens, nutrients or water deficit.	(Bareth et al., 2016; Geipel et al., 2014; Kachamba et al., 2017; Rey-Caramés et al., 2015; Zhou et al., 2017; Sanches et al., 2018; Gong et al., 2018; Zarco-Tejada et al., 2013; Shields and Testa, 1999; Smith et al., 2015; Faithpraise et al., 2015; Yue et al., 2012; Cardil et al., 2017; Moriya et al., 2017)
d. Soil fertility	Estimation of soil organic carbon content, soil residue cover, soil moisture and soil erosion.	(Aldana Jague et al., 2016; Kavoosi et al., 2018; d'Oleire-Oltmanns et al., 2012; Bazzoffi, 2015; Acevo-Herrera et al., 2010; Sugiura et al., 2007)
e. Weeds and other non-crop plants	Weed detection, characteristics and management.	(Shields et al., 2006; Rasmussen et al., 2013; Pelosi et al., 2015; Peña et al., 2013; Peña et al., 2015; Pantazi et al., 2017; Pérez-Ortiz et al., 2015)

3.1 Biodiversity conservation

Species identification and monitoring in agricultural landscapes, from natural and semi-natural habitats to cropland, is fundamental for biodiversity conservation (Fig 1). UAVs derived information on plant and animal occurrence, movement and health status is providing important information for appropriate management. Besides the intrinsic value of biodiversity, animals and plants are also important for production in agricultural landscapes given the number of ecosystem services they provide (Balvanera et al., 2006; García-Feced et al., 2015).

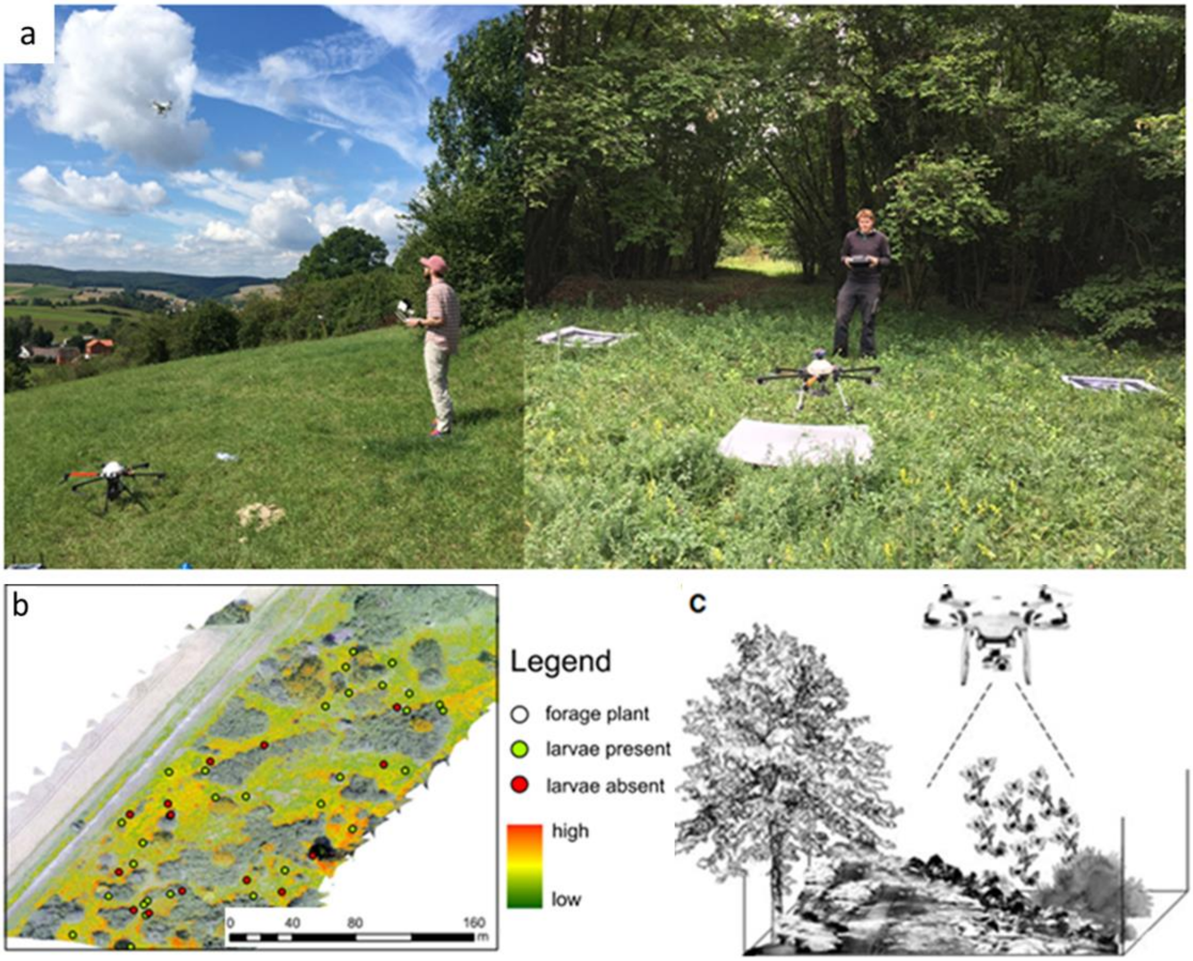

Fig. 1 a) Plant diversity assessment and floral resources mapping in grasslands of central Germany. Notice two different multirotor UAVs (one quadracopter and one hexacopter) performing image acquisition tasks in habitats of high plant diversity. b) UAV high-resolution imagery, based on a habitat suitability model of two lycaenid butterflies in Germany (modified from Habel et al., 2016, used with permission). Open circles represent presence of the butterfly´s forage plants. Green circles depict presence of butterfly larvae and red circles absence of it. Warmer colors indicate areas of high habitat suitability. c) Butterfly tracking in South Korea (modified from Ivosevic et al., 2017, used with permission).

a. Plant diversity

The expansion of monocultures and herbicide overuse has caused a dramatic decline in plant diversity in agricultural landscapes with negative consequences for ecosystem multi-functionality and production sustainability (Egan et al., 2014; Hooper et al., 2012). To alleviate this situation and increase landscape heterogeneity, measures including crop diversification, adjacent natural vegetation protection and agri-environmental schemes, have been promoted by state agencies in many countries (Batáry et al., 2015; Fahrig, 2017). Efficient plant diversity assessments in agricultural landscapes are fundamental for the success of these measures.

RGB (red-green-blue) cameras mounted on UAVs have enabled identification of not only conspicuous species in savannas (Cruzan et al., 2016), pastures (Silva et al., 2014) and riparian forest (Michez et al., 2016), but also biodiversity in deciduous forests (Getzin et al., 2012). Although comparatively cheap and simple, RGB cameras have been shown to achieve similar performances as LiDAR systems (Zahawi et al., 2015). Multispectral sensors (i.e. those able to capture 4-10 spectral bands) move a step forward, as they allow for more detailed vegetation classification and monitoring. In particular, those able to capture near-infrared spectra have been used in temperate systems to distinguish among land-cover classes and individual species with accuracies of ~90% (Ahmed et al., 2017; Knoth et al., 2013; Lu and He, 2017; Mora et al., 2015). They have also been successfully used to identify and monitor invasive plants (Samiappan et al., 2016b; Samiappan et al., 2016a) as in the case of *Harrisia pomanensis* in South Africa (Mafanya et al., 2017).

The general methodology implies the construction of orthomosaics from RGB or multispectral imagery (e.g. with AgiSoft software) followed by a segmentation process through object-based image analysis (OBIA). Later, spectral vegetation indices are derived from the imagery and tested for their capacity to identify the specific species or cover types (e.g. with random forests' algorithms). Finally, accuracy tests are performed (Michez et al., 2016). Knoth et al. (2013), for example, used this procedure to analyse a bog complex in Germany using color infrared images with a modified digital camera. Thanks to the small spatial resolution achieved in the study (1.5 - 3 cm/px) they were able to discriminate a moss (*Sphagnum* spp), a herbaceous plant (*Eriophorum vaginatum*) and a deciduous tree (*Betula pubescens*) with high accuracy (Table S1). In a different study system, Ahmed et al. (2017), were able to precisely distinguish individual deciduous tree species, shrub communities and agricultural crops, by deriving orthomosaics and normalized difference vegetation index (NDVI) maps from true-color and multispectral imagery.

Although RGB and multispectral sensors may be sufficient for many objectives, hyperspectral sensors are usually regarded with the best potential for mapping purposes given the possibility to capture more than 200 bands in a broad spectral range (~350 – 2500 nm) and high spectral resolution (~10 nm) when mounted on manned or unmanned aerial vehicles (Colomina and Molina, 2014). The spectral diversity/variability hypothesis proposes that the number of plant species increases with the diversity of spectra observed (Heumann et al., 2015; Palmer et al., 2002; but see Schmidtlein and Fassnacht, 2017) and has been tested with hyperspectral sensors mounted on satellites or manned aerial systems (Mapfumo et al., 2016; Möckel et al., 2016; Wachendorf et al., 2018). This data has been used for biodiversity assessment in a wide range of ecosystems, including tropical forests (Cochrane, 2000), costal zones (Lange et al., 2004), wetlands (Gross and Heumann, 2014; Heumann et al., 2015) and grasslands (Lopatin et al., 2017; Möckel et al., 2016). However, in complex habitats, such as grasslands, accurate biodiversity assessment demands higher spatial resolution than manned aerial or satellite systems can reach (Capolupo et al., 2015; Lopatin et al., 2017), highlighting the relevance of UAVs as the only current remote solution available for biodiversity assessments in these habitats (Fig. 1a).

Until very recently, hyperspectral sensors were only available for manned aircraft and satellite systems (Mulla, 2013) given UAVs' payload limitations (Adão et al., 2017). Additionally, high costs associated to commercial hyperspectral sensors (ranging from USD 25,000 to USD 100,000; Association for Computing Machinery, 2017; CBRNE Tech Index, 2019) prohibited their wider public use. However, the increase in UAVs' payload capacity (up to 15kg multirotor and up to 50kg fixed wing UAVs, Chen et al. 2016), in addition to the emergence of light and non-commercial low-cost hyperspectral sensors (USD700~USD2,000; Adão et al., 2017; Colomina and Molina, 2014; Nevala and Baden, 2018; Sigernes et al., 2018) in the last few years, are making it possible for a larger public to have access to UAV-on-board hyperspectral sensors. Cao et al. (2018), for example, used a 470g commercial hyperspectral camera (USD 50,000), with a spectral resolution of 4nm, to identify mangrove species in China. Sigernes et al. (2018), on the other hand, constructed a light (200g) low-cost (USD 700) hyperspectral sensor and successfully produced orthomosaics from NDVI image sequences taken from a UAV octocopter.

In practice, the fact that commercial hyperspectral sensors adapted for UAVs are still approximately ten times more expensive than multispectral ones highlights the importance of carefully considering the most cost-efficient sensor for each specific objective. Multispectral or RGB imagery may offer cheaper and easier solutions than hyperspectral imagery in ecosystems where all types of sensors record similar accuracy levels for species classification, such as forests (Michez et al., 2016). Nonetheless, limitations need to be overcome in terms of automated image classification methods (e.g. by including elevation data, Cruzan et al., 2016). Furthermore, given the high spatial resolution needed for vegetation identification at the species level and the current resolution of most current commercial RGB and multispectral sensors, UAVs need usually to be flown at very low altitudes (< 20m). This makes it impractical to cover big areas given the amount of time needed for the flights and image mosaicking (Bertacchi et al., 2019). These problems might soon be overcome by the development of new sensors with increased resolution power.

b. Animal diversity

Data on the availability of vegetation used for food is fundamental to understand animals' occurrence (Forbey et al., 2017). The capacity of sensors mounted on UAV to deliver high resolution images, combined with high UAV spatio-temporal flexibility for mapping and characterizing microhabitats, provides new opportunities for animal species habitat preference detection (Habel et al., 2016). UAVs' sensors have been used to measure structural properties (e.g. height metrics and phytochemical features) in forest, grass and shrub ecosystems (Anderson and Gaston, 2013; Forbey et al., 2017) and consequently the identification of areas with high protection value is expected to become more precise and efficient (Habel et al., 2016).

Conservation strategies (e.g. agri-environmental schemes), especially those directed towards specific species, may improve by employing UAVs. For example, the monarch butterfly (*Danaus plexippus)* relies almost exclusively on milkweed (*Asclepias syriaca)* as a larval food-plant. A recent decline in milkweed populations, due to increased use of glyphosate in maize and soya plantations in the USA, is threatening the butterfly survival (Pleasants and Oberhauser, 2013). Mapping and protecting milkweed populations is hence critical to protect this flagship species (Lu and He, 2017). In this context, the combination of UAVs' surveys precision, range, speed and cost-efficiency could help to overcome former strategies' limitations and therefore to avoid the species' extinction.

Wildlife detection and management have also benefited from UAVs (Fig. 1c). Wildlife detection within field and in the field surroundings is an important component for the concept of biodiversity-friendly agricultural landscapes for two main reasons. On the one hand, an increased detection rate would reduce the number of animals unintentionally killed in agricultural landscapes during fieldworks (e.g. harvest period). Thermal cameras mounted on UAVs can be used to detect endothermic animals, therefore avoiding animal mortality and also increasing farmers harvest efficiency, as has been shown for deer fawn (Cukor et al., 2019), lapwing (Israel and Reinhard, 2017 - 2017) and Montagu´s Harrier (Mulero-Pázmány and Negro, 2011). On the other hand, detection of certain animal species in the agricultural landscape might contribute to a better planning of agricultural and conservation strategies and eventually lead to win-win scenarios. Given its high conservation value and its role in rodent biological control in cereal fields, the Montagu´s Harrier protection constitutes one of these mutually benefiting scenarios between conservation science and agricultural production.

Wasps' nests identification would be likewise important in agricultural landscapes given their importance as pest predators of many crops and their eventual danger to humans when undetected (Medeiros et al., 2019; Prezoto et al., 2019; Southon et al., 2019). Given the higher temperature of social wasps' nests compared to the surrounding environment (i.e. 5-10°C, Klingner et al., 2005), thermal cameras could also be applied to identify them, although, to our knowledge, this possibility has not yet been explored. Furthermore, vertebrate pollinators, such as hummingbirds and bats, would also be fundamental to detect given their crucial role in plant reproductive success (Rader et al., 2016). Their absence reduces fruit and/or seed production by 63% on average (Ratto et al., 2018). Bats are known for their importance as biological control agents, seed dispersers and pollinators of several wild plants and crops (Kunz et al., 2011), such as the *Agave* spp. (Trejo-Salazar et al., 2016). Birds are also fundamental pest predators (Boesing et al., 2017), the endemic lemon-bellied-white-eye *Zosterops chloris*, for example, was found to be the main bird predator in cacao agroforestry landscapes in Indonesia (Maas et al., 2015) and is therefore a key element for efficient biological pest control. Quantitative and spatially explicit information on the presence of these important animal groups (e.g. gathered with thermal cameras on UAVs) would be a tipping point for the design of biodiversity-friendly agricultural landscapes and for smart farming.

Density data collection over large areas has significantly improved and spread thanks to the advent of UAVs, given the avoidance of traditional aerial survey biases, greater spatio-temporal resolutions, and to the reduced impact of noise on wildlife (Chrétien et al., 2016). Multispectral imagery, in particular, has been recognized as more efficient than traditional human visual detection for animal discrimination, especially in the case of bird and mammal surveys (Chrétien et al., 2016). UAV-derived counts of colony-nesting birds, for example, are an order of magnitude more precise than traditional ground counts (Hodgson *et al.* 2016). For small but fixed objects, such as birds' nests, UAVs can obtain very detailed data from images, such as nestlings' age and number of eggs (Weissensteiner et al., 2015). Moreover, the possibility of using multispectral imagery and, in particular, the combination of visual and infrared spectrum sensors, allows tracking animals more efficiently and even at night (Chrétien et al., 2016; Ward et al., 2016). This may be particularly relevant to track small, low contrasting and nocturnal animals (e.g. rodents) that may otherwise be difficult to follow (Gonzalez et al., 2016). Images can be used for abundance estimates (with both manual and automated methods) and also to track changes in animal size, body shape and nutritive condition (Goebel et al., 2015).

3.2 Agricultural land monitoring

Agricultural land monitoring refers to the set of activities related to crop health and grow from soil fertility to yield calculation (Fig. 2). Early and precise plant physiological stress detection caused by pests, pathogens, nutrients or water deficit is of major importance (Lichtenthaler, 1998; Maimaitiyiming et al., 2017), not just for crop development and yield, but also for conservation objectives in agricultural land (e.g. biodiversity protection). Detecting a crop pest outbreak early enough, for example, may allow low-cost and environmentally friendly treatment, e.g. with biological pest control agents (Barrera, 2008; Gerling et al., 2001).

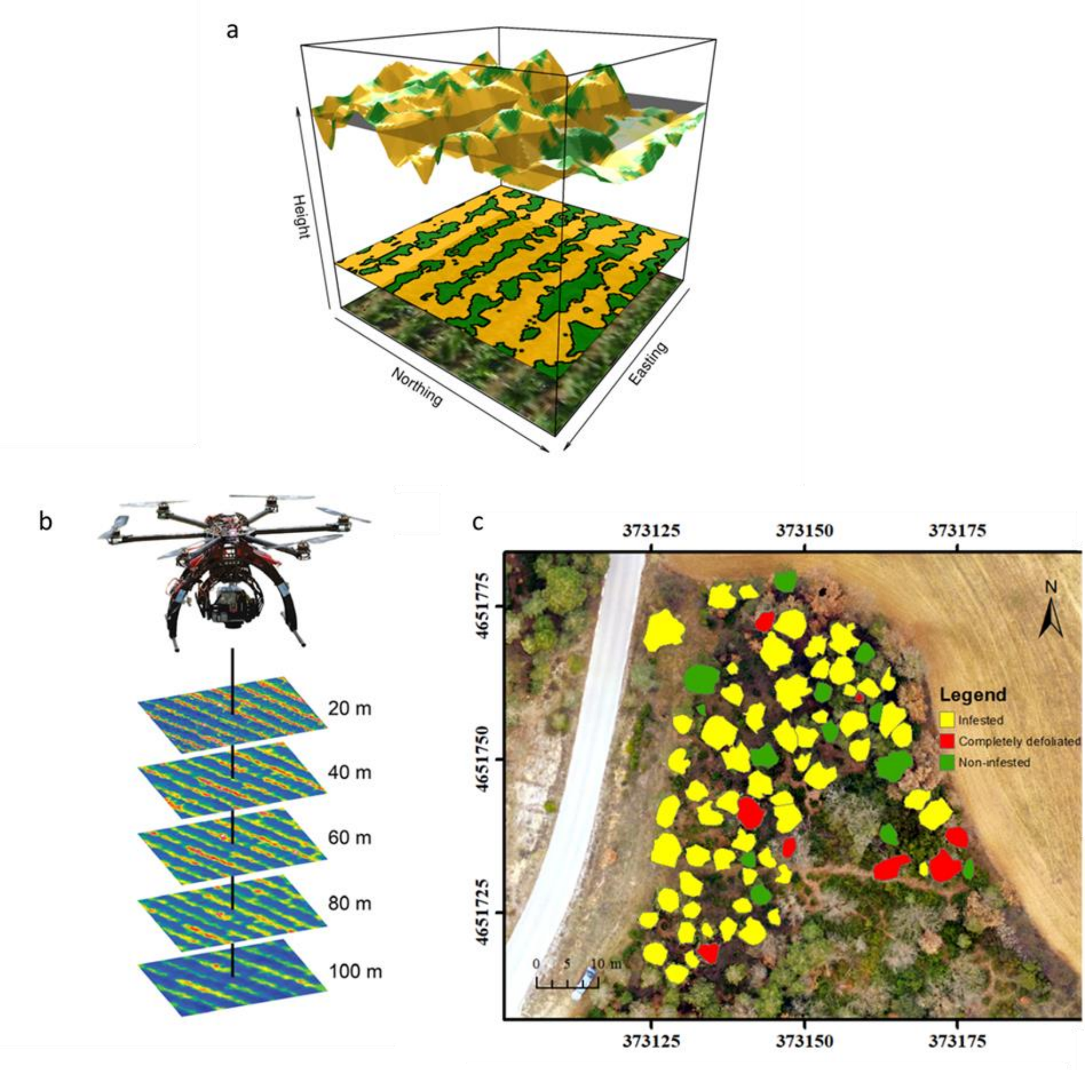

Fig. 2 UAV applications for vegetation monitoring in crops and forests. a) Plant height computation of a corn field (modified from Geipel et al., 2014). The lower part of the figure shows an RGB orthoimage and a classification layer based on the Excess Green Index (ExG) where green represents crop and yellow soil. The upper part shows the corresponding crop surface model height information as a 3D representation, colored by the ExG-classification. b) Surface temperatures at different heights from potato fields (modified from Faye et al. (2016), used with permission). Red stands for higher temperatures and blue for lower ones. c) Pine processionary moth defoliation assessment in Catalonia (modified from Cardil et al. (2017), used with permission). Yellow depicts infested trees, red completely defoliated trees and green non-infested trees.

a. Plant height and biomass

In precision farming, management strategies often rely on estimations of biomass, crop growth, light use efficiency and carbon stocks to predict total yields and spatial yield variations, and to determine harvest dates (Bendig et al., 2014; Chen et al., 2012; Li et al., 2016). Plant growth is a good indicator of plant response to heat, drought or nutrient stress and therefore of crop performance. Bareth et al. (2016) used RGB imagery from a UAV and computer vision techniques to construct multi-temporal crop surface models of barley at three growth stages and found that plant height estimations derived from this method were as accurate as the more commonly used terrestrial laser scanning (Table S1). Furthermore, UAV multispectral imagery can also produce crop height estimates as accurate as those coming from LiDAR systems (Sofonia et al., 2019), at much lower costs.

Above-ground biomass is another important measure for agricultural and natural systems that can be applied to monitor ecosystem health, impacts of climate change and human activity (Liang et al., 2016). Above-ground biomass allows to estimate carbon sequestration, which is important for the global carbon cycle and for carbon emissions estimation and can be used for carbon conservation programs (Chen et al., 2012). In the past, the above-ground biomass of plants in an area was extrapolated by measuring the height (and width of trees in forests) of a sample of plants on the ground or by destructively sampling plants to directly measure their biomass (Gao et al., 2013). Today parameters such as canopy height, ground cover, and vegetation indices (e.g. NDVI) can be estimated using UAVs imagery and later used to model above-ground biomass (Bendig et al., 2014; Grüner et al., 2019). At small to medium scales, UAVs can produce consistent biomass estimates at significant smaller costs than manned aircraft (Kachamba et al., 2017).

Common procedures for plant height and biomass estimation involve the generation of 3D point clouds from RGB or multispectral imagery (e.g. with structure from motion techniques), followed by the construction of digital surface models (DSMs) and digital elevation models (DEMs) with software as Agisoft or Pix4D (Table S1). In grasslands, above-ground biomass estimations help to predict production (e.g. livestock forage), carbon storage, and wind erosion potential (Gao et al., 2013; Liang et al., 2016). Möckel et al. (2016), for example, used airborne hyperspectral data for fine-scale biodiversity predictions through pigment content and biomass analyses, based on the negative correlation between plant species diversity and above-ground biomass. Given the recent miniaturization and price reduction of UAVs, these habitats could be now studied at a much lower price. In fact, the use of UAVs enables us to non-destructively sample areas and to make small-scale estimations of above-ground biomass, which can be used for site-specific agricultural decision making in croplands and grasslands (Geipel et al., 2014; Liang et al., 2016).

Accurate tree height and biomass estimation is also possible through UAVs imagery based on color-infrared (Zarco-Tejada et al., 2014), multispectral (Shin et al., 2018) and hyperspectral sensors (Adão et al., 2017). This is especially important for orchards (e.g. olive and fruit trees), silvopastoral systems (Surový et al., 2018) and forestry (Tang and Shao et al., 2015). Forestry management, for example, might particularly benefit from these advances considering that tree height and biomass information are fundamental to determine productivity and harvesting time. Pine (Guerra-Hernández et al., 2017), eucalyptus (Wallace et al., 2016) and oak (Surový at al., 2018) plantations have already profited from UAV monitoring.

Although most studies report good accuracies for plant height and biomass estimation (Table S1), it is important to note that structure from motion approaches retrieve in general lower accuracies in heterogeneous crops, compared to homogeneous ones, such as monocultures. Increased spatial resolution and plant density information might contribute to higher accuracy in those scenarios (Grüner et al., 2019).

b. Yield and nutrient status

Yield prediction is naturally of principal interest for farmers, given its direct effect on income. However, it is also fundamental to adaptive crop management and balancing input applications (e.g. fertilizers). Avoidance of unnecessary inputs, as nitrogen and phosphorous, has positive effects on ecosystem functioning and biodiversity (Mozumder and Berrens, 2007). Therefore, yield and nutrient status predictions are central to the design of biodiversity-friendly agricultural landscapes. The Leaf Area Index (LAI), defined as the area of single sided leaves per area of soil, can link multispectral remote sensing to crop growth, yield and other biological measurements (López-Lozano and Casterad, 2013; Wu et al., 2007). Multispectral information can be used to calculate spectral indices related to LAI such as the NDVI (normalized ratio between the red and near infrared bands, Lelong et al., 2008). These spectral indices provide information about important vegetation properties, such as the chlorophyll concentration, water stress and plant productivity (Gago et al., 2015; Nemeskéri et al., 2019). LAI can be calculated at multiple phenological stages using RGB, TIR (thermal infra-red) and hyperspectral sensors and has been used in potato plantations (Roosjen et al., 2018), wheat (Yao et al., 2017), sorghum (Potgieter et al., 2017) and vineyards (Kalisperakis et al., 2015).

Imagery datasets from UAVs have allowed yield prediction in crops such as corn (Geipel et al., 2014), vineyards (Rey-Caramés et al., 2015), rice (Zhou et al., 2017) , sugarcane (Sanches et al., 2018) and oilseed rape (Gong et al., 2018). The combination of spectral vegetation indices maps (e.g. Excess Green Index) with 3D surface models is a particularly important method for yield estimation (Geipel et al., 2014). However yield estimation accuracy based on imagery has not yet reached that of traditional methods in some crops (Geipel et al., 2014; Yin et al., 2011).

Nutrient status assessment through spectral indices has been studied in many crops (Liu et al., 2018; Schirrmann et al., 2016) and particularly well in vineyards. In the latter, leaf carotenoid content estimation, vigour and development have been estimated using high resolution hyperspectral (Zarco-Tejada et al., 2013) and multispectral imagery (Rey-Caramés et al., 2015), acquired from UAVs. It has been demonstrated that, given its higher spatial resolution, UAV imagery outperforms satellite decametric imagery in vineyard vigour assessment (Khaliq et al., 2019). Moreover, LAI estimation with hyperspectral data or 3D canopy models was found to be more accurate than estimations based on RGB 2D data (Kalisperakis et al., 2015).

Current methods for yield and nutrient status estimation show already satisfactory results (Table S1). Research is now focused on increasing efficiency in terms of costs/time reduction and increased accuracy. Cost reduction is mostly associated to technology development and will continue in the years to come as UAVs and sensors tend to get more economic. Reduced time involves finding the optimal spatial resolution for each objective, where important vegetation details can be captured without increasing data noise. Avoiding unnecessary high resolution also reduces image processing and aerial campaigns time, as UAVs might be flown at higher altitudes, covering more area per flight.

c. Pest and pathogen damage

Some pests and pathogens have potential to gain uncontrolled outbreak character causing dramatic losses to agriculture (Singh and Satyanarayana, 2009). Attempts to reduce these losses cost farmers a considerable amount of time, money and effort (Deutsch et al., 2018; Oliveira et al., 2014). Chemical pest control, the most used pest control method, is also an important driver of biodiversity loss, negatively affecting surrounding areas and beneficial insects such as pollinators (Gill et al., 2012; Jong et al., 2008; Woodcock et al., 2017). Furthermore, pesticides costs might take a substantial part of farmers' budget, making the production chain more expensive and compromising the sustainability of small and medium farmers' livelihoods (Bourguet and Guillemaud, 2016). Therefore, early and precise detection of incipient pests and pathogens means a breakthrough for agriculture and conservation, as these could be treated fast and locally, well before reaching economic thresholds. Consequently, this early detection could favour farmers' budget, biological conservation and ecosystem health and functioning.

Although in its infancy, crop pest and pathogen damage can be monitored with UAV-based imagery given the specificity of the structural and chemical changes occurring in attacked plants (Maes and Steppe, 2019; Mahlein, 2016). One of the main advantages of UAV imagery is the possibility to detect pest and pathogen attack before visual signs emerge. Thermal and fluorescence imaging can provide such early identification of attacked plants based on the modification of plant cuticular and stomatal conductance (Oerke et al., 2006) and chlorophyll fluorescence (Mahlein, 2016), respectively. However, both methods lack the capacity to distinguish among diseases.

UAV-based multispectral sensors can assist in early and specific pest and pathogen detection through spectral vegetation indices (Garcia-Ruiz et al., 2013). Although, UAV-based multispectral imagery was found to reach higher accuracy than aircraft imagery for this purpose; moderate overall accuracy levels and a high proportion of false negatives demand further improvements on these technics (Garcia-Ruiz et al., 2013). One possible improvement might be to combine multispectral and thermal imagery, which has retrieved encouraging results in legal opium poppy plantations (Calderón et al., 2014). The simpler RGB sensors might not be as appropriate for early detection objectives but, nonetheless, they can provide accurate maps of location and severity of affected plants (Cardil et al., 2017; Sugiura et al., 2016; Tetila et al., 2017). Considering the lower costs of RGB sensors compared to multispectral ones, it is important to adapt methods to research objectives in order to achieve cost-effective solutions (del-Campo-Sanchez et al., 2019).

Despite the above, hyperspectral imaging has the biggest potential for species specific, precise and early pest and pathogen detection (Mahlein et al., 2018), in particular when combined with thermal data (López-López et al., 2016). Vanegas et al. (2018), for example, developed a methodology to detect grape phylloxera (*Daktulosphaira vitifoliae*) attack in vineyards by combining digital surface models obtained from RGB imagery with spectral vegetation indices coming from multispectral and hyperspectral data (Table S1). Vanegas et al. (2018) used a methodology that produced promising results and could be adapted to other systems provided that information on the optical properties of healthy and attacked plants is available. Spectral signatures between healthy and unhealthy plants are usually not different across all spectral regions; therefore, it is important that the used sensors capture radiation at the correct wavelengths for the given study system (Moriya et al., 2017; Vanegas et al., 2018). Given the high amount of data generated with hyperspectral sensors (Mahlein, 2016), it is recommendable to carefully select just the informative spectral regions and the correct spatial resolution needed in order to optimize data analysis.

Non-imagery UAVs have also been applied in different studies to reduce pest and pathogen damage to crops. Smith et al. (2015), for example, studied the long distance dispersal potential of an insect pest (*Thrips tabaci*) transmitting a pathogenic virus in onion crops. They used UAVs equipped with sticky card traps to determine seasonal dynamics of insect occurrence in the planetary boundary layer and virus infection rates to better understand pest dynamics of *T. tabaci*. Likewise, UAVs have been used to deploy wasp and fly parasites of the African armyworm (*Spodoptera exempta*) in cereal crops, improving the quality of the crop and replacing pesticides (Faithpraise et al., 2015).

d. Soil fertility

RGB and multispectral imagery have also been used to estimate soil residue cover (Kavoosi et al., 2018), soil erosion (Bazzoffi, 2015; d'Oleire-Oltmanns et al., 2012), soil moisture (Acevo-Herrera et al., 2010; Sugiura et al., 2007) and soil organic carbon content in bare cultivated soils (Aldana-Jague et al., 2016b). Soil residue cover, for example, is fundamental to sustainable agriculture as appropriate residue cover improves soil and water quality and reduces soil erosion (Kavoosi et al., 2018). Kavoosi et al. (2018) used a combination of multispectral satellite imagery (Landsat 8 OLI) and RGB imagery from a UAV and found that multispectral imagery predicts soil residue cover with higher precision than RGB imagery.

Soil erosion is a serious problem in Europe (Bazzoffi, 2015) and especially in semi-arid regions (d'Oleire-Oltmanns et al., 2012), as it causes soil loss and degradation and is considered an indicator of desertification (López-Bermúdez, 1990). Soil erosion is accelerated by inappropriate human activities and is a useful indicator to monitor land degradation (Wang et al., 2016). Wang et al. (2016) and d'Oleire-Oltmanns et al. (2012) used commercial digital cameras (i.e. RGB imagery) mounted on UAVs to produce DEMs and sub-decimetre orthomosaic images through which they were able to precisely map, quantify and monitor gully erosion (Table S1). High resolution multispectral imagery has also proved useful in the prevention and management of soil erosion through the interactions between sediment connectivity and vegetation (Estrany et al., 2019).

Soil moisture estimates are essential for precision agriculture, coastal monitoring, fire risk estimation and flood prevention (Kumar et al., 2018; Wang et al., 2018). They have been calculated with high accuracy in agricultural fields using L-band radiometers (Acevo-Herrera et al., 2010), thermal cameras (Sugiura et al., 2007; Wang et al., 2018), multispectral sensors (Wang et al., 2018) and UAV hyperspectral imagery (Ge et al., 2019b). Finally, estimates of soil organic carbon are extremely important as this property is related to water holding capacity and nutrient availability of soils. It is also linked to climate regulation, as atmospheric CO_2 concentrations depend on terrestrial carbon, whose largest reservoirs are soils (Aldana Jague et al., 2016a). Although the most informative spectral bands related to soil organic carbon estimation occur in both, the visible near-infrared (350–1000nm) and the shortwave near-infrared (1000-2500nm) regions (Laamrani et al., 2019); Crucil et al. (2019) found that model predictions of soil organic carbon based only on the visible near-infrared spectral range perform as well as those based on both regions. Furthermore, they found that models based on multispectral narrow bands performed better than those of hyperspectral sensors. Crucil et al. (2019) key findings mean that expensive and heavy hyperspectral sensors (e.g. spectro-radiometers) are not needed for soil organic carbon estimation. Instead, lighter UAV adaptable hyperspectral sensors (i.e. typically those covering a spectral range of 400-1100 nm), and particularly multispectral sensors, might perform even better. The study of Aldana-Jague et al. (2016b), for example, used UAV multi-spectral imagery for soil organic carbon estimation in barley fields and obtained highly accurate models (average R^2= 0.95), staying in line with recent findings (Table S1).

e. Weeds and other non-crop plants

Given potential competition with crops, non-crop plants (e.g. arable weeds) are usually seen as enemies to yield and are therefore intensively fought with herbicides in conventional agriculture (Oerke, 2006). Widespread herbicide use has caused dramatic declines in arable plant species (Storkey et al., 2012), despite their importance as major basis for biodiversity and food webs, with bottom-up effects to insects and birds (Gerowitt et al., 2017). In Germany, 71% of all arable plant species per crop field have disappeared since 1950 (Meyer et al., 2013) and currently 35% of species are facing extinction (Albrecht et al., 2016). However, weeds are very diverse and some species may even exhibit net positive effects to agricultural systems thanks to a high biodiversity value and low levels of competition with crops (Marshall et al., 2003; Storkey, 2006). Beneficial weeds can decrease the damage caused by pests (Frank and Barone, 1999) and inhibit the proliferation of detrimental weeds and invasive plants, avoiding further costs for the farmers (Christina et al., 2015; Li et al., 2015; Vandermeer and Perfecto, 2017; Zhao et al., 2008).

The ability to distinguish and map beneficial and detrimental weeds within farms (see Storkey, 2006), can lead to a general reduction of herbicide application (Rasmussen et al., 2013) as farmers may opt to maintain beneficial weeds while removing detrimental ones. Selective herbicides constitute one method to achieve this. Alternatively, weed clusters could be treated at the sub-field level (Pelosi et al., 2015), exploiting the fact that weeds show often patchy distributions, naturally leaving a considerable proportion of land free of them (Rew and Cousens, 2001; Torres-Sánchez et al., 2013). Using a quadcopter equipped with a lightweight multispectral sensor, Peña et al. (2013) found that 23% of the area in a maize field was free of weeds, and the area with low weed coverage (<5% weeds) was 47%. These findings highlight the potential of UAV-based weed mapping to reduce the amount and time spent on herbicide spraying (Table S1).

Satellites and airplanes are unsuitable for this task because of their low spatial and temporal resolutions (Lopez-Granados, 2011). Conversely, UAV-based imagery can capture the spectral differences between weeds, crop plants and bare soil enabling successful identification of weed plants (Peña et al., 2013), with accuracy levels of > 90% (Pantazi et al., 2017; Peña et al., 2015). The success of these UAV operations in detecting weed plants has been shown to depend on the cameras used, resolution of images, as well as on time (i.e. days after sowing, Peña et al., 2015) .

Accuracy can also be improved when crop row detection/classification is included in the identification process (Pérez-Ortiz et al., 2015).

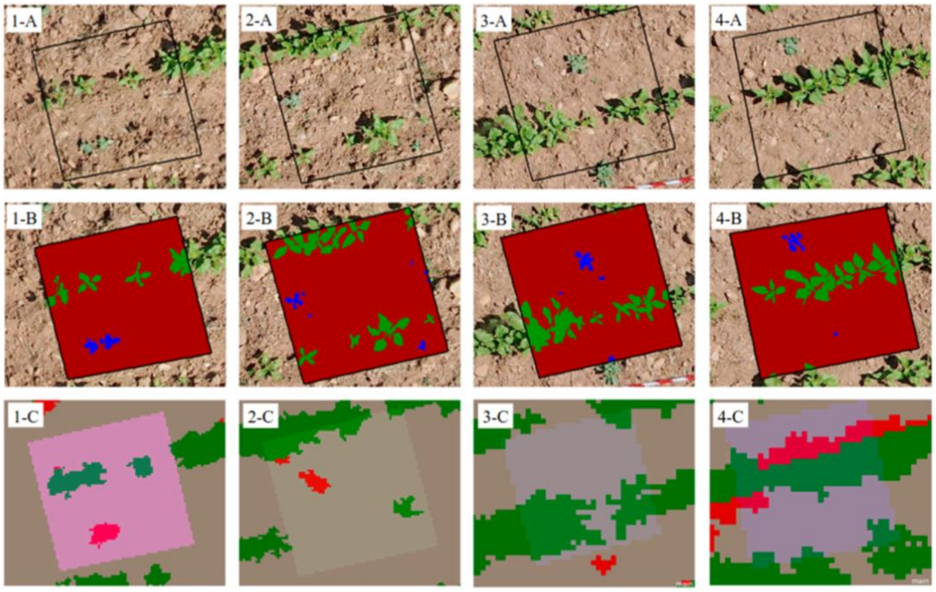

Fig. 3 Weed seedling detection in sunflower field from Spain (modified from Peña et al. (2015), used with permission). The first row includes on-ground photographs; the second shows manual classification of crop (green) and weeds (blue); and the third shows weed (red) and crop (green) detection with four different automatic classification methods (columns).

Precise weed detection has been shown to reduce herbicide applications ranging from 12.5% to 99% depending on the proportion of the field infested, herbicide and application threshold used (Andújar et al., 2013; Hamouz et al., 2013). Castaldi et al. (2017), for example, used multispectral UAV imagery from a modified digital camera and demonstrated that UAVs can save up to 39% in herbicide applications in maize fields (Table S1). Furthermore, UAVs can be used to monitor weeds by taking air samples from wind-dispersed weed seeds (Shields et al., 2006). Finally, UAVs can assist in identifying detrimental weed seed predators (see section 1b on animal diversity) such as certain insects, birds and small mammals (Bajwa et al., 2015), allowing for specific management practices for these species and therefore enhancing the provision of biological control services.

4 Perspectives on future research

Biodiversity-friendly management in agriculture has been limited by a lack of information on species location and condition, in particular if species cover large areas. Large-scale UAV applications will need collaboration between local and regional stakeholders to jointly take landscape scale measures. With current technology, UAV high spatial resolution imagery could be used to detect and map floral resources with high precision. Mapping and monitoring of flower resources from flower strips and set asides across landscapes is of major importance as these are fundamental for pollination and biological control services delivery (Sutter et al., 2018; Tschumi et al., 2015; Walton and Isaacs, 2011; Westphal et al., 2015). However, systematic monitoring of flower resources at the landscape scale in successive years has been practically unfeasible, given associated time and costs constrains.

UAVs' imagery, and in particular the emergent hyperspectral imaging from UAVs, opens a new set of possibilities for accurate mapping and monitoring of flower resources across entire landscapes by applying the spectral diversity/variability hypothesis. Additionally, multispectral sensors (especially those able to capture near-infra red radiation) could be used to provide a precise assessment of the activity and distribution of keystone animals (e.g. vertebrate pollinators, pests' predators and protected species), although arthropod activity is still mainly based on indirect evidence such as flower resources or plant damage (Xavier et al., 2018). UAV´s imagery has therefore a promising potential to increase the efficacy of agri-environmental schemes across European agriculture (Batáry et al., 2011).

Despite the considerable advance in wildlife tracking in Ecology and Conservation Science this knowledge has not yet been extensively applied to identify species of agricultural or conservation value in agricultural landscapes. In particular, to our knowledge, pests' predators and crops' pollinators have not been so far systematically monitored in agricultural systems. Given the above we exhort scientists, state agencies and agricultural practitioners to put this new technology and knowledge at the service of biodiversity and ecosystem services conservation in agricultural landscapes.

In the tropics, where agricultural landscapes are usually complex mosaics of different crops and remnants of secondary tropical forest (Ribeiro et al., 2009), UAV's RGB and multispectral imagery could be further exploited to assess the conservation value and quality of forest fragments through biodiversity assessments from the over- and understorey (Getzin et al., 2012; Hernandez-Santin et al., 2019). This information can improve landscape management and contribute to policy making based on scientific evidence (Metzger, 2010). Moreover, the advances on UAV research will increase the number of native habitat fragments within agricultural landscapes that can be protected and allow further exploration of their interactions with cropland.

Premature and precise identification of crop damage due to pests and pathogens opens the possibility for a new set of tailored responses. Heavy, expensive and systemic pesticide application may become a method of the past as much cheaper, easier and biodiversity-friendly strategies can be applied, provided that pest damage is targeted early enough, before economic damage thresholds are reached. These strategies gain further importance considering the consistent move to insecticide and herbicide banning in developed countries (Storck et al., 2017). Additionally, systematic chemical control provokes emergence of resistant pest and weed (Schütte et al., 2017) populations, such as the Colorado potato beetle (*Leptinotarsa decemlineata*), which has developed resistance to ≥ 50 different insecticides (Alyokhin et al., 2007; Mota-Sanchez et al., 2006). Therefore, reduced insecticide use means costs avoidance, preservation of yield enhancing pollinators (e.g. bees), and less contamination of soil and water (Arias-Estévez et al., 2008; Bretagnolle and Gaba, 2015; Geiger et al., 2010; Gerhardson, 2002; Potts et al., 2010; Wilson and Tisdell, 2001).

The detection of local and incipient pest focuses, such as those of the coffee-leaf-miner (*Leucoptera coffeella*) in coffee plantations, would become possible by identifying the particular necrotic areas caused in the leaves and may be mitigated by deployment or facilitation of natural enemies such as wasps, birds and bats (Librán-Embid et al., 2017). Identification of pest and pathogen presence in the agricultural landscape may also help to better understand how different land-use types and linear elements like flower strips and hedgerows affect their distribution. Control agents may then better contribute to a more biodiversity-friendly approach of pest and pathogen control in agricultural, natural and semi-natural land. Collaboration and coordination among local and regional stakeholders might become increasingly important under this scenario as many of these processes are affected by management at the local and landscape level (Redlich et al., 2018).

In general, conservation science has not yet fully integrated recent advances in plant monitoring coming out of precision agriculture, which could help to better monitor fragile ecosystems under climate change and biotic pressures. On the other hand, precision agriculture should incorporate the latest developments in species detection coming from conservation science, especially to distinguish among detrimental and beneficial arable weeds (see section 2e. *weeds and other non-crop plants*). This would benefit farmers' economy in terms of reduced time and herbicide costs, increased ecosystem services and would also contribute to the protection of biodiversity given the high proportion of arable weeds threatened with extinction (Albrecht et al., 2016; Meyer et al., 2013).

Yield is frequently negatively associated to biodiversity although management options to increase yield with less impact on biodiversity have been proposed (Clough et al., 2011; Cunningham et al., 2013). This apparent trade-off is, however, mainly caused by high agrochemical input associated to non-biodiversity-friendly agricultural intensification. We posit that UAVs can establish a new scenario in which the antipode between yield and biodiversity conservation may not be the rule. UAVs' based imagery is changing the way inputs are applied as it is allowing to identify where, when and how much input is needed with high precision. This produces two major benefits: first, yields increase as plants receive the exact treatment they need at the right time, avoiding nutrient, water and herbivory stress, and leading to reduced input costs for farmers. Second, reduced amounts of pesticides directly benefit naturally occurring insects (Geiger et al., 2010), which is not only fundamental for conservation science, but also increases the availability of beneficial agents such as pollinators and pest predators, thereby also reducing the necessity for inputs (Chaplin-Kramer et al., 2011; Cohen et al., 1994; Holland et al., 2012). In sum, these developments may constitute a synergistic win-win scenario.

5 Conclusions

Future agricultural landscapes must meet two major objectives: 1) increase food, fiber and fuel production and 2) do so in a biodiversity-friendly way. Here we show that UAVs are helping to reconcile these oft-considered discrepant objectives, by enhancing the efficiency of fertilizer, pesticide and herbicide applications, while simultaneously increasing yield and reducing impacts on biodiversity. UAV-based information on species' habitat use and movement through the landscape supports more efficient large-scale management of beneficial animals and increased success in biological conservation. Therefore, UAVs are expected to become common tools for the management of agricultural landscapes, in particular when combined with promising developing technology, such as light-weight hyperspectral sensors. UAV-based imagery will not substitute the use of manned aircraft or satellite imagery for regional and global assessments but will greatly contribute to local management at small to medium scales (up to 50 ha). The main current limitations for a more widespread adoption of UAVs are the high price of multispectral and especially hyperspectral sensors; the lack of established image processing methods in some applications; and the lower estimation accuracy for yield estimations in certain crops, compared to traditional methods. Nevertheless, these current limitations may be offset in the near future by rapid advances in sensor technology and decreasing prices, thereby increasing the suitability of UAVs for applications in agriculture and conservation science.

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Supplementary material

From 1995 to 2018 UAVs publications showed a growth rate of 30.64% resulting in a doubling of output in less than 2.3 years, therefore nearly tripling the mean publication growth rate in science (Larsen and Ins, 2010; Bornmann and Mutz, 2015).

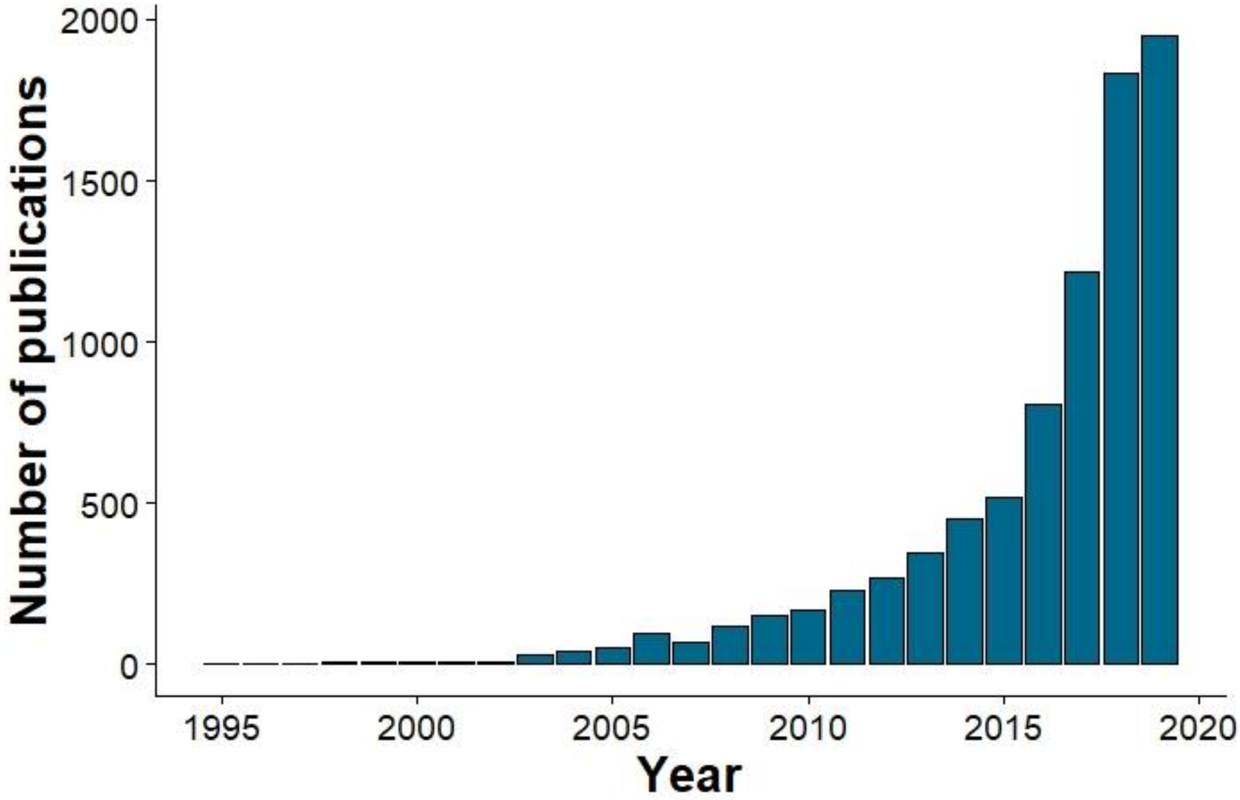

Figure S1. Total number of publications per year in Web of Science core collection under the topic "unmanned aerial" from 1995 to 2019 as of October 10th 2019.

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Table S1. Technical details of all studies using UAVs cited throughout the review sections.

UAV application	Authors	Study objective	Sensor	Platform	Flight height (m)	Indices used	Processing software	Built products	Resolution (cm): GSD or cell size	Accuracy	Other data sources used	Comments
3.1 Biodiversity conservation *a. Plant diversity*	Ahmed et al., 2017	Vegetation classification	Sony DSC-WX220 (RGB) and Parrot Sequoia (multispectral)	SenseFly eBee (fixed-wing)	120	NDVI	ENVI	RGB: Orthomosaics, point clouds and DSM Multispectral: Colour-balanced orthomosaics, non-balanced 'raw' reflectance and NDVI maps	RGB: 2.6- 3.5 Multispectral: 5.7	Overall accuracy 78-95% depending on sensor, resolution and classification detail.	Reflectance data calibrated with spectral reflectance measurements obtained with an ASD Field Spectrometer	-
	Cruzan et al., 2016	Plant species and vegetation types distributions	RGB	DJI Phantom 2 Vision+ (quadcopter)	40	None	AgiSoft PhotoScan	Orthomosaic and DSM	~2	Not reported	No	R scripts used for automated habitat delineation
	Getzin et al., 2012	Forest biodiversity assessment	RGB	Fixed-wing	~250	GSCI	ArcGIS	Shapefiles	7	R2 = 0.47–0.74, P values <0.001	No	Gap polygons from orthophotos manually segmented to create shapefiles.
	Habel et al., 2016	Butterflies micro-habitat mapping and characterization	GoPro HERO 4 Black (RGB)	DJI Phantom 2 (quadcopter)	40	None	AgiSoft Photoscan Professional	Georeferenced orthomosaic and HSM	2	HSM feeding plants: AUC = 0.72, COR = 0.39 HSM for larvae: AUC = 0.72, COR = 0.22	Verification in the field	Input variables for HSMs were aerial pictures decomposed into RGB channels
	Knoth et al., 2013	Restoration monitoring	Modified Canon Ixus 400 (captures NIR) and modified Panasonic Lumix LX-3 (captures VIS and NIR)	Mikrokopter and Microdrone MD4-1000 (quadcopters)	15-100	NIR/blue ratio to generate NIR-albedo variation	ERDAS Imagine including the Leica Photogrammetry Suite and eCognition Developer	CIR orthomosaic	3 and < 1.5	Overall accuracy 84-95%	No	-
	Lu & He, 2017	Grassland species classification	Modified Canon PowerShot ELPH 110HS (captures VIS and NIR)	Tarot T15 (octocopter)	70	Blue NDVI and Green NDVI	Agisoft Photoscan, ArcGIS and ENVI	Orthomosaics	5	R^2 = 0.6-0.95	Canopy reflectance data collected using a spectroradiometer.	-
	Michez et al., 2016	Riparian forest species classification and health condition	Ricoh GR3 camera (RGB)	Gatewing X100 (fixed-wing)	114-404	Multiple	Agisoft Photoscan Professional	Orthomosaic	10-25	Species clasification: 48.5-84.1% depending on site and scale of analysis. Health condition: 81±10.8-90.6±0.7	LiDAR digital terrain model (DTM)	-
	Silva et al., 2014	Grassland species mapping	Canon Ixus-90 (RGB) and modified RG715 (captures NIR)	Helium balloon	35	Foliage projective cover and LAI	Open source: "Bundler", "GRASS", "SAGA" and "gbm" R-package	DSM	1	AUC 0.81-0.99. AUC= 0.88 in average	Field Spectroscopy with the field spectrometer (Handyspec-14)	Also used R and Python languages

	Zahawi et al., 2015	Monitor tropical forest recovery	Canon ELPH 520 HS (RGB)	HiSystems Mikrokopter (hexacopter)	30–40 m above canopy	None	Agisoft Photoscan and ArcGIS	Point clouds, DTM and CHM.	30	$R^2 = 0.53$-0.85	Compared to LiDAR measurements	Also used R and Python languages
b. Animal diversity	Chrétien et al., 2016	Wildlife surveys	FLIR Tau640 sensor (thermal) and D7000 sensor (RGB)	ING Robotic Responder (helicopter)	60	None	Not specified	Orthomosaics	RGB: 0.8 Thermal: 5.4	100% detection rate open land deer. 52% detection rate overall	No	-
	Cukor et al., 2019	Reduce mortality of roe deer fawns	LWIR Workswell WIRIS 2nd generation (thermal)	GD HX-1100F ZODIAC (hexacopter)	40	None	DJI GO application and WorkswellCorePlayer	Thermogram	~10	100% search success rate	No	-
	Gonzalez et al., 2016	Wildlife monitoring	FLIR Tau 2-640 (thermal) and Mobius (RGB)	S800 EVO (hexacopter)	20,30, 60 and 80	None	Not specified	Thermal and RGB images	RGB: ~17 - ~ 70 Thermal: ~5 - ~20	100% accuracy at < 60 m height	No	Used two algorithms to automatically classify and count wildlife (Python)
	Hodgson et al., 2016	Bird colony estimation	Canon EOS M mirrorless camera (RGB)	X8 3D Robotics (octocopter) and FX79 airframe conservation drone (fixed-wing)	75 and 120	None	Adobe Photoshop	Composite	1.5	UAV counts ten times more accurate than ground counts	No	-
	Israel & Reinhard, 2017	Reduce mortality of lapwings	Tau 640 infrared (thermal) and GoPro 3 Black Plus (RGB)	Falcon 8 from Ascending Technologies (octocopter)	40	None	Not specified	Thermogram	3.18	93%	No	MbOpt algorithm to improve detectability
	Mulero-Pazmany & Negro-Balmaseda, 2011	Reduce mortality of Montagu´s Harriers	Panasonic Lumix LX3 (RGB)	Fixed-wing	70	None	Arc GIS	Georeferenced aerial photographs	~5	64% search success rate	No	-
	Ward et al., 2016	Wildlife detection and monitoring	FLIR Lepton (thermal)	3DR IRIS (quadcopter)	10	None	Not specified	Thermogram	Not specified	-	No	Open-source detection algorithms (written in Python)
	Weissensteiner et al., 2015	Nesting status evaluation of canopy-breeding birds	RGB	DJI Phantom 2 Vision (quadcopter)	10-30	None	-	-	< 1	Nestling number accuracy 75%. UAV nesting status assessment 7.4 times faster than climbing ($P < 0.005$)	No	-

3.2 Agricultural land monitoring *a. Plant height and biomass*	Bareth et al. 2016	Barley monitoring	Panasonic Lumix GX1(RGB)	HiSystems MikroKopter MKOkto (octocopter)	50	None	Agisoft PhotoScan Professional	Georeferenced CSM	0.9	$R^2 = 0.91$	Compared to terrestrial laser scanning	-
	Bendig et al., 2014	Plant height estimation	Panasonic Lumix GX1(RGB)	HiSystems MikroKopter MKOkto (octocopter)	50	None	Agisoft PhotoScan Professional	Georeferenced CSM	1	$R^2 = 0.71\text{-}0.92$	No	-
	Grüner et al., 2019	Grassland biomass prediction	DJI FC300S (RGB)	DJI Phantom 3 Advanced (quadcopter)	20	None	Agisoft PhotoScan Professional	DSM	0.7-0.8	$R^2 = 0.58\text{-}0.81$;	No	Compared to destructive biomass sampling and ruler height measurements
	Guerra-Hernández et al., 2017	Tree growth estimation	Canon Powershot S110 (RGB)	SenseFly eBee (fixed-wing)	170	None	Pix4D	Orthomosaics and DSMs	6	$R^2 = 0.96$ Detection rate 100%	No	-
	Kachamba et al., 2017	Biomass estimates in dry tropical forests	Canon IXUS127 HS (RGB)	SenseFly eBee (fixed-wing)	325	None	Agisoft Photoscan Professional	Normalized point cloud to generate canopy height variables	~ 20	$R^2 = 0.31\text{-}0.64$	No	-
	Li et al., 2016	Maize canopy height and aboveground biomass estimation	SONYA6000 (RGB)	Not specified multiple-rotor system	150	7 greenness VIs	Smart3DCapture to generate point clouds	Orthorectified image and DSM	2	$R^2 = 0.88$ (multiple stepwise linear regressino model); R^2=0.78 (random forest regression)	No	-
	Shin et al., 2018	Forest canopy fuels estimation	multispectral	SenseFly eBee (fixed-wing)	120	NDVI	Pix4D, ENVI and CloudCompare	Orthomosaics	15	$R^2 = 0.72$	No	-
	Surový et al., 2018	Tree position and height estimation	Samsung K-Zoom (RGB)	DJI F550 (hexacopter)	50	None	Agisoft Photoscan and ArcGIS	Orthomosaic and DEM	Orthomosaic: 3.5 DEM: 4.5	Detection rate 43-80%	No	.
	Wallace et al., 2016	Forest structure assessment	Canon 550D (RGB)	Droidworx Skyjib (octocopter)	30	None	Agisoft Photoscan Professional	Point cloud	10	$R^2 = 0.68.0.84$	Laser scanner data	-

	Zarco-Tejada et al., 2014	Tree height quantification	Modified Panasonic Lumix DMC-GF1 (CIR detection)	mX-SIGHT (fixed-wing)	200	None	Pix4D	Ortho-mosaics and DSMs	5	$R^2 = 0.83$	No	-
b. Yield and nutrient status	Capolupo et al., 2015	Grassland structural and chemical trait analysis	Wageningen UR Mapping System (hyperspectral)	Aerialtronics Altura AT8 v1A (octocopter)	70	Multiple narrow vegetation indices	-	-	Hyperspectral: 20 RGB: 2	R^2= 0-0.86 (see tables 6 and 7 in manuscript)	No	Comparison of statistical approaches: partial least squares regression vs narrow Vis. 400-950nm
	Geipel et al., 2014	Spectral and spatial modeling of corn yield	Canon Ixus 110 IS (RGB)	Modified MikroKopter Hexa XL	50	ExG, NGRDI and PPRb	Agisoft PhotoScan	Vegetation index-orthoimages and 3D crop surface models	2-10	R^2 of up to 0.74	Combined with vegetation index maps	Three early- to mid-season growth stages
	Gong et al., 2018	Estimation of rapeseed yield	Modified Tetracam Mini-MCA (multispectral)	SZ DJI S1000 (hexacopter)	50	Multiple vegetation indices	-	-	2.5	R^2 = 0.33-0.81	In situ hyperspectral measures of samples spectra	Six spectral bands 490-900nm.
	Kalisperakis et al., 2015	Leaf area index estimation in vineyards	Headwall Photonics Micro-A-Series (hyperspectral) and GoPro Hero3 (RGB)	OnyxStar multicopter (octocopter)	Not specified	LAI, NDVI and GRVI	SfM for 2D orthomosaics and not specified algorithms for 3D canopy surface models	2D orthomosaics and 3D canopy surface models	Not specified	R^2 >73%	No	380nm-1000nm
	Khaliq et al., 2019	Vineyard variability assessment	Parrot sequoia (multispectral)	Octocopter	35	NDVI	Agisoft Photoscan	NDVI maps	5	-	Compared to satellite multispectral imagery	UAV-NDVI maps significantly predicted three vigor classes
	Lelong et al. 2008	Quantitative monitoring of wheat crop	CANON EOS 350D (RGB) and SONY DSC-F828 (Red, Green, Blue, and Cyan).	L'Avion Jaune powered glider (fixed-wing) and ABS-Aerolight motorized parachute	20-100	NDVI, SAVI , GNDVI and GI	Not specified	LAI and nitrogen uptake maps	10	R^2 = 0.82-0.92	No	-
	Liu et al. 2018	Nitrogen status diagnosis in winter oilseed rape	Mini-MCA 6 (multispectral)	SZ DJI S1000 (hexacopter)	40	NDVI, VARI, MSAVI2, $CI_{red\ edge}$, RVI1, RVI2	Agisoft Photoscan Pro	Orthomosaics	2.2	R^2 = 0.45-0.83	Ground sampling campaigns. LAI and oilseed rape spectra measured (hyperspectral data)	-

	Potgieter et al., 2017	Assessment of sorghum leaf area dynamics	MicaSense RedEdgeTM (multispectral)	3D Robotics X8+ multi-rotor (quadcopter)	20	LAI, NDVI, EVI and NDRE	Pix4D	Geo-referenced multi-layer orthomosaic	0.5	R² = 0.19-0.85	No	-
	Rey-Caramés et al., 2015	Vineyard variability characterization	MCA-6 Tetracam (multispectral)	RPAS Md4-1000 (quadcopter)	250	Multiple indices	ENVI	Orthomosaic	17	R² = 0.32-0.69	No	-
	Sanches et al., 2018	Sugarcane yield prediction	1/2.3”CMOS (RGB)	DJI Phantom 3 (quadcopter)	25	LAI and GRVI	Drone Deploy	Orthomosaic	5	$R^2_{GRVI} = 0.69$ $R^2_{LAI} = 0.34$ $R^2_{GRVI+LAI} = 0.79$	No	-
	Zarco-Tejada et al., 2013	Leaf carotenoid estimation in vineyards	MCA-6 Tetracam (multispectral) and Micro-Hyperspec VNIR (hyperspectral)	mX-SIGHT (fixed-wing) and ELIMCO Viewer (fixed-wing)	150 (multispectral) and 575 (hyperspectral)	LAI, R515/R570 and TCARI/OSAVI	PARGE	Ortho-rectified hyperspectral scenes	15 for multispectral and 40 for hyperspectral	R² = 0.5-0.99	No	-
	Zhou et al., 2017	Rice yield prediction	EOS 5D Mark III (RGB) and Mini-MCA6 (multispectral)	HiSystems MK (octocopter)	100 (multispectral) and 50 (RGB)	Multiple indices	IDL script within ENVI and Agisoft PhotoScan Professional	Orthomosaic	5.4 for multispectral and ~2 for RGB	R² = 0.33-0.79	Target´s reflectance measured with a FieldSpec 4 Spectroradiometer	-
c. Pest and	Calderón et al., 2014	Downy mildew detection in opium poppy	ADC Lite Tetracam (multispectral) and MIRICLE 307 (thermal)	mX-SIGHT (fixed-wing)	200 (multispectral) and 100 (thermal)	NDVI and R550/R670	Not specified	Multispectral and thermal scenes	20	-	Reflectance of attacked leaves measured with Li-Cor 1800-12 Integrating Sphere spectrometer	-
	Cardil et al., 2017	Pine-processionary-moth defoliation assessment	RGB	DJI Phantom 3 (quadcopter)	80-100	None	Agisoft PhotoScan Professional	Point clouds, 3D reconstruction, orthomosaic, DSMs, DEM and CHM	1.5-2.5	Overall accuracy 79%. R² = 0.55 of linear regression model	No	Videos at 20 m altitude for validation
	Del-Campo-Sanchez et al., 2019	Pest quantification in vineyards	SONY αILCE-5100L (RGB)	microdrone md4-1000 (quadcopter)	80	None	Agisoft PhotoScan and LAIC	Point clouds, orthomosaics and affection maps	1.5	Overall accuracy radiometric 79%. Overall accuracy radiometric + geometric 99.3%.	5 m resolution DEM used	The automated identification of affected vegetation with LAIC
	Garcia-Ruiz et al., 2013	Infected citrus trees identification	miniMCA6 Tetracam (multispectral)	HiSystems GmbH (hexacopter)	100	Seven vegetation indices	PixelWrench2, ENVI, Matlab	Georeferenced false color images	5.45	Overall accuracy 67-85%.	No	Compared with 50 cm/pixel airborne hyperspectral images

pathogen damage	Moriya et al., 2017	Sugarcane mosaic virus mapping	DT-0014 Fabry-Perot Interferometer (hyperspectral) and Ultracam-XP (RGB)	SX8 multirotor UAS (octocopter)	160	None	Radiometric processing done with BRDF model. Classification Process with spectral information divergence (SID) in ENVI	Orthomosaic and digital surface model	11 for hyperspectral images. 40 for RGB camera. 50 for DSM and orthomosaic	Overall accuracy 92.5%.	Spectral library of sick and healthy leaves made with an ASD handheld FieldSpec UV/NIR spectroradiometer	Up to 25 bands from selectable wavelengths. spectral range 500 -900 n
	Sugiura et al., 2016	Assessment of potato late blight resistance	Sony NEX-5N (RGB)	HiSystems GmbH Mikrokopter (quadcopter)	80	None	Not specified	Potato damage maps	2.4	R^2 = 0.73-0.77	No	-
	Tetila et al., 2017	Identification of Soybean Foliar Diseases	Sony EXMOR (RGB)	DJI Phantom 3 (quadcopter)	1-16	None	Visual classification of superpixels	Disease classification maps	0.043-0.691	Overall accuracy 98.34%.	No	Uses SLIC superpixels algorithm for segmentation
	Vanegas et al., 2018	Plant pest surveillance in vineyards	Canon 5DsR camera (RGB), MicaSense RedEdge (multispectral) and Headwall Nano-Hyperspec (hyperspectral)	S800 EVO (hexacopter)	60-100	Multiple indices	Agisoft Photoscan, Headwall SpectralViewer, MATLAB, Scyllarus and ArcMap	3D models, orthomosaics, DSM and DVM	3.26-6.74 for multispectral imagery	positive correlation ($r > 0.4$) with 7 different indices	Google Earth imagery	-
d. Soil fertility	Aldana-Jague et al., 2016b	Soil carbon mapping	Mini-MCA6 (multispectral)	Mikrokopter-XL (octocopter)	100	None	AutoPano Giga and ArcGISTM. Support Vector Machine (SVM) algorithm to predict SOC from the soil spectra in R	Orthomosaic	12	$R^2 > 0.9$	No	Six spectral bands 450-1050nm
	Bazzoffi, 2015	Rill erosion measurement	SONY NEX-5 (RGB)	Falcon 8 (octocopter)	30	None	Agisoft PhotoScan Pro and ESri ArcGis	Digital elevation model	1-6	R2 = 0.87	No	-
	d'Oleire-Oltmanns et al., 2012	Soil erosion monitoring	Panasonic Lumix GF1 (RGB)	Sirius I (fixed-wing)	70-400	None	Leica Photogrammetry Suite and MAVinci	Digital Terrain Models (DTMs) and orthomosaics	~1-10	Not specified	No	Coordinates for well-defined points, were taken from a Quickbird satellite scene
	Estrany et al., 2019	Ecosystem dynamics assessment and management	Canon PowerShot ELPH 110HS (multispectral)	Mikrocopter (hexacopter)	52	BNDVI	Agisoft Photoscan Professional and ArcGIS	Orthomosaic and DEMs	1.4	Not specified	No	MATLAB for image processing

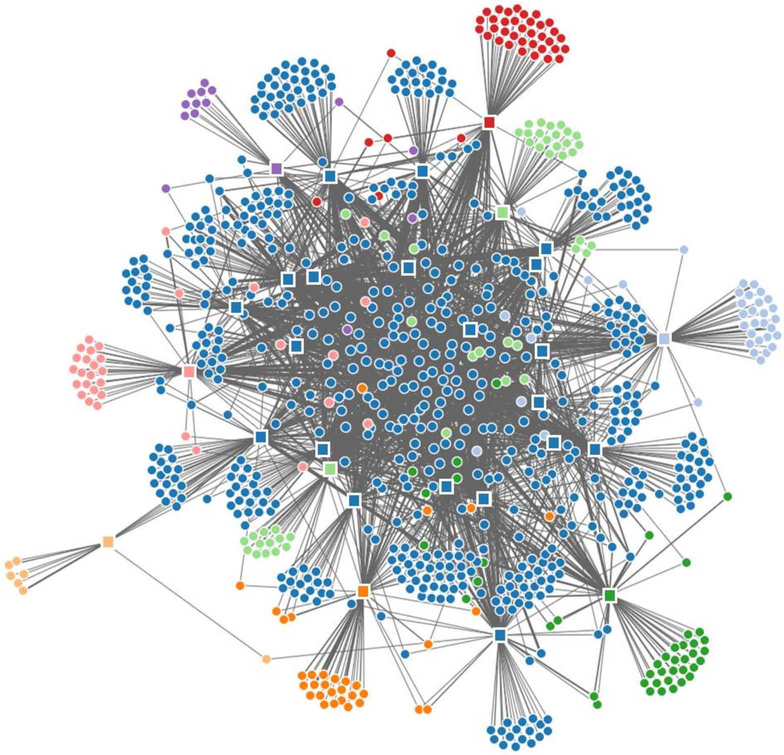
	Ge et al., 2019	Soil moisture monitoring	Headwall Nano-Hyperspec (hyperspectral)	DJI Matrice 600 Pro (hexacopter)	100	30 different indices	Image smoothing and model calibration, evaluation and comparison in MATLAB	Orthomosaic	4	R2 = 0.15-0.66 for common spectral indices. R^2=0.91 for perpendicualr index random forest	No	Spectrometer range 400–1000 nm.
	Kavoosi et al., 2018	Soil residue cover monitoring	Sony EXMOR (RGB)	DJI Phantom 3 professional (quadcopter)	5-10	14 different visible spectrum indices	RGB bands separated with MATLAB. Spectral indices calculated in Excell	None	0.23-0.45	R2 = 0.84	Landsat 8 OLI data (satellite)	-
	Sugiura et al., 2007	Soil water status estimation	Thermal camera	Unmanned helicopter	40	None	Used a correction model to get real temperature values based on emissivity and transmissivity.	Thermal infrared maps	~12	R2 = 0.62-0.69	No	Ground-truth measurement
	Wang et al., 2016	Gully erosion mapping and monitoring	Sony EXMOR (RGB)	Phantom 3 Professional (quadcopter)	120	None	Pix4Dmapper and ArcGIS	Orthomosaic and DSM	4.4	Overall accuracy 90%.	Pleiades-1A imagery (satellit e)	-
e. Weeds and other non-crop plants	Castaldi et al., 2017	Maize herbicide spraying analysis	Modified Canon s110 (multispectral) and AIRINOV Agrosensor (multispectral)	eBee (fixed-wing) and SF6	150 and 35	LAI and NDVI	Support vector machine algorithm in ENVI CAN-EYE to calculate LAI	Weed, prescription and biomass maps.	8-9 and 5	R2 ≥ 0.80	No	-
	Pantazi et al., 2017	Weed mapping	Canon S110 (NIR sensor)	eBee (fixed-wing)	115	None	Pix4Dmapper Pro	Orthomosaic, point cloud and DSM.	50	>98%	No	-
	Peña et al., 2013	Maize weeds mapping	Tetracam mini-MCA-6 camera (multispectral)	md4-1000 (quadcopter)	30	NDVI	PixelWrench2 and eCognition Developer	OBIA output (geo-referenced weed map)	2	R2=0.89	No	-
	Peña et al., 2015	Weed seedling detection	Olympus PEN E-PM1 (RGB) and Tetracam mini-MCA-6 camera (multispectral)	md4-1000 (quadcopter)	40-100	NDVI	eCognition Developer and Agisoft Photoscan Professional	Orthomosaic and OBIA output (geo-referenced weed map)	RGB: 1.52-3.81 Multiscpectral: 2.16-5.41	RGB: 19-71% accuracy Multispectral: 43-71% accuracy	No	-
	Pérez-Ortiz et al., 2015	Sunflower weeds mapping	Olympus PEN E-PM1 (RGB) and Tetracam mini-MCA-6 camera (multispectral)	md4-1000 (quadcopter)	30-100	NDVI and ExG	Agisoft Photoscan Professional	Orthomosaic	RGB: 1-4 Multiscpectral: 2-5	75%	No	-

Definitions: Ground sampling distance (GSD), digital terrain model (DTM), digital surface model (DSM), digital vigour model (DVM), digital elevation model (DEM), habitat suitability model (HSM), crop surface model (CSM), canopy height model (CHM), area under the receiver operating characteristic curve (AUC), point-biserial correlation coefficient (COR), colour infrared (CIR), Near infra-red (NIR), vegetation indices (VIs), gap shape complexity index (GSCI), green-red vegetation index (GRVI), excess green index (ExG), normalized green-red difference index (NGRDI), plant pigment ratio (PPRb), normalized difference vegetation index (NDVI), blue normalized difference vegetation index (BNDVI), enhanced vegetation index (EVI) and normalized difference red edge index (NDRE), soil-adjusted vegetation index (SAVI), green normalized difference vegetation index (GNDVI), greenness index (GI), visible atmospherically resistance index (VARI), modified soil adjusted vegetation index 2 (MSAVI2), red edge chlorophyll index (CIred edge), ratio vegetation index 1 (RVI1), ratio vegetation index 2 (RVI2), structure from motion (SfM), ground control points (GCPs), microbolometer optimization (MbOpt), Leaf Area Index Calculation software (LAIC), Simple Linear Iterative Clustering (SLIC).

Software details: Agisoft Photoscan and Pix4D are used for mosaicking and orthorectification. ArcGIS and ENVI allow geometric and radiometric correction, respectively. Adobe Photoshop permits image merging.

Chapter 2

A plant-pollinator metanetwork along a habitat fragmentation gradient



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Article in preparation

Abstract

To understand how plant-pollinator interactions respond to habitat fragmentation we need novel approaches that can capture properties that emerge at broad scales, where species engage across multiple communities in metanetworks. Here we studied plant-pollinator interactions over two years on 29 calcareous grassland fragments selected along independent gradients of habitat size and surrounding landscape diversity. We associated the centrality of plant-pollinator interactions and grassland fragments with their traits. Interactions involving habitat specialist plants and large-bodied pollinators were the most central, implying that species with these traits form the metanetwork core, maintaining its integrity. Large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality; however, small fragments harbored a high share of unique interactions not found on larger fragments. Our results emphasize the need to keep a conservation focus on both small and large habitat fragments as well as on landscape diversification.

Introduction

To understand the impacts of global change on species survival and community composition, we need to look beyond the species richness level and incorporate the fact that all species are connected by ecological interactions (Valiente-Banuet et al., 2015). Ecosystem functions and services, many of which are essential to human well-being, are underpinned by species interactions (Galetti et al., 2013; Traill et al., 2010). Plant-pollinator interactions, for example, are mutualistic associations fundamental to the reproductive success of 88% of all flowering plants and consequently to the functioning of natural and agricultural systems (Ollerton et al., 2011). Plant-pollinator interactions organize themselves in intricate networks based on the local plant and pollinator pools (Bascompte et al., 2003; Delmas et al., 2019; Memmott, 1999). Studying the properties of these networks gives information about their functionality and stability, which ultimately determines species persistence (Burkle et al., 2013; Landi et al., 2018). Understanding changes in ecological networks following habitat fragmentation, from local community to broader metacommunity levels, would greatly advance basic knowledge needed for successful species conservation (Emer et al., 2018; Tylianakis et al., 2010; Tylianakis and Morris, 2017).

The effects of habitat fragmentation on plant-pollinator networks have been studied to some extent (Ferreira et al., 2013; Pellissier et al., 2018). Most studies have used bipartite approaches at local scales that have helped to understand network changes in terms of structure and stability (Grass et al., 2018; Spiesman and Inouye, 2013). However, local approaches cannot capture the properties of plant-pollinator interactions emerging at broader scales, where species engage across multiple communities in metacommunities (Hagen et al., 2012). To overcome this limitation, plant-pollinator interactions can be studied in a metanetwork framework in which local communities are connected by the interactions they share (Emer et al., 2018). From a conservation perspective, it is fundamental to identify and protect the most important nodes within a metanetwork (i.e. central interactions or habitats, Emer et al., 2018). Node importance can be quantified through the concept of node "centrality" (Jordán, 2009). Central nodes are those that maintain network cohesiveness and stability, and, when lost, have the strongest detrimental effects for the whole structure of the network (Estrada, 2007; Freeman, 1978; González et al., 2010). The loss of central nodes can lead to the breakdown of a spatial metanetwork resulting in isolated communities and the extirpation of ecological functions at the landscape level (Emer et al., 2018).

Species traits determine their centrality in local networks (Morán-López et al., 2020). Likewise, trait combinations of interacting partners may determine the centrality of an interaction within a metanetwork perspective. Among the different species traits that can be related to centrality, body size and habitat specialization are of particular ecological importance (Grass et al., 2018). For instance, wing and body size are correlated with flying capacity in bees and butterflies (Gathmann and Tscharntke, 2002; Stevens et al., 2013; Westphal et al., 2006). In a scenario of habitat fragmentation and low-risk matrix (Fahrig, 2007), large species would be expected to be able to cross the matrix and use habitat patches that are out of reach for smaller species (Thomas et al., 1992). High habitat specialization entails that a given species is mostly restricted to a certain habitat (Segura et al., 2007). Therefore, at the landscape level, habitat specialists cannot establish viable populations in the matrix, being restricted to available habitat fragments. Habitat specialization and body size can thus be used to identify key interactions of metanetworks, as well as to identify changes in plant-pollinator interactions caused by habitat fragmentation at the landscape scale.

In addition, the metanetwork approach can be used to identify key traits of habitat fragments that are fundamental to maintain metacommunity cohesiveness. Fragment size and fragment spatial connectivity (i.e. measure of proximity to other sites) could predict fragment centrality, as these characteristics are related to the number of individuals that a certain fragment can support and to the frequency of immigration events, respectively (Hanski and Ovaskainen, 2000; Steffan-Dewenter and Tscharntke, 2002). Furthermore, the characteristics of the matrix in the surroundings of a fragment can also influence fragment centrality, given that the matrix composition affects available food resources and is known to affect the capacity of organisms to cross it (Boesing et al., 2018; Nowicki et al., 2014; van Halder et al., 2017).

Here we studied plant-pollinator interactions along a habitat fragmentation gradient in calcareous grasslands, which are threatened hotspots of plant and pollinator diversity in Europe (Habel et al., 2013). We identified central plant-pollinator interactions in a metanetwork context and related these to the traits of the species involved in those interactions. We also explored the characteristics of the most central habitat fragments that maintain metanetwork cohesiveness at the regional level.

We hypothesized that: (i) the overall metanetwork structure will be poorly connected and highly modular because of the presence of many interactions performed by small-sized species, not able to cross the matrix and therefore restricted to single fragments; (ii) interactions involving habitat specialist species are more central than those involving habitat generalists, because habitat specialist are better adapted to exploit the resources of calcareous grasslands, as they depend exclusively on them across the fragmented landscape; (iii) interactions involving large-bodied pollinators are more central than those involving small-bodied ones, given that large-bodied species can exploit resources at greater distances and potentially cross the matrix, and that (iv) larger-sized and more connected fragments with higher diversity of cover types in the surrounding landscape show higher centrality.

Methods

Study system

Calcareous grasslands are the most species-rich habitats in central Europe and are therefore considered biodiversity hotspots (Habel et al., 2013; van Swaay, 2002). Once widely spread, they have been greatly reduced due to agricultural intensification and the abandonment of the historically common extensive grazing, essential to avoid bush encroachment (Cremene et al., 2005; WallisDeVries et al., 2002). Although highly fragmented, they still harbour many rare and specialized plant and invertebrate species (Steffan-Dewenter and Tscharntke, 2002) and are therefore protected by law in Germany and other European countries (Filz et al., 2013).

Study area

Our study region around the city of Göttingen (Germany) comprises 285 sharply delimited semi-natural calcareous grasslands that differ in size, spatial connectivity, management and successional stage (Krauss et al., 2003b). These grasslands are embedded in an agricultural matrix mainly composed of arable land (42%) and managed European beech (*Fagus sylvatica*) forests (37%) (Krauss et al., 2003a). We conducted our study on 29 calcareous grassland fragments during the spring and summer of 2017 and 2018 (April-September). These fragments were selected in a previous study (Krauss et al., 2003a) along independent (i.e. non-correlated) gradients of habitat area and spatial connectivity.

Landscape metrics

We characterized the calcareous grasslands at the local (fragment area and fragment spatial connectivity) and landscape levels (percentage of cover types and Shannon diversity of cover types) using the “landscapemetrics” package (Hesselbarth et al., 2019). Fragment size ranged from 82 m² to 52557 m², excluding zones dominated by shrubs. The distance between study fragments with respect to the closest neighbouring grassland ranged from 55 m to 1894 m (Krauss et al., 2003a). Fragments’ spatial connectivity was quantified with a connectivity index developed by (Hanski et al., 1994) and considered all calcareous grasslands in a radius of 2 km around the study grasslands (see SM for details). Larger values of this index indicate higher spatial connectivity (Table S1). We calculated percentages of land cover types at multiple radii from our focal fragments (i.e. fragment centroids) from 100 m until 500 m radius in 50 m intervals, based on reported spatial scales at which bees and butterflies perceive their environment (Gathmann and Tscharntke, 2002; Steffan-Dewenter and Tscharntke, 2002; Stevens et al., 2013; Westphal et al., 2006). The mapped land cover types were: oilseed rape, grainfield, maize, other crops, forest open, forest closed, field margin, hedgerow, pasture, calcareous grassland, orchard, settlements, water bodies, streets, grassroads and bare soil. We tested the effect of arable land (mainly composed of oil-seed-rape, wheat and maize plantations), semi-natural habitat (including calcareous grasslands, orchards, hedgerows, field margins and flower strips) and the Shannon diversity of cover types, on site centrality (see section Statistical analyses). To choose the optimal scales at which these variables had the strongest effects on fragment centrality, we compared linear models at different spatial scales, and chose the scale with the highest predictive value, using the corrected Akaike information criterion for small samples (AICc). Shapefiles of land use were constructed using ArcGis 10.5.1 and all statistics were performed in R (R Development Core Team 2019).

Field data collection

Each calcareous grassland was visited three times per year in order to capture the succession of flower visitors (hereafter pollinators) and wildflower species throughout the season. We established seven observation plots in each site, totalizing 1218 observations of 10 min each. Surveys were carried out from 9:00 to 17:00 on days with a minimum temperature of 15 °C and at least 50% clear sky, or with a minimum temperature of 18 °C in any sky condition (van Swaay et al., 2012). Sites were surveyed at different times of the day to avoid any potential confounding effect of daytime.

Observation plots were circular (3 m radius, 28.3 m^2) and were established in flower-rich areas. Within these, all interactions between pollinators (butterflies, Lepidoptera: Papilionoidea; burnet moths, Lepidoptera: Zygaenidae; and bees, Hymenoptera: Apiformes) and flowering plants that occurred in a ten-minute period were registered. A visit by a pollinator was considered to be an interaction as soon as the insect touched the plant reproductive organs. Pollinators not easily recognizable at a distance were captured with a sweep net and photographed or collected for later identification by taxonomists. The timer was paused while handling insects. We excluded interactions involving *Apis mellifera* as the presence of this species in the region is solely related to the existence of bee keepers in the surroundings. *A. mellifera* interactions accounted for 1181 from a total of 8114 interactions registered and were present in all sites (range 1-166 *A. mellifera* interactions per site).

Plant-pollinator traits

Plants and pollinators were classified according to their life-history traits. Habitat specialization followed Piqueray et al. (2011) for plants, Jauker et al. (2013) and Hopfenmüller et al. (2014) for bees, and van Swaay (2002) and Brückmann et al. (2010) for butterflies. Body length values for bees were taken from Westrich (2018) and wing length values for butterflies were taken from Sterry and Mackay (2004). All values were standardized to make them comparable by subtracting the mean and dividing by the standard deviation of each group. Butterflies were considered large whenever their wing length was equal or larger than 16 mm (median wing length of butterflies), otherwise they were classified as small. On the other hand, bees were considered large when having a body length of 10 mm or more (median body length of bees) and were otherwise considered small (Fig. S2).

Metanetwork structure

A metanetwork was built by pooling the 29 calcareous grasslands into an a*ij* adjacency matrix, in which *i* are the studied sites and *j* the pairwise plant-pollinator interactions. First, we characterized the overall structure by calculating: (1) pollinator richness, plant richness and plant-pollinator interaction richness; (2) connectance: here defined as the realized proportion of plant-pollinator interactions per fragment regarding all possible interactions at the metanetwork level (Dunne et al., 2002); (3) modularity: here, the organization in sub-groups of fragments and interactions that are highly connected among themselves but less with other sub-groups; estimated using the DIRTLPAwb+ algorithm (Beckett, 2016).

Second, we estimated the centrality (Freeman, 1978; González et al., 2010) of the metanetwork nodes by calculating: (4) interaction degree, as the number of fragments in which a given interaction occurs; (5) interaction weighted degree, as the frequency of an interaction across all fragments; (6) fragment degree, as the number of unique pairwise interactions that a given fragment holds (i.e. interaction richness per site); (7) fragment weighted degree, as the frequency of interactions that a given fragment holds (i.e. interaction frequency per site).

All network metrics were calculated using the “bipartite” package in R (Dormann et al., 2008).

Statistical analyses

First, we assessed the significance of the metanetwork connectance and modularity against independent null models that constrain network size while randomizing the distribution of links among rows and columns, but holding the marginal totals constant (Dormann et al., 2009). That is, fragments maintain the same number of interactions in the null models, and interactions maintain the same number of fragments in which they occur. We obtained the mean and standard deviation of 100 iterations of each null model to test against the observed values of each corresponding metric (i.e. obtaining their z-scores). In a post hoc analysis we used linear and generalized linear models to explore local (fragment area and connectivity) and landscape (diversity of cover types) level effects on the number and proportion of single-fragment interactions per fragment.

Second, we tested whether species traits affected the centrality of plant-pollinator interactions (i.e. interaction degree and interaction weighted degree) using generalized linear mixed models. Specifically, we tested for the effects of the plant and pollinator habitat specialization, as well as pollinator size and guild (i.e. bumblebee, solitary bee or butterfly), on the centrality of the interactions they perform. Our full models included the mentioned explanatory variables, all their two-way interactions, the plants’ and animals’ active period regarding season (categorical with three levels: Spring, Summer or Spring and Summer) and number of months active. Furthermore, we included plant’s and animal’s identity as crossed random intercepts.

Finally, we tested whether the previously described fragment and landscape traits affected the centrality of the calcareous grassland fragments. Specifically, we tested the effects of (log) fragment area, (log) connectivity index and the Shannon index of cover types (hereafter, landscape diversity). Percentage of semi-natural habitat was excluded from the analyses as it was correlated with fragment area (Pearson's corr = 0.66, $P < 0.001$) and with landscape diversity (Pearson's corr = 0.51, $P = 0.004$).

We used a truncated negative binomial distribution and the “glmmTMB” package in all centrality models (Magnusson et al., 2017). We selected the minimum adequate models using backwards model selection with likelihood ratio tests. All non-significant explanatory variables ($P > 0.05$) were sequentially removed. Post-hoc tests were performed with the “lsmeans” package (Lenth, 2017). All network and statistical analyses were performed in R (R Development Core Team 2019).

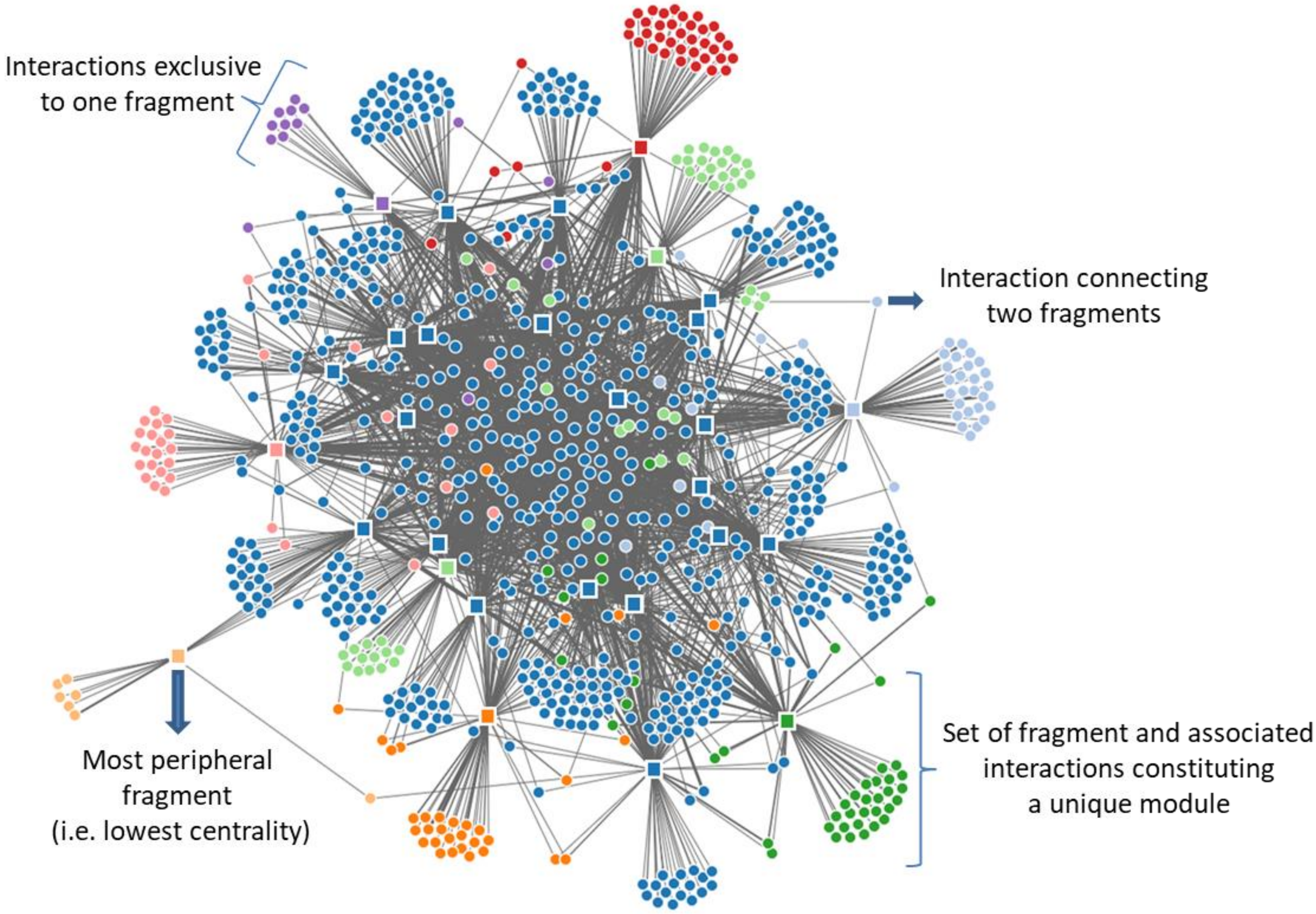
Results

Metanetwork structure

The metanetwork had a total of 6936 plant-pollinator interaction events from a pool of 842 unique pairwise plant-pollinator combinations among 131 plant species and 118 pollinator species on 29 calcareous grassland fragments (Fig. 1). From those, 4722 (68.1%) plant-pollinator interactions occurred among 46 butterfly species and 99 plant species, comprising a total of 474 unique pairwise plant-butterfly interactions (56.3%). On the bees’ side, we found 12 bumblebee species interacting 1891 (27.3%) times with 89 plant species, totalizing 214 unique pairwise plant-bumblebee interactions (25.4%). In addition, we found 320 (4.6%) interactions among 60 solitary bee species and 50 plant species, involving 154 unique pairwise plant-bee interactions (18.3%). On average, each fragment comprised 28.2 ± 6.7 (mean ± s.d.) pollinator species, 22.3 ± 5.2 plant species and 71.5 ± 21.7 unique pairwise interactions.

Overall, the metanetwork was significantly less connected ($C = 0.08$, $P < 0.001$) and more modular ($M = 0.39$, $P < 0.001$) than expected from null models (Fig. S1). The modular structure was organized around 17 modules, with an average of 1.7 fragments and 49.5 unique interactions per module.

a)



Interactions exclusive to one fragment

Interaction connecting two fragments

Set of fragment and associated interactions constituting a unique module

Most peripheral fragment (i.e. lowest centrality)

b)

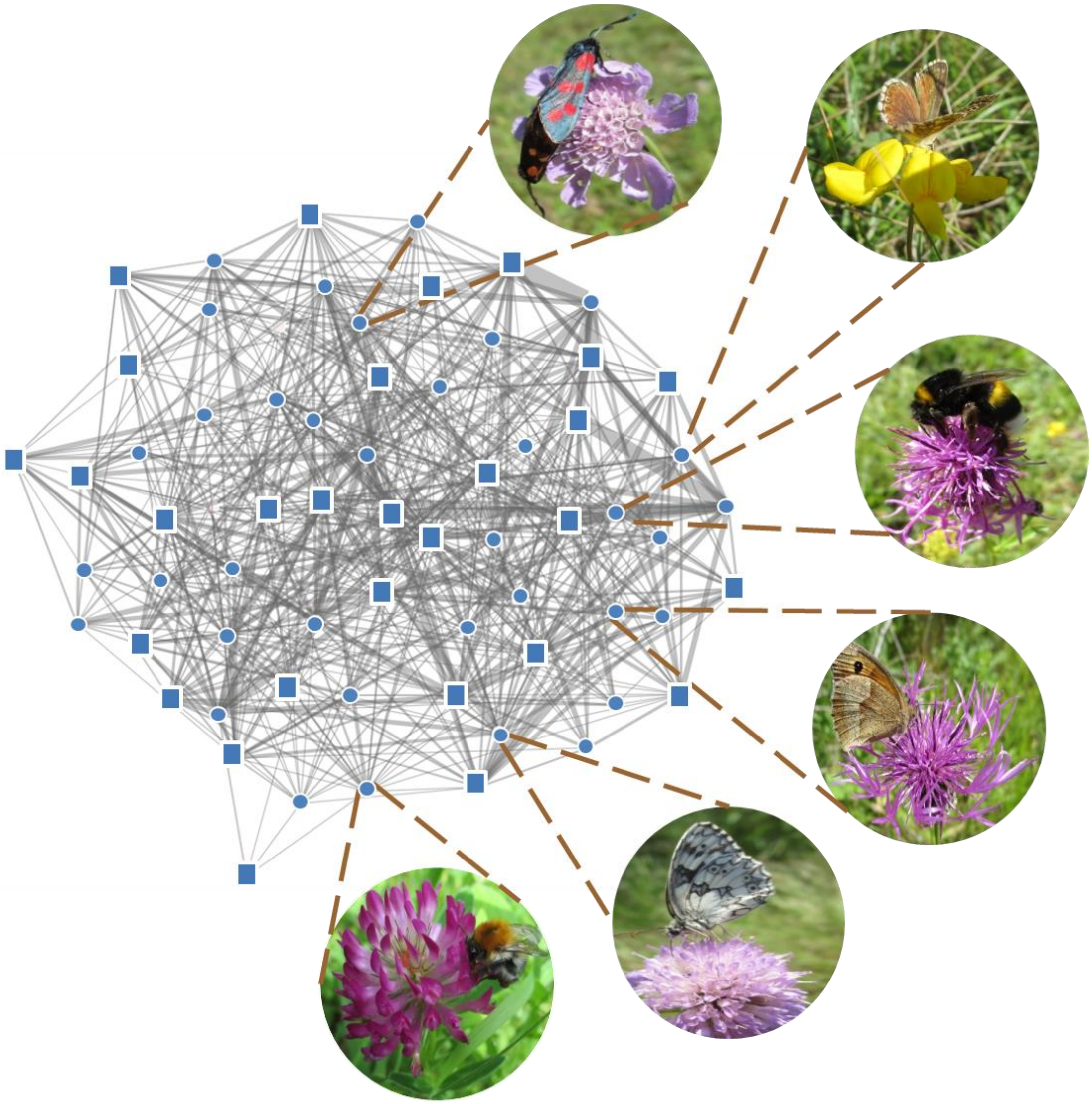
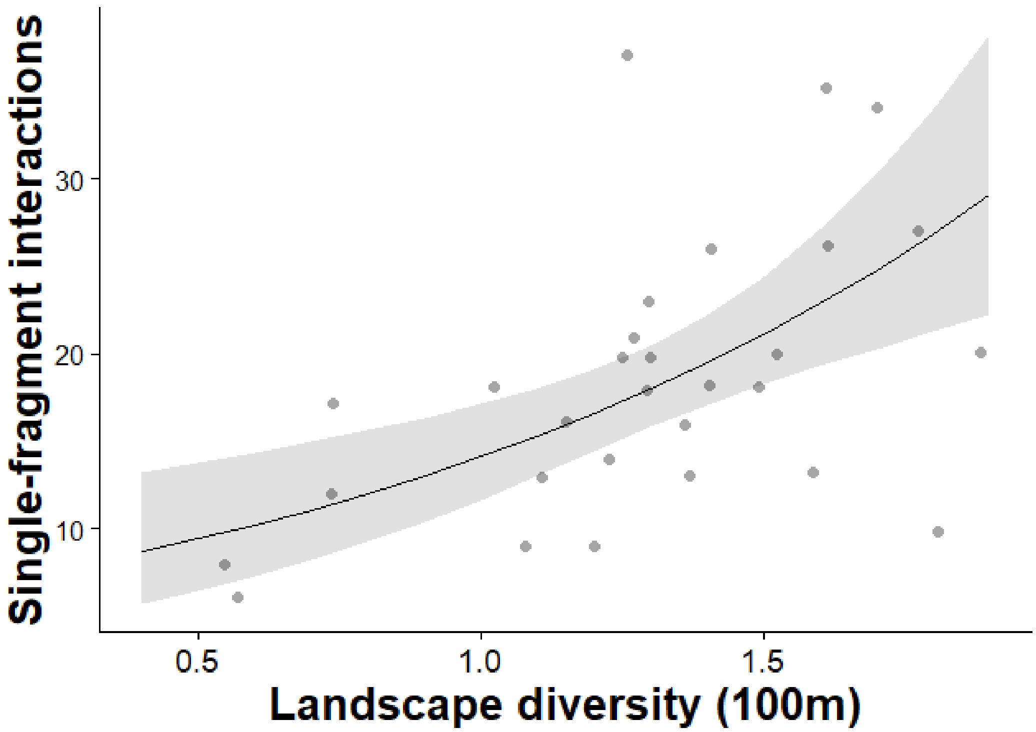


Figure 1. a) The plant-pollinator metanetwork structure of the calcareous grassland fragments. Circles indicate unique pairwise combinations of plant and pollinator species that perform pollination interactions (n = 842) and squares represent the studied sites (n = 29). Interactions occurring in at least two sites form links connecting them. The thickness of links (gray lines) is proportional to interaction frequency (range 1-254). Colors represent metanetwork modules based on the Walktrap community-finding algorithm (igraph package). This algorithm indicates the presence of sub-graphs that constitute a distinctive community. Nodes with greater centrality occur in the central positions of the graph based on the "gravitational force" on degree (Bannister et al., 2013). b) Sub-graph of the metanetwork, zooming on the core plant-pollinator interactions (here those present in more than 10 sites).

Single-fragment interactions

Only 305 (36.2%) unique pairwise plant-pollinator interactions occurred in at least two fragments, but these made up for the majority of observed plant-pollinator interactions (6171, or 89%). This means that more than half of the unique plant-pollinator combinations were rare and local (i.e., occurred in a single fragment). Landscape diversity had a positive effect on the number of single-fragment plant-pollinator interactions ($X^2 = 12.25$, $P < 0.001$, Fig. 2a) and a negative effect on the proportion single-fragment interactions respect to all unique interactions in a certain fragment ($F = 8.08$, $P = 0.008$, Fig. 2b). Fragment area and fragment connectivity did not have significant effects on the number of single-fragment interactions or their proportion respect to all interactions (Table S3).

a)



b)

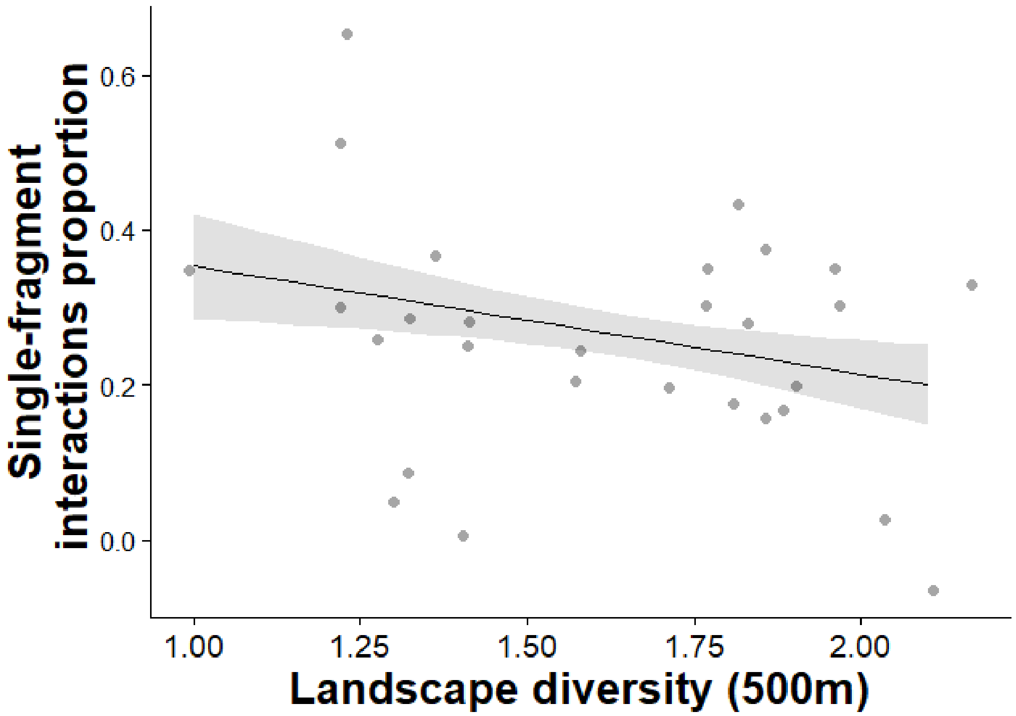


Figure 2. Relationship between a) the number of single-fragment interactions (i.e. those that occur in only one fragment from the 29 fragments studied) and b) the proportion of single-fragment interactions, with landscape diversity. The proportion is the number of single-fragment interactions divided by interaction richness in a specific fragment.

Interaction centrality and biological traits

Plant habitat specialization was a significant predictor of interaction degree ($X^2 = 12.78$, $P < 0.001$, Table S2). Specifically, interactions involving habitat specialist plants had significantly higher degree than those involving habitat generalist plants (Fig. 3a). Additionally, pollinator identity and the interaction between plant habitat specialization and pollinator size were found to be significant predictors of interaction weighted degree (Table S2). Specifically, interactions involving habitat specialist plants and large-bodied pollinators had higher weighted degree than those involving habitat generalist plants and small-bodied pollinators ($X^2 = 5.28$, $P = 0.021$, Fig. 3b). Moreover, interactions performed by butterflies ($t = -2.50$, $P = 0.034$) and bumblebees ($t = -2.75$, $P = 0.016$) had higher weighted degree than those performed by solitary bees (Fig. 3b).

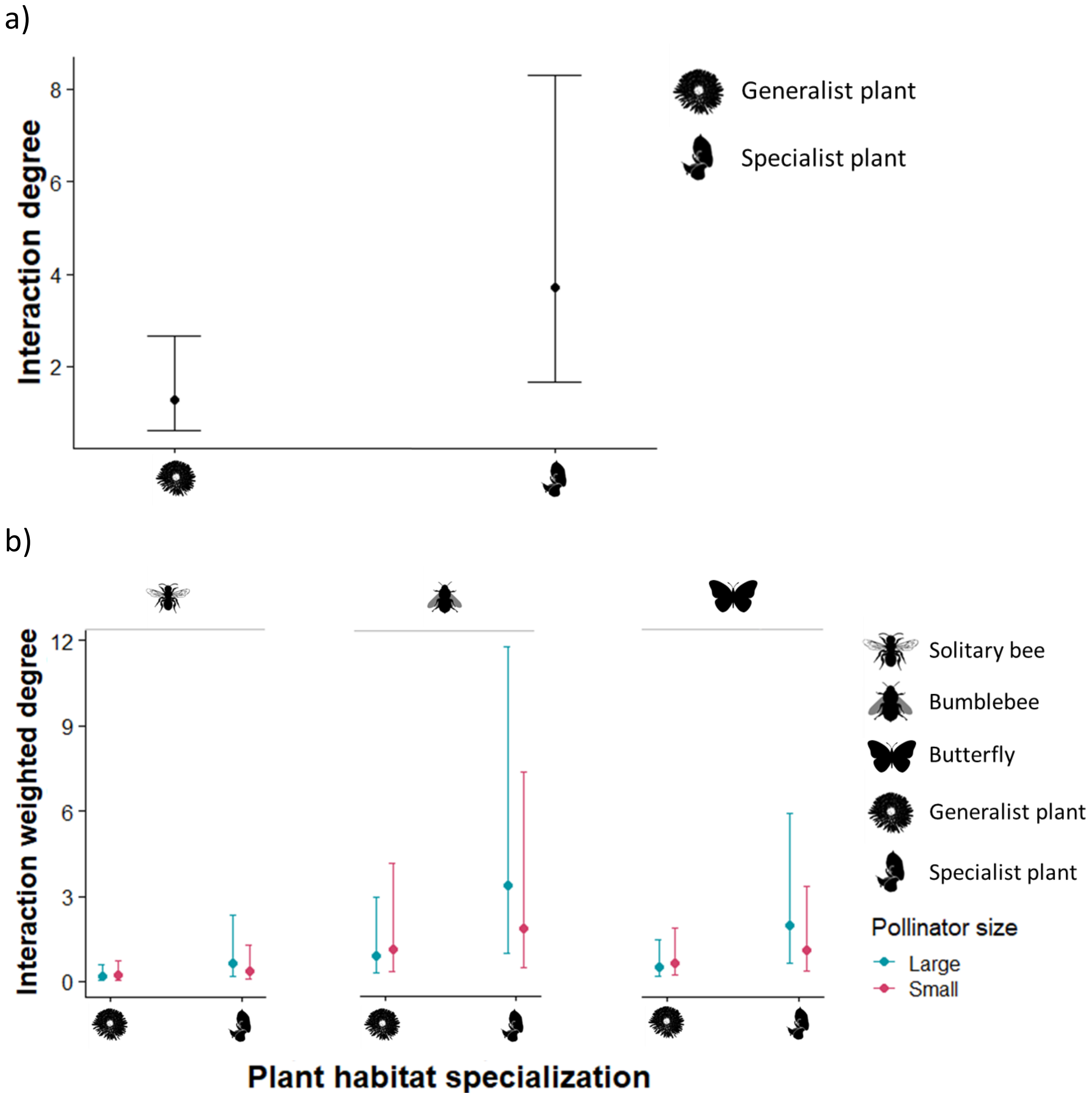
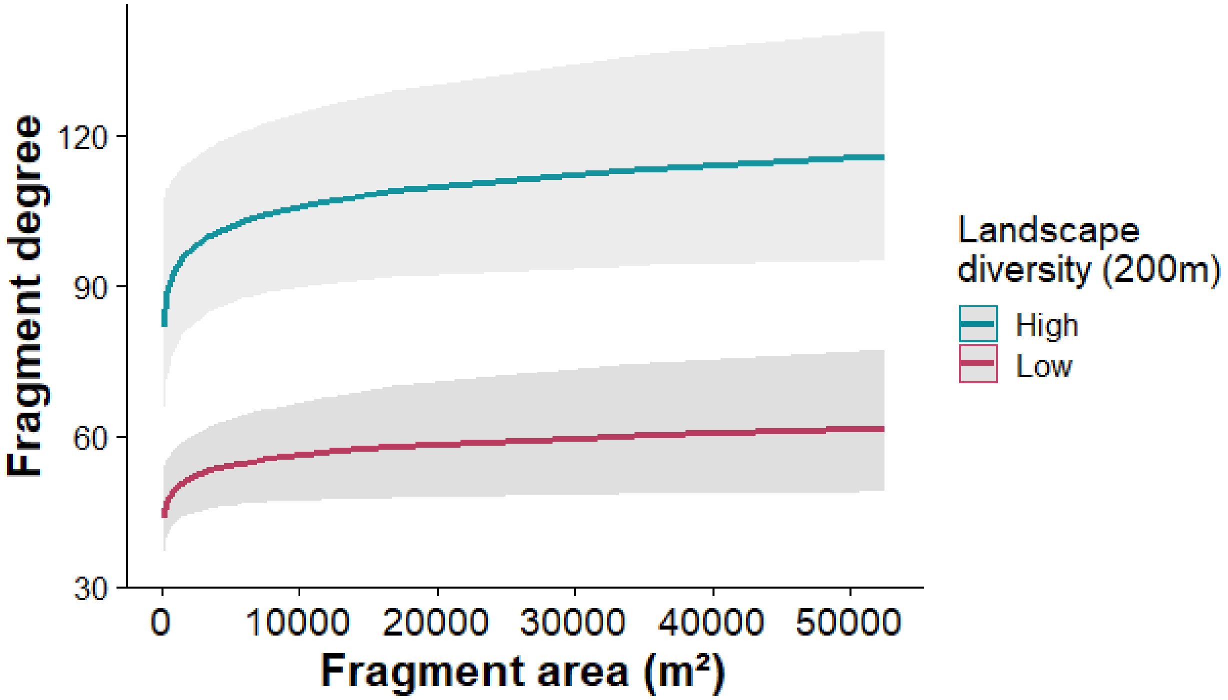


Figure 3. Relationship between a) interaction degree (i.e. number of fragments on which a specific plant-pollinator interaction pair occurs) with plant habitat specialization and b) interaction weighted degree (i.e. interaction frequency across all fragments) with plant habitat specialization, pollinator size and pollinator identity. Bars represent 95% confidence intervals.

Fragment centrality and landscape features

Larger calcareous grassland fragments were more central in the metanetwork, as indicated by the positive effect of fragment area on fragment degree ($X^2 = 4.24$, $P = 0.04$) and fragment weighted degree ($X^2 = 11.40$, $P < 0.001$, Fig. 4). In addition, landscape diversity had also a positive effect on fragment centrality as evidenced by increased fragment degree ($X^2 = 4.67$, $P < 0.001$) and weighted degree ($X^2 = 12.54$, $P < 0.001$). Conversely, fragment connectivity and arable land had no significant effects on fragment degree ($X^2 = 0.95$, $P = 0.33$; $X^2 = 1.27$, $P = 0.26$) nor on fragment weighted degree ($X^2 = 0.013$, $P = 0.91$; $X^2 = 2.37$, $P = 0.12$).

a)



b)

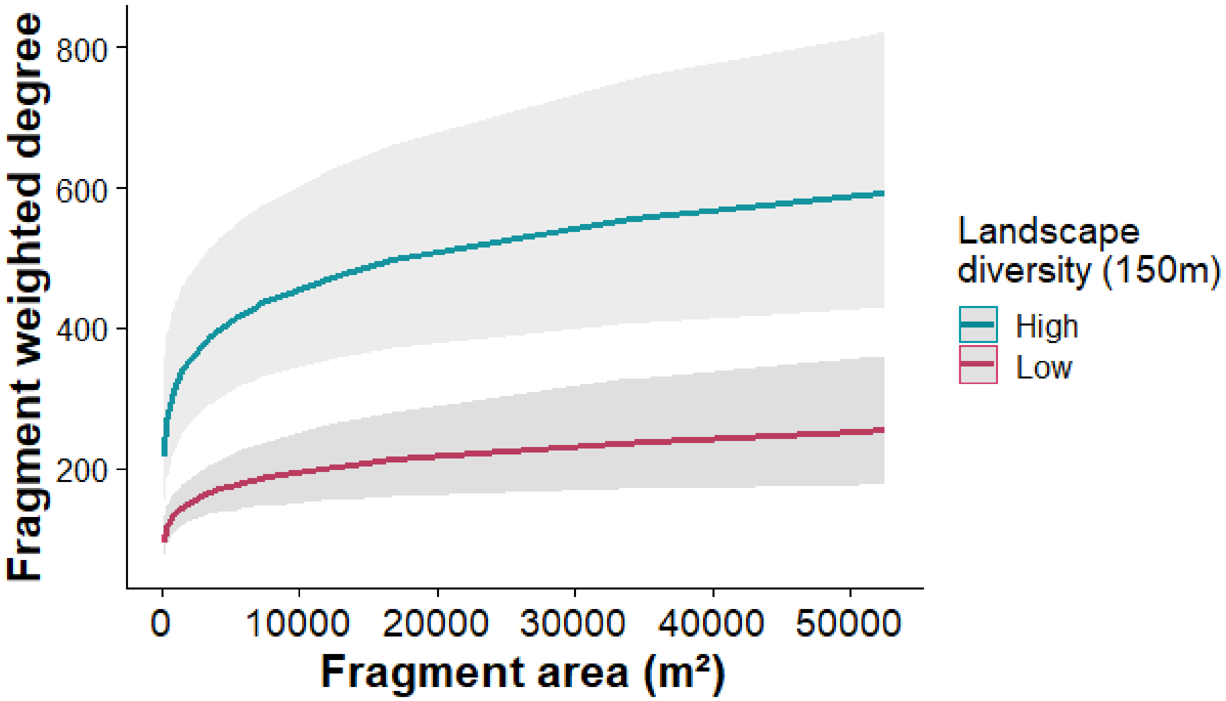


Figure 4. Effects of calcareous grassland fragment size and landscape diversity (here calculated as the Shannon diversity index of cover types) on a) interaction richness and b) interaction frequency. Grey areas represent 95% confidence intervals.

Discussion

Here we analyzed a plant-pollinator metanetwork along a habitat fragmentation gradient over a two-years period. We found that plant-pollinator interactions involving habitat specialist plants and large-bodied pollinators were the most central in our system. Bumblebees and butterflies established more central interactions than solitary bees. Moreover, large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality, while small fragments harbored a high share of unique interactions not found on larger fragments.

Plant-pollinator metanetwork structure

As predicted, the plant-pollinator metanetwork was more modular and less connected than expected by chance. The different modules within the metanetwork appear to reflect the presence of unique pools of interacting species in different fragments of calcareous grassland where local species tend to establish specific associations among each other. Interestingly, compared to the only previous study applying the same methodology, a plant-frugivore metanetwork in the Brazilian Atlantic Forest (Emer et al., 2018), our plant-pollinator metanetwork was less modular. This might be explained by two reasons, namely the difference in the biology of the systems and the difference in scale. The extent of the study region and the size of the fragments were smaller in our study. This is related to the larger size of the Brazilian Atlantic Forest fragments compared to the calcareous grasslands fragments in our region (Ribeiro et al., 2009). Considering that some large-bodied pollinator species should be able to actually cross the matrix and reach some of the nearest neighboring grasslands in our system (Steffan-Dewenter and Tscharntke, 1999), the present study constitutes a more applied version of the metanetwork concept than in the case of (Emer et al., 2018), where the chance of a bird reaching a neighboring studied fragment was small (minimum distance among studied fragments was 26 km). The pollinators recorded in our study may thus act as mobile links among fragments reducing modularity, which is supported by the strong core of central interactions in our metanetwork (Fig. 1b).

Network theory predicts that modularity can reduce the sensitivity of interconnected systems to perturbations as these will not easily spread to the whole network (Dormann et al., 2017). However, modularity has also been associated to reduced stability in mutualistic networks (Thébault and Fontaine, 2010). A highly modular network depends on the presence of connector species (i.e. species establishing interactions across modules) to maintain its integrity and prevent it from breaking apart into separate modules. Once modules are disconnected, they become smaller independent networks on their own and consequently become more prone to collapse given their smaller size and higher sensitivity to stochastic events (Traveset et al., 2017; Tscharntke et al., 2002).

As established by (Olesen et al., 2007), only a small proportion of species are structurally important to a network, however, when these are lost, cascades of extinctions might occur, leading to a general collapse of the network. In our case, the species involved in the interactions showed in Figure 1b are the most important to the metanetwork, as they are the key connections among otherwise segregated modules. Interestingly, all pollinator species involved in the most central interactions of our system were habitat generalists (except for *Polyommatus coridon*), but most plant species were habitat specialists, i.e. characteristic species of the studied calcareous grasslands. This means that in addition to protecting habitat specialist species of calcareous grasslands by targeted management strategies (Filz et al., 2013), biodiversity-friendly measures in the matrix, such as flower strips, hedgerows and crop diversification, could help to protect central pollinators acting as mobile links (Kleijn et al., 2006; Sirami et al., 2019). Protecting habitat generalist pollinators, in turn, maintains the cohesiveness of the metanetwork, thereby also protecting habitat specialist plant species (directly) and habitat specialist pollinator species (indirectly). In other words, conservation measures aiming at this core group of generalist species may indirectly help to conserve also specialist species. Furthermore, protecting *Polyommatus coridon* might also be possible by including *Hippocrepis comosa* into seed mixtures of agri-environmental schemes (Batáry et al., 2015), as it is its solely larval food plant in western Europe (Schmitt, 2015).

Unique pairwise plant-pollinator interactions

All unique pairwise interactions, including single-fragment interactions, increased with landscape diversity (Fig. 2a and Fig. 4a), but the proportion of single-fragment interactions decreased with it (Fig. 2b), i.e. the rate at which all unique pairwise interactions increase with landscape diversity is higher than that of single-fragment interactions. This result may be related to the high amount of interactions established by large-bodied habitat generalist butterflies. As a consequence of their high mobility, these butterflies are expected to connect the metanetwork by reaching multiple calcareous grassland fragments. Hence, differently from bees, that are spatially attached to their nests, the majority of the interactions established by large-bodied habitat generalist butterflies may not be restricted to a single fragment.

Interaction centrality and species traits

Our results show that interactions between habitat specialist plants and pollinators are fundamental to the metanetwork (Fig. 3). Despite representing only 17.6% of the plant species found and despite being involved in only 38.9% of all unique pairwise interactions, interactions conformed by habitat specialist plants and pollinators were more central than those involving habitat generalist plants. Hence, habitat specialist plants in calcareous grasslands establish interactions that provide cohesiveness and stability to the metanetwork, highlighting the importance of their conservation. Contrastingly, although habitat generalist plants establish numerous interactions, those interactions do not belong to the core interactions of the plant-pollinator metacommunity in calcareous grasslands. A notable exception is the habitat generalist plant *Knautia arvensis*, which established many central interactions particularly with large-bodied butterflies. Whether this is a consequence of interaction rewiring due to the absence of the related habitat specialist *Scabiosa columbaria* remains to be studied.

As expected, large-bodied pollinators established more central interactions than small-bodied ones. Movement capacity is positively correlated to body size (Stevens et al., 2014). Large pollinators have larger foraging ranges (Greenleaf et al., 2007), which may allow them to reach a higher amount of calcareous grassland fragments, increasing the number of plant species available with which they can potentially interact. From the plant species perspective, it is reasonable for habitat specialist plants to specialize more on large-bodied pollinators that are not constrained to the focal fragment and can eventually disperse their pollen at greater distances. This assumption is supported by our finding that the core of the most central interactions is in fact formed by habitat specialist plants and large-bodied pollinators (Fig. 1b and Fig. 3b). Whether this pattern is a consequence of habitat fragmentation or a characteristic feature of calcareous grasslands needs to be further explored, for example, by analyzing plant-pollinator interactions exclusively in large continuous calcareous grasslands.

Solitary bees were found to be involved in interactions of lower centrality than those of butterflies and bumblebees. In comparison to social bees, such as bumblebees, solitary bees typically have much more restricted movement capacity (Gathmann and Tscharntke, 2002; Westphal et al., 2006). Also, bumblebees establish numerous interactions with both specialist and generalist plants given their high abundance favored by their social life in colonies (Hass et al., 2019; Leidenfrost et al., 2020). Nonetheless, all bees are somehow attached to the nest position to which they need to come back regularly, independent of whether they are social or solitary species. Butterflies, on the other hand, are not attached to a nest and therefore can potentially move longer distances than bees throughout their lives. In particular, this may be the case for large-bodied generalist butterflies, as small specialist butterflies have a much smaller capacity and probability to cross the matrix and reach other fragments (Habel et al., 2020).

Fragment centrality and landscape traits

As expected, habitat fragment size had a positive effect on fragment degree and on fragment weighted degree (Fig. 4). This result is not surprising given that larger fragments tend to harbor larger species populations and consequently have a higher probability of interaction establishment. Although larger fragments might favor the presence of area-sensitive, monophagous and rare specialist species (Rösch et al., 2015; Steffan-Dewenter and Tscharntke, 2002), it has been demonstrated that in a fragmented landscape many small fragments harbor a larger amount of habitat specialist species than a single large fragment of the same area (Rösch et al., 2015; Tscharntke et al., 2002). Given the high amount of unique interactions involving habitat specialist species that were restricted to small fragments, a similar importance of small fragments seems to hold for species interactions. Therefore, it needs to be highlighted that although large fragments are fundamental for the metanetwork stability and cohesiveness, small fragments contribute many unique pairwise interactions that cannot be conserved by only focusing on large fragments.

Interestingly, fragments embedded in landscape with high land cover diversity exhibited higher fragment centrality, meaning that these fragments had higher numbers of unique and total plant-pollinator interactions. This finding has important implications for conservation as it highlights the essential role of not only protected habitats, but also the surrounding landscape to protect plant-pollinator interactions. A diverse landscape multiplies the number of resources available for pollinators, such as nectar, pollen and nesting opportunities, and therefore contributes to their persistence in the landscape (Landis et al., 2005). Furthermore, the presence of linear elements such as flower strips and hedgerows can facilitate animal movement through the landscape and between fragments (Davies and Pullin, 2007; Holzschuh et al., 2009; Klaus et al., 2015; van Geert et al., 2010). The ability of large-bodied specialist butterflies, such as *Polyommatus coridon*, to cross the matrix and reach surrounding calcareous grasslands needs to be further explored. However, some studies have found that a small proportion of individuals of this species can cross matrix gaps of a few hundred meters and exceptionally a few kilometers (Schmitt et al., 2006; Schmitt, 2015). The protection of this particular butterfly species and the interactions it establishes appears fundamental for the integrity of the metanetwork system.

Conclusion

We analyzed a plant-pollinator metanetwork along a habitat fragmentation gradient over a two-year period. We identified the most central plant-pollinator interactions and habitat fragments in the metanetwork and traits associated to their centrality. We found that plant-pollinator interactions involving habitat specialist plants and large-bodied pollinators were the most central and thus structurally important in our system. Furthermore, bumblebees and butterflies established more central interactions than solitary bees, highlighting the importance of social bees and mobile butterflies for maintaining plant-pollinator interactions in fragmented landscapes. Importantly, large fragments embedded in landscapes with high land cover diversity exhibited the highest centrality. Conserving large grasslands fragments and diversifying the agricultural matrix is thus fundamental for the cohesiveness and stability of plant-pollinator metanetworks. In particular, crop diversification and conservation schemes such as agri-environmental schemes may promote metanetwork stability. However, although large fragments were the most central in our system, small fragments also need protection as they harbor a high proportion of unique interactions not found in large fragments.

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Supplementary material

Connectivity index based on Hanski et al. 1994

$$I = \sum e^{-dij} A_j$$

Aj is the size in m² of neighbouring calcareous grasslands and dij is the distance in km from the neighbouring grassland j to the study site I (following Krauss et al. 2004). The 2 km radius was chosen to capture the maximum biologically meaningful distance for the largest pollinators (see also Krauss et al. 2010). Larger values of "I" indicate higher connectivity (Table S1).

Table S1. Landscape metrics for each study site: Area in m², management, Shannon diversity index of cover types in a 200m radius and connectivity index.

Study site	Habitat area (m²)	Management	Shannon index (200 m)	Connectivity index
Huhnsberg	52557	Grazing	1.50	52162
Mühlenberg	50673	Grazing	1.89	15805
Aschenburg	35479	Grazing	1.45	19917
Ellershagen	33186	Grazing	0.68	7145
Lengender Burg	16804	Unmanaged	1.68	4914
Dehnerberg	12724	Grazing	1.85	3671
Mackenrodt	11612	Mowing	1.71	637
Burgbreite	7641	Grazing	1.28	7335
Gladeberg	7288	Grazing	1.19	3814
Weinberg	6641	Grazing	1.71	25941
Hackelberg	5823	Mowing	1.58	28463
Am Graben	5535	Unmanaged	1.93	1186
Tiefetal	4132	Grazing	1.36	4617
Südlicher Riesenberg	3535	Unmanaged	1.76	6103

Ossenfelder Bahndamm	3504	Grazing	1.86	1111
Kleiner Knull	3467	Grazing	1.55	8083
Kuhberg	3465	Grazing	1.78	10797
Eschenberg	1861	Unmanaged	1.36	306
Vor dem roten Berge	1462	Unmanaged	1.23	21676
Auf dem Klee	778	Unmanaged	1.45	25575
Schweineberg	701	Mowing	1.70	114
Am Hopfenberge	693	Unmanaged	1.34	19917
Unter den Niederwiesen	406	Mowing	0.49	5332
Emme	381	Unmanaged	0.85	10015
Gieseberg Süd	353	Unmanaged	1.71	15953
Mühlenberg 2	228	Mowing	1.12	47366
Zipfel am Lindenberg	227	Unmanaged	1.37	10518
Lieseberg	144	Unmanaged	1.24	2943
Heikenrott	82	Mowing	1.28	6152

Table S2. Minimum adequate models for interaction and fragment degree centrality selected with likelihood ratio tests (via “drop1”). Significance levels: ***p<0.001. **p<0.01, *p<0.05

Response variable	**Model**	**Fixed effects**	**LRT (Chi^2)**	***P***
Interaction degree	1	Months active plant	42.30	< 0.001***
		Months active pollinator	24.80	< 0.001***
		Plant habitat specialization	12.78	< 0.001***
Interaction weighted degree	2	Pollinator identity	8.74	0.012*
		Months active plant	24.86	< 0.001***
		Months active visitor	6.64	0.010*
		Plant habitat specialization: Pollinator size	5.28	0.021*
Fragment degree	3	(log) Fragment area	4.24	0.040*
		Landscape diversity (200 m)	16.04	< 0.001***
Fragment weighted degree	4	(log) Fragment area	11.40	< 0.001***
		Landscape diversity (150 m)	12.54	< 0.001***

Table S3. Full and minimum adequate models for unique interactions and unique interactions' proportion. Minimum adequate models were selected with likelihood ratio tests (via "drop1"). Significance levels: ***p<0.001. **p<0.01, *p<0.05

Response variable	**Model**	**Fixed effects**	**LRT**	***P***
Unique interactions	Full	Landscape diversity (100 m) (log) Fragment area (log) Connectivity Index	9.34 0.092 0.60	0.002** 0.76 0.44
Unique interactions	Min	Landscape diversity (100 m)	12.52	< 0.001***
Unique interactions' proportion	Full	Landscape diversity (500 m) (log) Fragment area (log) Connectivity Index	6.88 0.88 2.30	0.014* 0.36 0.14
Unique interactions' proportion	Min	Landscape diversity (500 m)	8.08	0.008**

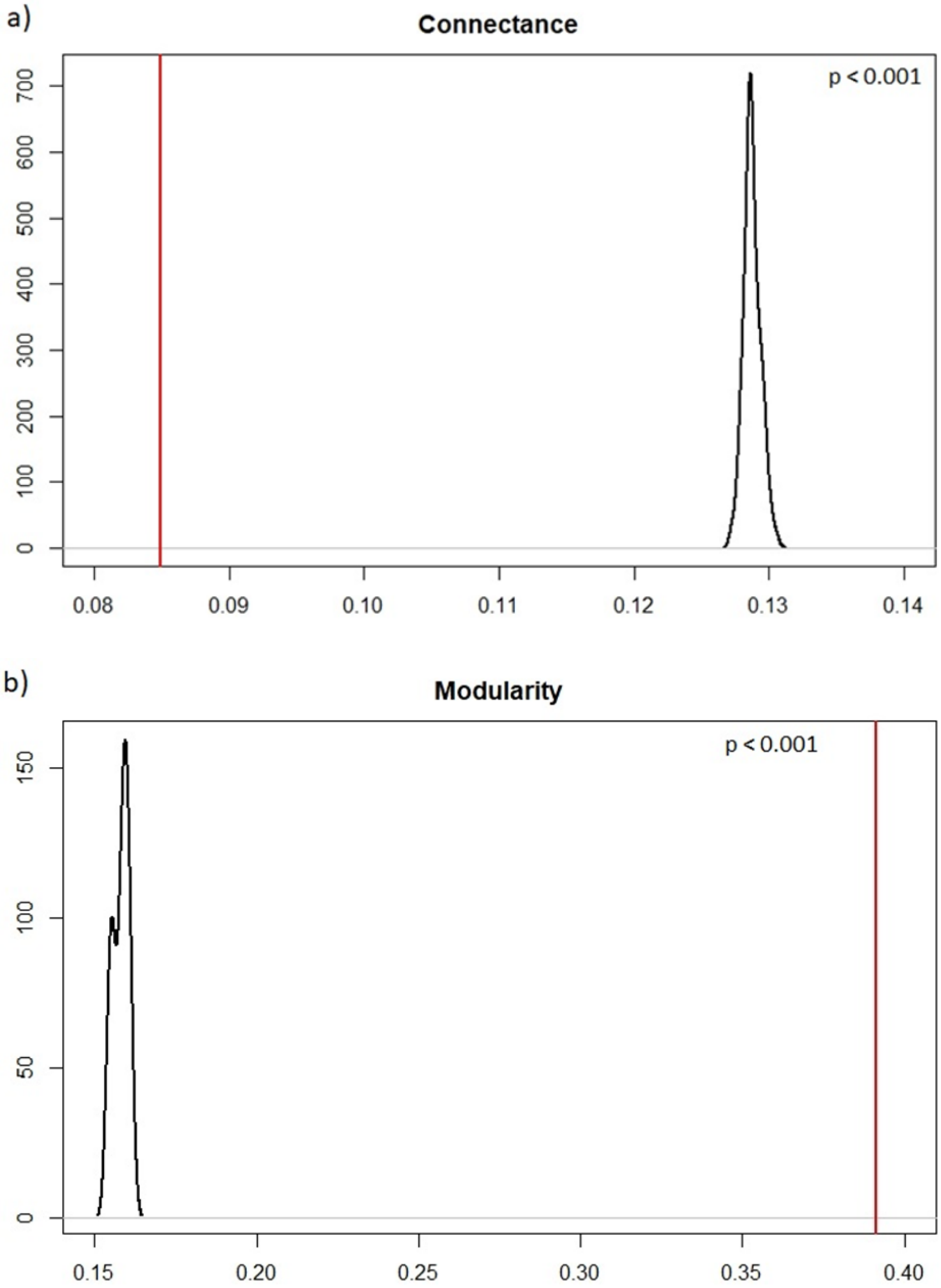


Figure S1. Connectance (a) and modularity (b) of our plant-pollinator metanetwork (red vertical line) compared to null models (grey distribution).

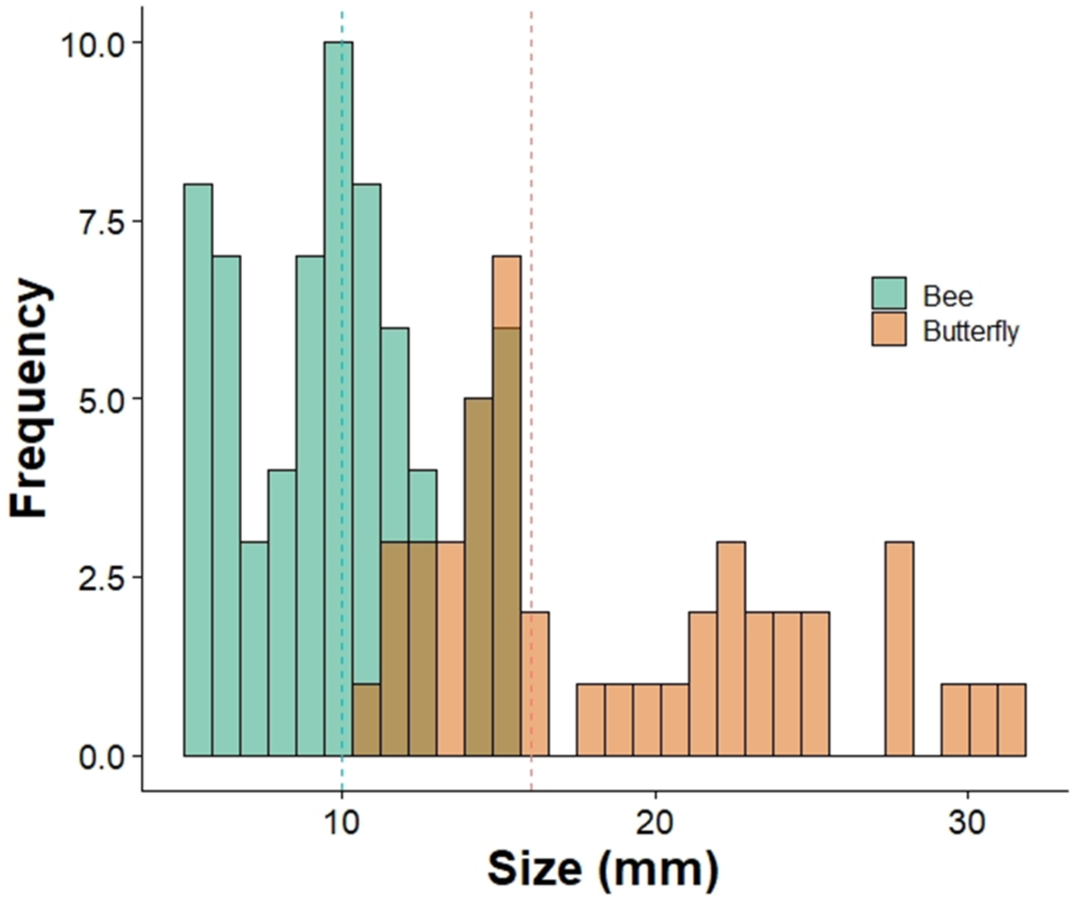
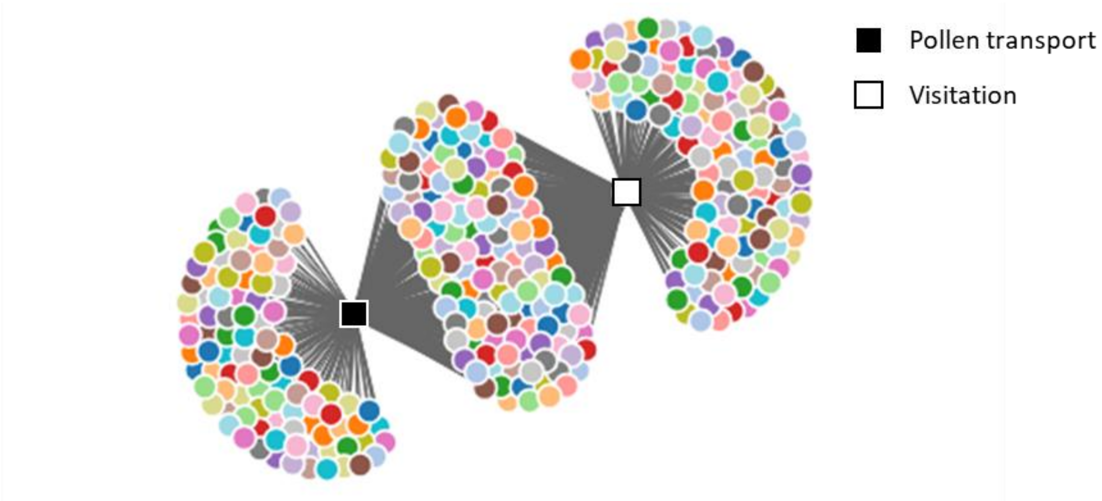


Figure S2. Histogram of bees' and butterflies' sizes (body size and wingspan, respectively. The dashed vertical lines represent the median size for each group.

Chapter 3

Pollination networks in fragmented landscapes are more specialized for pollen transport than flower visitation



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Article in preparation

Abstract

Plant-pollinator networks are key to the functioning of natural and human-modified ecosystems. Habitat fragmentation and landscape simplification effects on mutualistic networks have been studied to some extent, but studies comparing pollination networks based on flower visitation and those based on pollen loads across landscape gradients are missing. Here we contrasted visitation with pollen transport networks in 29 fragments of calcareous grassland, a highly endangered biodiversity hotspot. We found that only 37% of the total unique pairwise interactions occurred in both types of networks, 28% of these were only registered through pollen load analyses and 49% of the observed flower-pollinator interactions did not translate into pollen transport. Network specialization was higher in pollen transport networks and was negatively related to the diversity of land cover types in the surrounding landscapes. The number of single-fragment interactions as well as the proportion of single-fragment interactions increased with landscape diversity in the pollen transport networks. Finally, at the metanetwork level, the most central plant and pollinator species are shared between the visitation and pollen transport metanetworks. In conclusion, our results reveal that flower visitation and pollen transport data give different, but complementary information, while none can be used as a surrogate of the other. Higher specialization of pollen transport networks indicates that network vulnerability could be higher than hitherto expected from visitation networks. Our results also reveal a surprisingly high number of rare pollen transport interactions, particularly in diverse landscapes, which would have been undetected in a classical flower visitation study.

Introduction

Plant-pollinator networks have been traditionally constructed using data on flower visitation (Ballantyne et al., 2015). However, in order for pollination to occur, viable pollen grains need to be transported from the anthers of a flowering plant to a receptive stigma of a conspecific. Therefore, the solely visitation of an animal to a flower is expected to be a poor predictor of its capacity as a pollinator (King et al., 2013). For instance, many flower visitors forage exclusively for nectar (e.g. most butterflies) and do not contact flower anthers; other species lack morphological traits to carry pollen and thus cannot act as pollinators (Genini et al., 2010; Stavert et al., 2016). Two methods have been proposed to overcome this challenge. First, stigmas and styles can be analyzed to identify pollen deposition after an animal visit (Emer et al., 2015). Yet, this method is extremely time-consuming and consequently prohibitive for landscape scale studies. Alternatively, flower visitors' pollen loads can be analyzed to check for their pollen transport capacity (Zhao et al., 2019). Although not as close to pollination as direct pollen deposition measures, this method can also provide valuable information regarding an animal capacity as a pollinator. Furthermore, given its relative simplicity, it is suitable for large scale studies.

Pollen transport networks have been recently constructed at singular sites and local scales (Alarcón, 2010; Gresty et al., 2018; Lopezaraiza-Mikel et al., 2007). However, landscape scale effects, and in particular, habitat fragmentation effects on plant-pollinator networks are essential to understand their dynamics under land use change (Grass et al., 2018; Xiao et al., 2016). In spite of this, to our knowledge, there is no study analyzing landscape scale effects on pollen transport networks over a gradient of habitat size and isolation. Originating from the concept of "multilayer" networks (Pilosof et al., 2017), metanetworks (i.e. a group of scattered local networks connected by species dispersal) are an emerging approach to study the consequences of habitat fragmentation on ecological networks at landscape and regional scales (González et al., 2018; Hagen et al., 2012). The identification of the most important species for metanetwork integrity can guide environmental policy and conservation efforts. A metanetwork can be constructed using habitat fragments and plant or pollinator species as the interacting units (i.e. nodes).

Node importance can be quantified through the concept of node centrality (Domínguez-García and Muñoz, 2015; Jordán, 2009). Central nodes are characterized by having the most detrimental effects on the integrity of a metanetwork once removed (e.g. most associated co-extinctions; González et al., 2010). Moreover, species traits can be related to species centrality in ecological networks (Morán-López et al., 2020). In particular, species body size and habitat specialization have been found to affect species' ecological roles and functions (Gathmann and Tscharntke, 2002; Grass et al., 2018; Westphal et al., 2006). Species traits can also determine the probability of an interaction being detected with flower visitation observations, pollen loads analyses or both. For example, given that social bees are usually more effective pollen vectors (sensu Freitas, 2013) and more abundant than solitary bees, interactions established by social bees should have a higher probability of occurrence in visitation and pollen transport networks simultaneously. Furthermore, habitat specialist plants, differently from habitat generalists, can have adaptations to maximize pollen dispersal through pollinators (Miller-Struttmann, 2013) and, hence, should also establish interactions with a higher probability of occurrence in both types of networks.

Here, we constructed pollination networks at the flower visitation and pollen transport levels, over a gradient of habitat fragmentation of European calcareous grasslands, a highly threatened biodiversity hotspot, characterized by a vast number of rare and endangered species (Habel et al., 2013). We compared the structure of local visitation and pollen transport networks in terms of network specialization and connectance. Furthermore, we explored fragmentation effects on them. To this end, we identified the most central species in both metanetworks and studied their functional traits (body size, habitat specialization). In addition, we aimed to analyze the differences and similarities among the observational and pollen loads data for the description of the plant-pollinator networks dynamics and to explore the consequences of the conclusions derived from both methods. Therefore, we analyzed which functional traits of the plant-pollinator interaction pairs relate to the probability of them occurring in the visitation and pollen transport networks. Finally, we studied the effects of landscape structure on the occurrence of single-fragment interactions in local networks.

We hypothesized that: (i) the specialization of local pollen transport networks will be higher than that of local visitation networks given that not all flower visitors are expected to carry pollen on their bodies; (ii) network specialization will decrease in larger and more connected habitats and also with landscape diversity, as the presence of more species should increase the probability of multiple interacting partners; (iii) due to many rare and ineffective interactions (i.e. interactions that contribute little to the plant reproductive success, sensu Freitas, 2013), a high number of interactions unique to the visitation and pollen transport metanetworks is expected; (iv) the most central species at the metacommunity level are expected to be the same in the visitation and pollen transport metanetworks, despite projected differences between network types; (v) the probability of interaction occurrence in both network types depends on pollinator identity (i.e. bumblebee or solitary bee) and plant habitat specialization; (vi) finally, we expect that the number and proportion of single-fragment interactions increases with landscape diversity and with habitat size and connectivity in both types of networks.

Methods

Study area

Data was collected from April until August 2018 on 29 calcareous grasslands in the surroundings of the city of Göttingen (Germany). These grasslands were selected in a previous study (Krauss et al., 2003a), from a larger regional pool (~300), to vary along independent gradients of size and isolation from other calcareous grasslands. Arable land and European beech (*Fagus sylvatica*) forests are the two main land use types in the region with 31% and 38% land cover, respectively (Krauss et al., 2003a).

Landscape metrics

We tested the effects of fragment size, fragment connectivity and landscape diversity of cover types on the structure of local fragment networks in terms of specialization and connectance and also on the number and proportion of single-fragment interactions per fragment. Fragment area was calculated with ArcGis 10.5.1 and ranged from 82 m² to 52557 m², excluding zones dominated by shrubs. Fragment spatial connectivity and the Shannon diversity of cover types (as a measure of landscape diversity) were calculated using the "landscapemetrics" package (Hesselbarth et al., 2019). For fragments' spatial connectivity we used a connectivity index developed by Hanski et al. (1994) and considered all calcareous grasslands in a radius of 2 km around the study grasslands (see SI for details). Larger values of this index indicate higher spatial connectivity (Table S1). The mapped cover types were: oilseed rape, grainfield, maize, other crops, forest open, forest closed, field margin, hedgerow, pasture, calcareous grassland, orchard, settlements, water bodies, streets, grassroads and bare soil. Shapefiles of land use were constructed using ArcGis 10.5.1 and all statistics were performed in R (R Development Core Team 2019).

Flower visitation data

We performed three rounds of sampling throughout the season in each calcareous grassland to capture the succession of flower visitors (hereafter, pollinators) and wildflower species. Seven observation plots of 10 min were established in each site. We followed a protocol established by van Swaay et al. (2012) to carry out our surveys. We collected data from 9:00 to 17:00 on days with a minimum temperature of 15 °C and at least 50% clear sky, or with a minimum temperature of 18 °C in any sky condition. To avoid any confounding effect of daytime sites were surveyed at different times of the day.

Our observational plots were established in flower-rich areas and were circular (3 m radius, 28.3 m^2). Within these, all interactions between bees (Hymenoptera: Apiformes) and flowering plants were registered. A visit by a bee was considered to be an interaction as soon as the insect touched the plant reproductive organs. Bees not easily recognizable at a distance were captured with a sweep net and photographed or collected for later identification by taxonomists. The timer was paused while handling insects. We excluded interactions involving *Apis mellifera* as the presence of this species in our region was solely related to the existence of bee keepers in the surroundings. *A. mellifera* interactions accounted for 334 from a total of 1499 interactions registered and were present in all sites (range 1-75 *A. mellifera* interactions per site). Bees were classified in solitary bees or bumblebees (hereafter, bee identity). All bumblebees are social and belong to the genus *Bombus spp.*. Within the group of "solitary bees", seven species present some degree of sociality but were grouped within the solitary bees because of the morphological and genetic similarities with these. The seven species are: *Andrena scotica* (communal), *Halictus confusus*, *Halictus rubicundus*, *Halictus tumulorum*, *Lasioglossum calceatum*, *Lasioglossum morio* and *Lasioglossum pauxillum*.

Plant-pollinator traits

Plants and pollinators were classified according to their life-history traits, following Piqueray et al. (2011), Jauker et al. (2013) and Hopfenmüller et al. (2014) for plants' and bees' habitat specialization, respectively. Bees were considered large when having a body length of 10 mm or more (median body length of bees) and were otherwise considered small. All body length values for bees were taken from Westrich (2018). We consider *Cirsium sp.* (cluster of four species mostly represented by the habitat specialist *Cirsium acaule*) and *Ononis sp.* (cluster of two hybridizing species including the specialist *Ononis repens*) as habitat specialists.

Pollen load data

Pollen was taken from bees' bodies, head and antennae by bathing bees in Eppendorf tubes filled with distilled water (modified protocol from Dafni, 1992). As some interactions were very abundant, we established a maximum of 6 pollen samples taken from the same interaction in each site and round. Samples were later acetolysed (Jones, 2014) using a protocol lab technique and analyzed using light microscopy at 40x magnification. We also created a reference collection of pollen from the flowering plants of the region to aid sample pollen identification. We did not consider slides with less than 30 pollen grains. From the remaining ones we counted 200 pollen grains in each slide, except five slides which had 50-200 pollen grains. Following Bosch et al. (2009), we considered the presence of at least 10 pollen grains in our samples as proof of true visitation to the corresponding flowering species.

Network and statistical analysis

Our study involved two levels of complexity: (i) local scale, in which we zoomed-in to compare flower-visitation vs pollen-transport networks types; (ii) regional scale, in which we scaled-up, from local fragment networks, to regional metanetworks. Below, we describe how we analyzed that complexity in the light of our hypotheses.

We constructed local quantitative bipartite networks (one for each fragment) and regional metanetworks using data on flower visitation (hereafter, visitation networks) and pollen loads (hereafter, pollen transport networks), respectively. Local bipartite networks were constructed as a_{ij} adjacency matrices in which *i* are the plant species and *j* the pollinator species. At the landscape level, metanetworks were built by pooling the 29 calcareous grasslands into a_{kl} adjacency matrices in which *k* are the studied sites and *l* the plant or pollinator species. To make visitation and pollen transport networks comparable we did not consider pollen from trees (e.g. *Picea spp* or *Pinus spp*), crops (e.g. *Vicia faba*), grasses (e.g. Poaceae) or ornamental plants (e.g. *Astrantia major*) as observations were done exclusively on herbaceous plants of calcareous grasslands.

To test whether pollen transport networks were more specialized than visitation networks at the local level (hypothesis 1), and whether they were affected by habitat fragmentation and landscape diversity (hypothesis 2), we calculated the H2' index which measures the specialization of the network for each fragment (Blüthgen et al., 2006). We used a linear mixed model with fragment identity as random intercept and network type, (log) fragment area, (log) connectivity index and landscape diversity at 350 m as explanatory variables. To choose the spatial scale at which effects were stronger, we compared models fitted at all scales from 100 m to 500 m in 50 m intervals and compared them using the corrected Akaike information criterion for small samples (AICc). As almost all indices of network structure are more or less affected by network size, we standardized H2' relative to a null model to allow for meaningful comparisons among networks of different fragments (Dormann et al., 2009; Dormann and Strauss, 2014). We followed Grass et al. (2018) by creating null distributions based on 1000 replicates of Patefield's algorithm.

We estimated the centrality of the metanetworks nodes (hypothesis 4) by calculating: (1) species degree, as the number of fragments where a species occurs; (2) species betweenness centrality (hereafter, species betweenness), as the number of shortest paths among fragments going through the focal species; (3) weighted betweenness centrality, same as species betweenness but weighted by species abundance and; (4) proportional generality, as the number of fragments, where the focal species occurs, in relation to the total number of fragments in the metanetwork weighted by the species abundance. Betweenness centrality > 0 indicates species that have the potential to connect the metanetwork to some extent, BC = 0 means that the focal node is exclusive to a single fragment. Network metrics were calculated using the "bipartite" package (Dormann et al., 2008).

We modelled the probability of the presence of interactions in both networks (hypothesis 5) using a generalized linear mixed model with binomial distribution and pollinator and plant species identity as crossed random intercepts. Network type was tested as a single explanatory variable. Finally, to study the relationship between landscape diversity and habitat fragmentation on the number and proportion of single-fragment interactions (hypothesis 6) we used generalized linear models with negative binomial distribution and linear models, respectively.

The minimum adequate models were found with backwards model selection using likelihood ratio tests. All non-significant explanatory variables (P > 0.05) were sequentially removed. All network and statistical analyses were performed in R (R Development Core Team 2019).

Results

We observed 1165 interaction events among 67 bee species and 71 plant species resulting in 250 unique pairwise interactions. Further, we analyzed pollen samples of 830 bee individuals and found 474 individuals carrying 0-30 pollen grains, 351 carrying ≥ 200 pollen grains and 5 carrying 50-200 pollen grains. In total we identified 44 bee species transporting pollen of 64 plant species, resulting in 222 unique plant-bee pairwise interactions. Of those, 31 (43.7%) plant species were only visited by bumblebees and 19 (26.8%) plant species were only visited by solitary bees, while 23 (32.4%) plant species were visited by both, totalizing 71 plant species visited (Fig. 1a, Table S2). Some examples include *Fragaria vesca,* which was only visited by solitary bees, and *Trifolium pratense, Salvia pratensis, Prunella grandiflora, Carlina vulgaris* and *Anthyllis vulneraria,* which were only visited by bumblebees (Table S2). Regarding pollen transport, 20 (31.3%) plant species were only pollen-transported by bumblebees and the pollen of 12 (18.8%) plant species was only transported by solitary bees (Fig. 1b, Table S3). The pollen of 32 (50%) plant species was transported by both groups, summing up to 64 plant species that got their pollen transported by flower visitors. For example, pollen of *Knautia arvensis* was only transported by bumblebees and pollen of *Potentilla sp.* was only transported by solitary bees (Table S3).

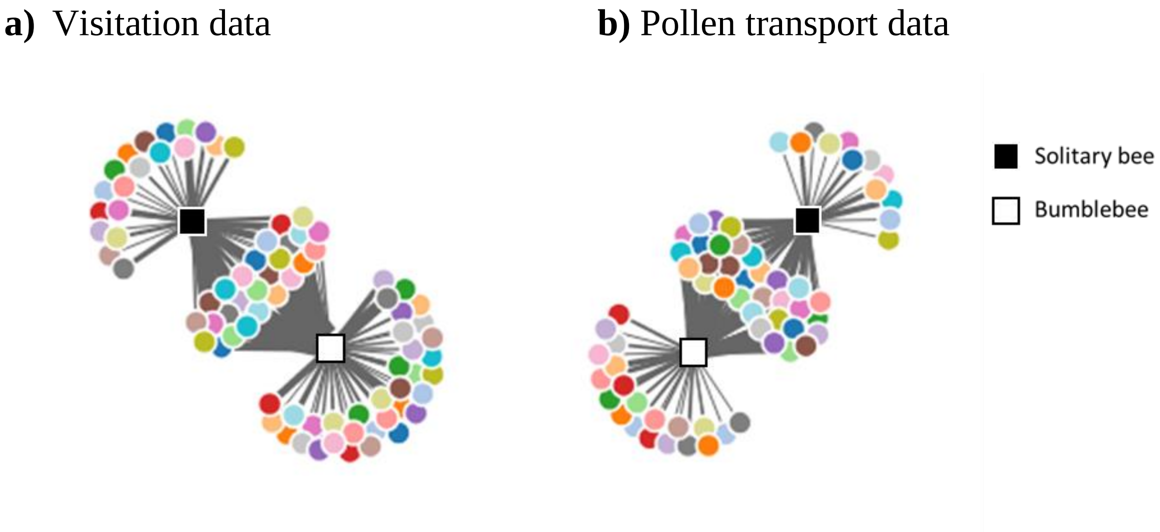


Figure 1. Network representation of the established interactions among bumblebees (white squares) and solitary bees (black squares) with plant species (circles) in a) the visitation dataset and b) the pollen transport dataset. Plants visited by both groups occur between the squares.

At the local network level, our results show that pollen transport networks were significantly more specialized than visitation networks (F = 11.33, P = 0.002, Fig. 2). We also found a negative effect of landscape diversity at the 350 m scale on specialization of both visitation and pollen transport networks (F = 13.56, P = 0.001, Fig. 2). On the other hand, network connectance did not differ between the visitation and pollen transport networks (F = 1.03, P = 0.32) and was also not affected by landscape diversity (F = 1.97, P = 0.17). Fragment area and fragment connectivity had no significant effects neither on network specialization nor network connectance (Table S4).

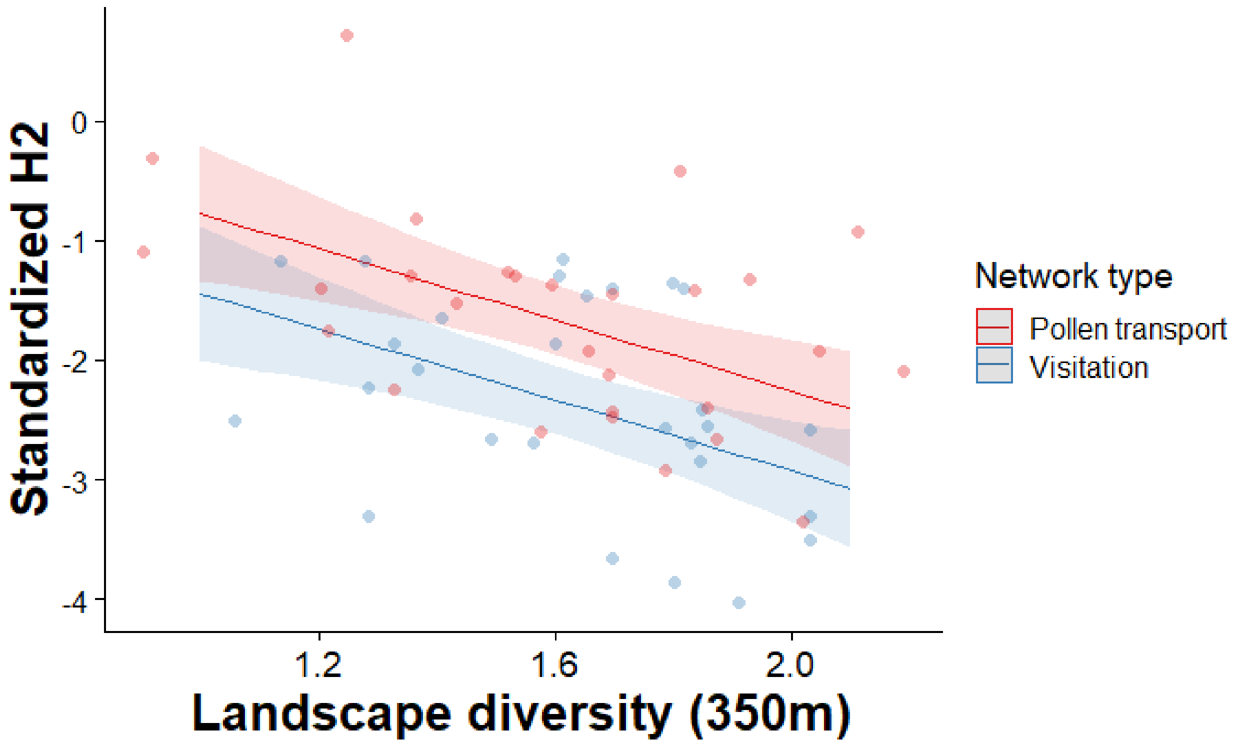


Figure 2. Relationship between standardized network specialization (H2), network type and landscape diversity (i.e. Shannon diversity of land cover types). Each network type includes 28 local networks (fragments) in each dataset (pollen transport and visitation). Bands represent 95% confidence intervals.

At the metanetwork level, we found a total of 345 unique combinations of plant-pollinator interactions considering both visitation and pollen transport metanetworks, from which 127 (36.8%) were found in both types (Fig. 3, Table S5). From a total of 222 unique pairwise interactions detected in the pollen transport metanetwork, 95 (42.8%) were exclusive to it (i.e. they were not registered in the visitation metanetwork, Table S6) and 123 out of 250 (49.2%) were recorded only in the visitation metanetwork (Table S7). Furthermore, we identified important differences in the number of interactions established by some plant species in both metanetworks (Table S8 and Table S9). The most outstanding case was *Knautia arvensis* (Caprifoliaceae*)*, which was visited by 19 different bees but only four of them transported its pollen.

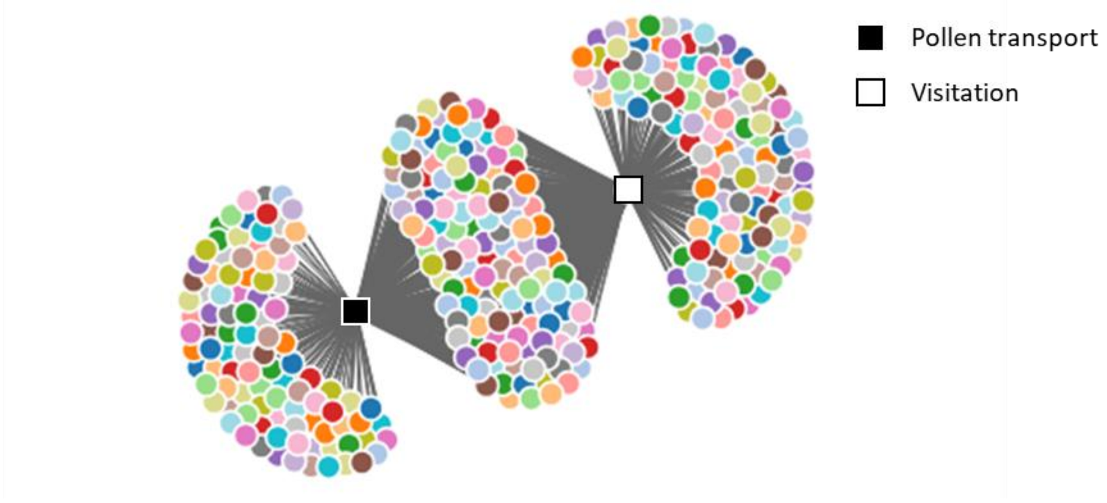
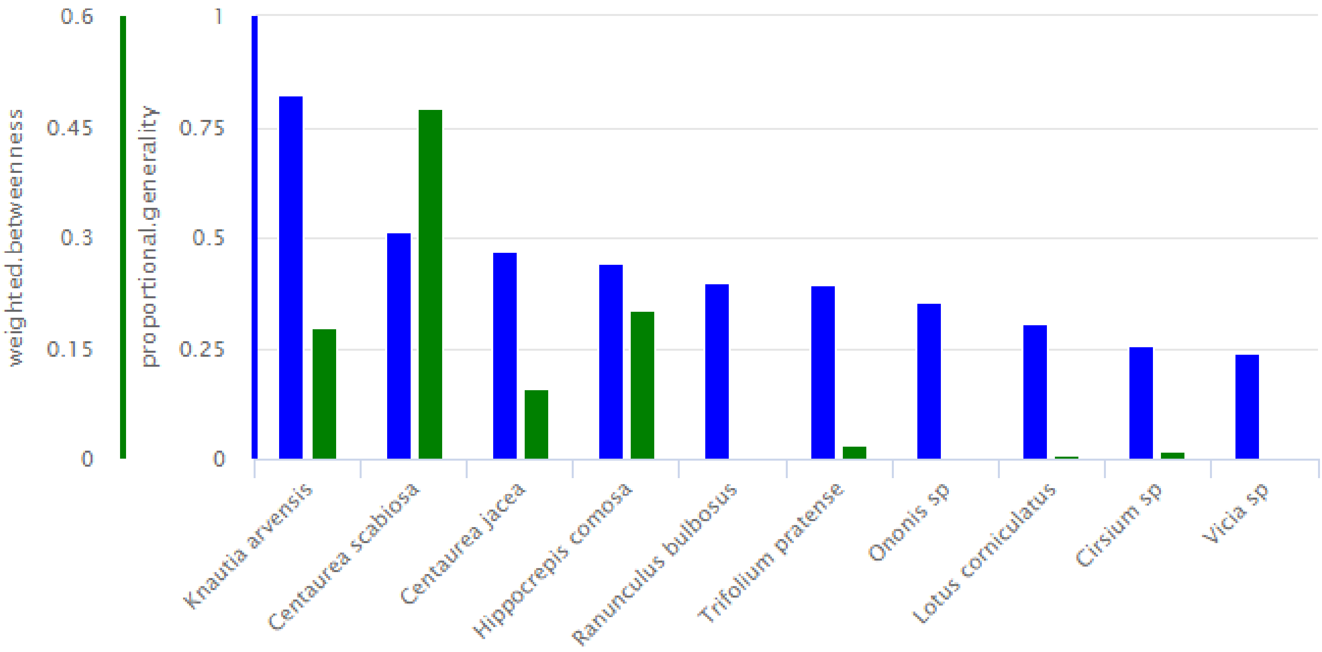


Figure 3. Diagram representation of the plant-pollinator interactions (circles) occurring in the pollen transport (black square) and visitation (white square) metanetworks. Those interactions exclusive to the pollen transport dataset occur to the left side of the black square and those exclusive to the visitation dataset are shown to the right side of the white square. Circles in between squares represent unique pairwise interactions occurring in both datasets.

Eight out of the 10 most central plant species in the visitation and pollen transport metanetworks, based on the proportional generality of the species, coincided (Fig. 4). The most central plant species in the visitation metanetwork, *Knautia arvensis*, did not fall among the ten most central plant species in the pollen transport metanetwork. On the other hand, *Trifolium pratense*, the most central plant species in the pollen transport network, only showed up at the sixth place in the visitation metanetwork. Moreover, centrality measures based on weighted betweenness differed from those based on proportional generality in both metanetworks. *Centaurea scabiosa* and *Hippocrepis comosa*, two habitat specialist plants, were consistently the two with the highest weighted betweenness in both metanetworks (Fig. 4).

a)



b)

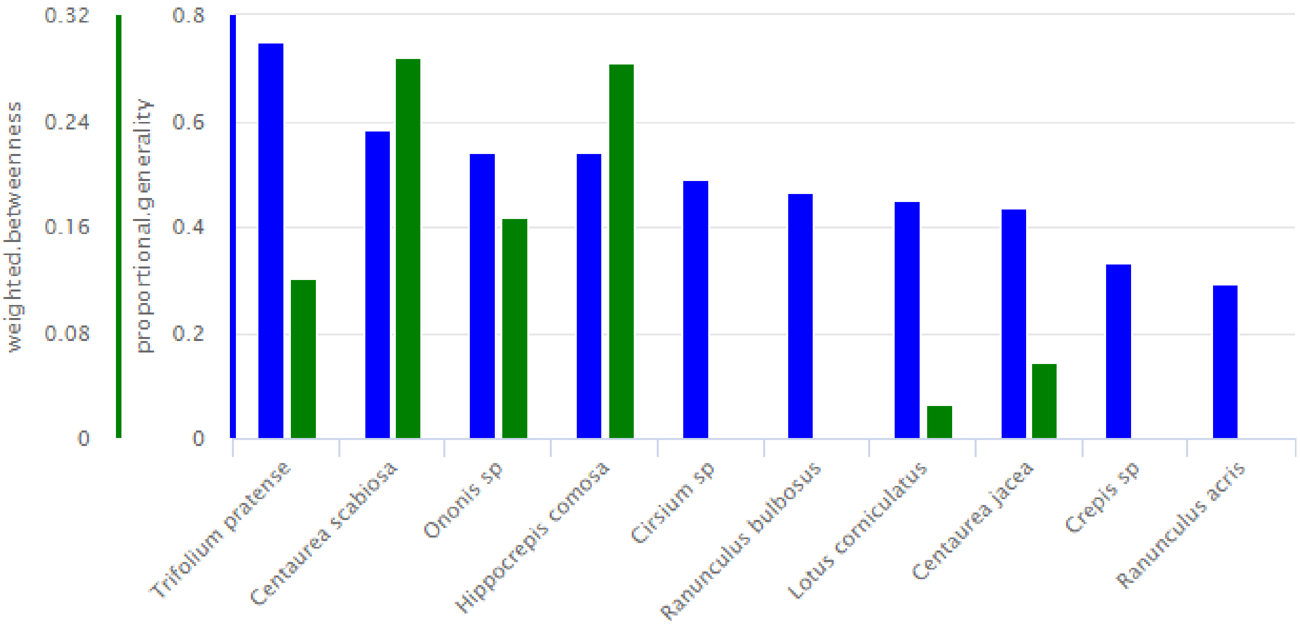


Figure 4. The ten most central plant species based on proportional generality in a) the visitation metanetwork and b) the pollen transport metanetwork.

Further, we found that the probability of the presence of an interaction in both datasets (i.e. visitation and pollen transport) was affected by the plant habitat specialization and the pollinator identity. Specifically, interactions involving habitat specialist plants (X^2 = 6.47, P = 0.011) and bumblebees (X^2 = 17.24, P = 0.0071), had a significantly higher probability of occurrence in both networks than those involving habitat generalist plants and solitary bees (Fig. 5).

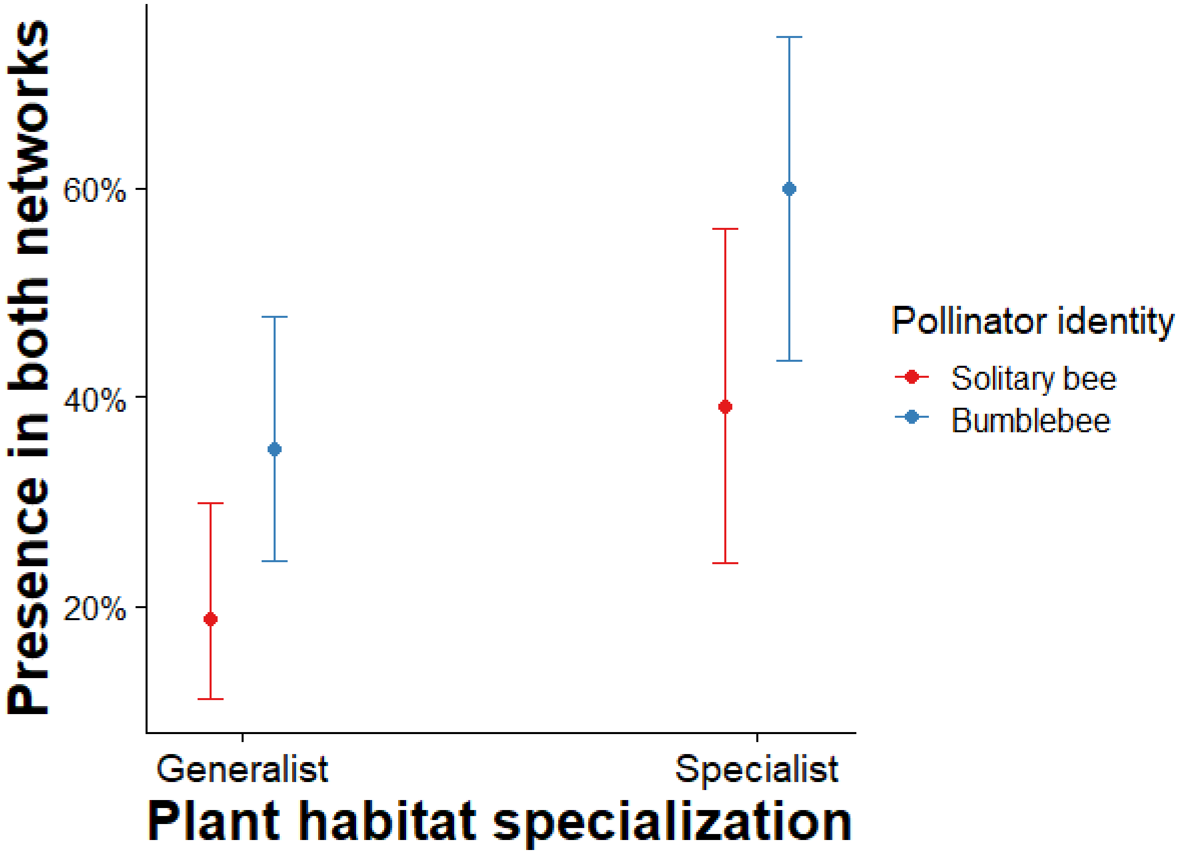


Figure 5. Effects of the plant habitat specialization and the pollinator identity on the probability of presence of an interaction in the visitation and pollen transport datasets simultaneously.

Finally, we found a significant positive effect of landscape diversity on the number of single-fragment interactions (Fig. S2). However, the spatial scale at which this effect was stronger differed for the visitation and pollen transport datasets. Specifically, the number of single-fragment interactions increased with landscape diversity at the 150 m scale for the visitation data (X2 = 4.59, P = 0.032, Fig. S2a) and at the 500 m scale for the pollen transport data (X2 = 5.96, P = 0.015, Fig. S2b). Moreover, landscape diversity at the 500 m scale was found to significantly increase the proportion of single-fragment interactions (F = 5.26, P = 0.030). Nonetheless, this effect was only found for the pollen transport data (Fig. 6). Fragment area and fragment connectivity had no significant effect on the number of single-fragment interactions or the proportion of single-fragment interactions (Table S10).

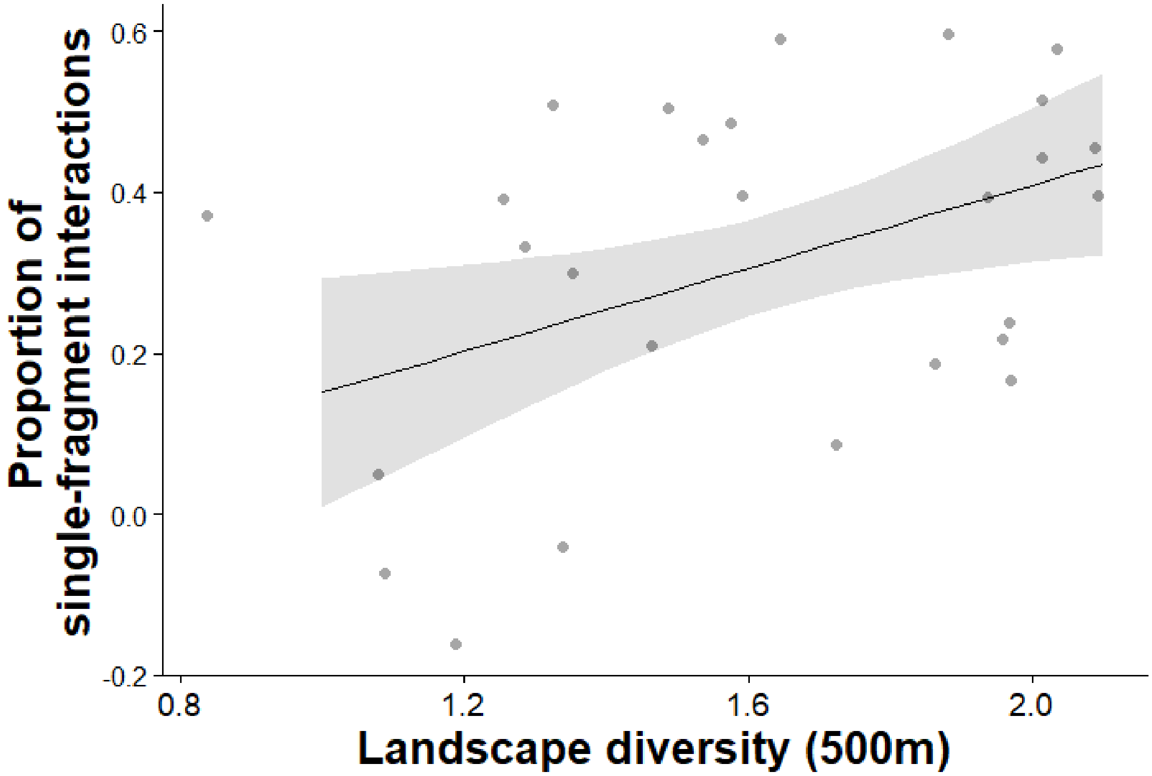


Figure 6. Effect of landscape diversity on the proportion of single-fragment interactions occurring in local networks based on the pollen transport dataset.

Discussion

In this study, we compared plant-pollinator networks from flower visitation data with those from pollen transport data across a gradient of habitat fragmentation and we identified their similarities and differences. Of all interactions found, 63.2% were exclusive to either the visitation or pollen transport networks, highlighting the numerous low-frequency interactions that are not captured by observations of flower visits (27.5%), and also a high number of interactions (35.7%) that do not translate into pollen transport. Pollen transport networks were more specialized than visitation networks. Also, the diversity of land cover types in the surroundings of a habitat fragment increased network generalization. The probability of being represented in both network types was larger for interactions involving habitat specialist plants and bumblebees, compared to those involving habitat generalist plants and solitary bees. Lastly, we found a positive effect of landscape diversity on the number of single-fragment interactions in the pollen transport and visitation networks as well as on the proportion of single-fragment interactions, which was found exclusively in the pollen transport dataset.

Network type and landscape diversity effects on network specialization

As expected, pollen transport networks were found to be more specialized than visitation networks (Fig. 2). This pattern supports previous studies (Alarcón, 2010; Zhao et al., 2019) and shows that many flower visits do not translate into pollen transport (King et al., 2013). Importantly, a higher specialization of pollen transport networks indicates that pollination networks might be more vulnerable to collapse following disturbance, as increased specialization can make networks less robust and more prone to co-extinction cascades (Classen et al., 2020; Thébault and Fontaine, 2010; Vanbergen et al., 2017, but see Benadi et al., 2013; Hoiss et al., 2015). The vast majority of plant-pollinator network studies are based on visitation data and conclusions regarding biodiversity conservation and ecosystem services provision are derived mostly from them. In light of our results, we call attention to the risk of an overestimation of plant-pollinator networks stability and robustness in past studies based solely on flower visitation data.

Landscape diversity had a negative effect on network specialization, i.e. plant-pollinator networks from fragments surrounded by a higher diversity of land cover types were more generalized. Plant-pollinator networks specialization has been shown to be affected by many variables, such as species richness and species behavior (Classen et al., 2020; Hoiss et al., 2015; Jauker et al., 2019). Analyzing plant-pollinator interactions in calcareous grasslands, Jauker et al., 2019, found that decreasing fragment size reduced networks generalization through the loss of species and interactions. Similarly to habitat fragmentation, landscape simplification may decrease the availability of interacting partners as a consequence of reduced population sizes or local extinctions. The absence of interacting partners can have opposite effects on species specialization. On the one hand, pollinators may visit more plant species to compensate for missing resources, therefore increasing their generalization (Brosi and Briggs, 2013). However, in case of limited behavioral plasticity or high plant fidelity, specialization could increase after disturbance (i.e. loss of a plant partner) as pollinators would be unable to establish new interactions. For plants, losing a pollinator may directly increase plant specialization by reducing the number of interacting partners. Nonetheless, reduced competition for resources among pollinators could facilitate visitation from opportunistic (and usually less effective) pollinators, therefore increasing the plant generalization (Brosi and Briggs, 2013). Our results suggest that pollinators may not compensate for the missing plant partners and that plants do not get extra visits once a specialized pollinator is lost following landscape homogenization.

Visitation and pollen transport exclusive interactions

We found a high amount of interactions occurring exclusively in the pollen transport (27.5%) or visitation datasets (35.7%, Fig. 3). Plant-pollinator networks based on pollen transport and pollen transfer data were recently found to have topological differences compared to traditional networks based on flower visitation (Emer et al., 2015; Zhao et al., 2019). This suggests that conclusions derived from traditional studies may have to be revisited. Our results indicate that the structural differences between visitation and pollen transport networks could be larger than previously believed, based on the surprisingly high amount of interactions found exclusively in the visitation and pollen transport datasets. These results challenge the so far accepted assumption that visitation data is a sufficient surrogate of animal mediated pollen transport.

The large presence of flower visitors with a relatively small capacity for pollen transport raises many questions regarding their importance for pollination (Moquet et al., 2017). In theory, deposition of a single conspecific pollen grain could be enough for pollination to occur, but pollen deposition thresholds are common given that not all pollen deposited by pollinators is viable (Li et al., 2019). Therefore, a relatively high amount of conspecific pollen deposition is usually needed for a meaningful pollination success (Li et al., 2019). The concomitant deposition of heterospecific pollen is also an important factor considering its negative effects on pollination (Arceo-Gómez and Ashman, 2011; Brown and Mitchell, 2001). Actually, from a plant species perspective, a strategy based on maximizing pollinators’ visits might come at the cost of high heterospecific pollen deposition on their stigmas. Contrastingly, a strategy based on the attraction of a small number of specialized pollinators (and therefore larger potential for conspecific pollen deposition) comes at the cost of a higher dependence on a small group of pollinators and a lower probability of visitation. Habitat fragmentation and landscape homogenization may impose a reduced set of pollinator partners to interact with. As a consequence, higher plant specialization could arise as an indirect result of the lack of alternative partners and not as part of an ecological strategy to increase reproductive success.

The pollen transport networks revealed a high amount of rare interactions. This implies that plant-pollinator networks based only on flower visitation data are not just biased by the inclusion of interactions with no potential for pollination, but also by missing many rare interactions. Consequently, pollen loads analysis represents a better approach to study pollination systems, as the actual pollen dispersal across the plant community can be quantified. Visitation data, on the other hand, appears fundamental to understand the plant-pollinator interactions from the pollinator perspective, as competition among pollinators and the different foraging strategies that pollinators use to maximize their fitness can be eventually quantified.

The detection of interactions involving rare habitat specialist plants, such as *Scabiosa columbaria* (Angeloni et al., 2014; Bijlsma et al., 1994), indicates that pollen load analyses can contribute to improve conservation strategies by identifying remaining small populations of these rare species. For example, restoration efforts targeting these small populations could be undertaken in places where the plants were thought to be locally extinct. Then again, the high amount of interactions not translating into pollen transport might suggest a higher vulnerability of plant-pollinator networks to the loss of species.

Plant habitat specialization and pollinator identity on interaction presence probability

As predicted, interactions involving bumblebees had a higher probability of occurrence in both, the visitation and pollen transport networks (Fig. 5). Bumblebee species are bigger than most solitary bees, have dense hair and also the capacity to vibrate their bodies through thoracic muscle contractions to extract pollen from buzz pollinated plants (Stavert et al., 2016; Vallejo-Marín, 2019). These morphological and behavioral traits, in addition to their abundance, give bumblebees a high capacity for pollen transport (Velthuis and van Doorn, 2006; Willmer et al., 1994). Our results support this by demonstrating that the probability of a bumblebee carrying pollen after a flower visit is higher than that of solitary bees. However, studies on pollen transfer (i.e. pollen deposition in a conspecific stigma) after flower visits would be necessary to verify whether bumblebees are also able to deposit more pollen on stigmas than solitary bees, since pollen transport does not always translate into pollen deposition (Emer et al., 2015). Furthermore, the ratio between conspecific and heterospecific pollen deposition might also be important to analyze, as it is essential for plants' reproductive success (Arceo-Gómez and Ashman, 2011; Morales and Traveset, 2008).

We found a smaller representation of habitat generalist plants on pollen transport networks compared to habitat specialist ones (Fig. 5). The direct consequence of this result is that flower visits to habitat specialist plants have a higher probability to translate into pollen transport than visits to habitat generalist plants. A higher representation of habitat specialist plants in pollen transport networks cannot be solely related to a higher attractiveness of habitat specialist flowers or pollen, as interactions involving habitat specialist plants in the pollen transport dataset were less than half of the total interactions found (46.8%). This result is rather a consequence of different mechanisms that allow habitat specialist plants to allocate their pollen more frequently on flower visitors than habitat generalists. Habitat specialist plants are expected to have a long history of evolutionary adaptations to the local pollinator pool and, therefore, to have developed mechanisms for efficient pollen transport through those pollinators (Miller-Struttmann, 2013). Conversely, generalist plants should lack such adaptations as they would exhibit more opportunistic strategies to quickly adapt to different environments. The adaptations of plants to increase pollination success can occur at many levels including pollen vector attraction, pollen presentation, pollen transport and pollen germination (Minnaar et al., 2019). At the visitation level, traits such as flower size, flower abundance and the quantity and quality of offered flower rewards (i.e. pollen and nectar), may increase visitation rates (Conner and Rush, 1996). At the pollen transport level, plants may possess mechanisms to place larger amounts of pollen at specific places of the flower visitors´ body (Minnaar et al., 2019). At the pollen transfer level, plant traits such as the stigma type (i.e. wet or dry), pollen morphological traits or behavioral characteristics of pollinators may affect the quantity and quality of pollen deposition (Emer et al., 2015; Konzmann et al., 2019; Minnaar et al., 2019). Even after pollen deposition on stigmas, plants may exhibit mechanisms to regulate receptiveness depending on the characteristics of the flower visitor (Betts et al., 2015).

Plant and pollinator metanetwork hubs

Interestingly, seven out of the 10 most central pollinator species and eight out of the 10 most central plant species were shared between the visitation and pollen transport data, indicating that the most central species tend to be identical in both metanetworks (Fig. 4 and Fig. S1). In addition, six out of the 10 most central plant species were habitat specialist in both metaneworks, but only one pollinator species (*Andrena subopaca* and *Halictus scabiosae* in the visitation and pollen transport metanetworks, respectively) was a habitat specialist among the most central pollinator species in both metanetworks. These results reveal that the most central species in the metanetworks are asymmetric in terms of habitat specialization, implying that habitat specialists tend to interact with habitat generalist species. This is in agreement with previous findings of pollination networks in grasslands communities (Fantinato et al., 2019). Remarkably, the habitat generalist *Knautia arvesis*, the most central plant in the visitation metanetwork, was not included among the 10 most central plant species in the pollen transport metanetwork. This highlights how misleading it can be to draw conclusions on pollination dynamics based exclusively on flower visitation data. It is also important to highlight the presence of *Osmia bicolor* as the only solitary bee species representative in the group of most central pollinators in both metanetwork types. Furthermore, *O. bicolor* exhibited the third highest weighted betweenness in both datasets among all bee species (i.e. including bumblebees). This is an exceptional trait for a solitary bee species, considering that bumblebees are frequently considered the dominant pollinator group given their high abundance and large body size (Gorenflo et al., 2017; Willmer et al., 2017).

Pollinator identity

Our results support the hypothesis that visitation data is a poor predictor of a pollinator's ability to transport pollen, as the presence of a plant's pollen in transport networks does not necessarily correlate to how frequently visited that plant is (King et al., 2013). The habitat generalist *Knautia arvensis*, for example, was visited by many species of both bee guilds (bumblebees and solitary bees) being involved in a total of 105 interactions events. As a consequence, this plant exhibited the highest proportional generality in the visitation metanetwork. However, we found only ten interactions with *K. arvensis* in the pollen transport networks, involving only four bumblebee species and no solitary bees (Table S8 and Table S9). In contrast, the habitat specialist, *Onobrychis viciifolia*, got its pollen transported by all its seven species of visitors from both guilds (Table S8 and Table S9).

Solitary bees were fundamental for the pollen transport of many plant species. In particular, they transported pollen of 16 habitat specialist plants and were the only pollen vector of at least three of them (Table S3). Considering that many solitary bee species are vulnerable and threatened with extinction (Jauker et al., 2013; Nieto et al., 2017), these results signal to the importance of their role in calcareous grasslands and to the potential risk of their absence for habitat specialist plants reproductive success. Our findings reveal that both, bumblebees and solitary bees, are complementary for pollen transport of calcareous grasslands plant species.

Landscape diversity effect on single-fragment interactions

The number of single-fragment interactions increased consistently with landscape diversity (Fig. S4). This highlights that a diverse group of land cover types benefits the diversity of interactions, most likely by providing suitable conditions for both, habitat specialist and habitat generalist species. Interestingly, the spatial scale at which landscape diversity most strongly affected the number of unique interactions was larger for the pollen transport dataset compared to the visitation dataset. This suggests that landscape-scale conservation measures to protect plant-pollinator networks might be undertaken at the wrong spatial scales when solely based on flower visitation data.

When considering not only the number of single-fragment interactions, but the proportion of single-fragment interactions (i.e. number unique interactions divided by interaction richness), we found a significant positive effect of landscape diversity that was, interestingly, not captured in the visitation dataset (Fig. 6). This means that the increased number of single-fragment interactions is not solely related to a general increase in the total number of interactions with landscape diversification. Importantly, this effect was only captured with the pollen transport data and highlights that landscape structure effects can remain undetected in plant-pollinator studies solely based on visitation data. It also implies that landscape diversification has a disproportionally positive effect on the occurrence of single-fragment interactions compared to the total amount of interactions.

Conclusion

Here we analyzed plant-pollinator networks across a gradient of habitat fragmentation through data on flower visitation and pollen transport by bees. We found that pollen transport networks were more specialized than visitation networks, indicating that plant-pollinator networks could be more vulnerable than previously believed. Only 35.7% of the total amount of plant-pollinator interactions registered occurred in both, flower visitation and pollen transport networks. This challenges the widely held assumption that visitation networks are a sufficient surrogate of pollination systems. It also questions conclusions drawn from these studies, as the actual properties and dynamics of pollination networks can be strikingly different from current pollination paradigms. We found positive effects of landscape diversity on the proportion of single-fragment interactions for pollen transport, but not visitation networks, highlighting the importance of landscape level measures for the conservation of plant-pollinator networks. Interactions involving habitat specialist plants and bumblebees were significantly more represented in the visitation and pollen transport networks than interactions involving habitat generalist plants and solitary bees. Nonetheless, the pollen of several plant species was found to be only transported by solitary bees and we identified solitary bee species with disproportionally high importance for the metacommunity. Our study shows that conservation of pollination systems and related pollination services cannot be conceived without finer data on the biological processes underlying plant-pollinator interaction networks, such as pollen load analyses. Our results have important consequences for the understanding of the responses of plant-pollinator networks to habitat fragmentation and contribute to unveil important processes underpinning the dynamics of these networks.

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Supplementary material

Connectivity index based on Hanski et al. 1994

$$I = \sum e^{-dij} A_j$$

Aj is the size in m² of neighbouring calcareous grasslands and dij is the distance in km from the neighbouring grassland j to the study site I (following Krauss et al. 2004). The 2 km radius was chosen to capture the maximum biologically meaningful distance for the largest pollinators (see also Krauss et al. 2010). Larger values of "I" indicate higher connectivity (Table S1).

Table S1. Landscape metrics for each study site: Area in m², management, Shannon diversity index of cover types in a 200 m radius and connectivity index.

Study site	Habitat area (m²)	Management	Shannon index (200 m)	Connectivity index
Huhnsberg	52557	Grazing	1.50	52162
Mühlenberg	50673	Grazing	1.89	15805
Aschenburg	35479	Grazing	1.45	19917
Ellershagen	33186	Grazing	0.68	7145
Lengender Burg	16804	Unmanaged	1.68	4914
Dehnerberg	12724	Grazing	1.85	3671
Mackenrodt	11612	Mowing	1.71	637
Burgbreite	7641	Grazing	1.28	7335
Gladeberg	7288	Grazing	1.19	3814
Weinberg	6641	Grazing	1.71	25941
Hackelberg	5823	Mowing	1.58	28463
Am Graben	5535	Unmanaged	1.93	1186
Tiefetal	4132	Grazing	1.36	4617
Südlicher Riesenberg	3535	Unmanaged	1.76	6103
Ossenfelder Bahndamm	3504	Grazing	1.86	1111

Kleiner Knull	3467	Grazing	1.55	8083
Kuhberg	3465	Grazing	1.78	10797
Eschenberg	1861	Unmanaged	1.36	306
Vor dem roten Berge	1462	Unmanaged	1.23	21676
Auf dem Klee	778	Unmanaged	1.45	25575
Schweineberg	701	Mowing	1.70	114
Am Hopfenberge	693	Unmanaged	1.34	19917
Unter den Niederwiesen	406	Mowing	0.49	5332
Emme	381	Unmanaged	0.85	10015
Gieseberg Süd	353	Unmanaged	1.71	15953
Mühlenberg 2	228	Mowing	1.12	47366
Zipfel am Lindenberg	227	Unmanaged	1.37	10518
Lieseberg	144	Unmanaged	1.24	2943
Heikenrott	82	Mowing	1.28	6152

Table S2. Number of interactions per pollinator group in the visitation data

Plant	Bumblebee	Solitary bee
Ajuga reptans	5	0
Alliaria petiolata	0	1
Anemone sylvestris	3	0
Anthyllis vulneraria	11	0
Aquilegia vulgaris	10	1
Astragalus glycyphyllos	1	0
Campanula sp	4	0
Carduus nutans	2	0
Carlina vulgaris	21	0
Centaurea jacea	52	51
Centaurea scabiosa	285	32
Cerastium arvense	1	0
Cerinthe minor	2	0
Cirsium sp	22	2
Cirsium vulgare	2	0
Clinopodium acinos	2	0
Clinopodium vulgare	1	0
Cotoneaster integerrimus	17	1
Crataegus monogyna	2	1
Crepis sp	0	2
Dactylorhiza fuchsii	1	0
Daucus carota	5	0
Dictamnus albus	2	0
Echium vulgare	4	0
Euphorbia cyparissias	0	3
Filipendula vulgaris	0	1
Fragaria vesca	0	16
Genista tinctoria	7	5
Geum urbanum	0	1
Helianthemum nummularium	4	2
Hieracium cymosum	1	0
Hieracium lachenalii	0	1

Plant	Bumblebee	Solitary bee
Hieracium murorum	1	0
Hieracium pilosella	0	4
Hieracium umbellatum	2	0
Hippocrepis comosa	100	37
Hypericum perforatum	2	0
Knautia arvensis	105	25
Lathyrus sylvestris	0	1
Leontodon hispidus	0	2
Leucanthemum vulgare	1	5
Lotus corniculatus	30	6
Medicago falcata	1	0
Medicago lupulina	0	1
Medicago sativa	1	1
Melampyrum arvense	1	0
Myosotis arvensis	1	3
Onobrychis viciifolia	13	2
Ononis sp	54	4
Origanum vulgare	0	8
Orobanche rapum-genistae	0	1
Plantago lanceolata	1	1
Plantago media	1	0
Polygala comosa	1	0
Potentilla sp	0	8
Primula veris	3	19
Prunella grandiflora	15	0
Ranunculus bulbosus	1	16
Ranunculus repens	0	2
Rhinanthus minor	2	0
Salvia pratensis	10	0
Sanguisorba minor	1	0
Senecio sp	3	7
Silene dioica	1	0
Stellaria holostea	0	4
Taraxacum officinale	0	4

Plant	Bumblebee	Solitary bee
Trifolium pratense	38	0
Trifolium repens	1	0
Veronica austriaca	4	3
Veronica chamaedrys	1	5
Vicia sp	12	2

Table S3. Number of interactions per pollinator group in the pollen transport data

Plant	Bumblebee	Solitary bee
Ajuga reptans	4	1
Anthriscus sylvestris	3	0
Anthyllis vulneraria	2	0
Aquilegia vulgaris	4	2
Astragalus glycyphyllos	7	0
Campanula sp	3	2
Carduus nutans	2	0
Carlina vulgaris	7	0
Centaurea jacea	44	11
Centaurea jacobea	1	0
Centaurea scabiosa	61	11
Cerastium arvense	0	1
Cerinthe minor	4	1
Cirsium sp	20	1
Cotoneaster interregimus	0	1
Crepis sp	4	8
Daucus carota	3	0
Echium vulgare	3	0
Filipendula vulgaris	0	1
Fragaria vesca	2	14
Galium sp	7	1
Genista tinctoria	3	2
Geum urbanum	1	1

Plant	Bumblebee	Solitary bee
Helianthemum nummularium	3	4
Hieracium cymosum	1	0
Hieracium pilosella	0	3
Hippocrepis comosa	51	11
Knautia arvensis	10	0
Leucanthemum vulgare	0	1
Lotus corniculatus	32	2
Medicago falcata	1	0
Melampyrum pratense	3	0
Mentha type	1	0
Myosotis arvensis	0	1
Onobrychis viciifolia	6	3
Ononis sp	50	6
Plantago lanceolata	4	2
Plantago media	2	2
Potentilla sp	0	10
Primula veris	1	6
Prunella grandiflora	1	0
Pulmonaria sp	1	0
Ranunculus acris	5	6
Ranunculus bulbosus	6	13
Ranunculus repens	0	1
Rumex obtusifolius	1	0
Salvia pratensis	11	1
Sanguisorba minor	0	4
Saxifraga sp	4	3
Scabiosa columbaria	1	1
Senecio sp	7	1
Silene dioica	1	0
Silene vulgaris	0	1
Stellaria holostea	0	5
Taraxacum officinale	0	8
Trifolium pratense	43	3
Trifolium repens	4	1

Plant	Bumblebee	Solitary bee
Trifolium sp	5	1
Valeriana officinalis	2	0
Veronica austriaca	1	1
Veronica chamaedrys	5	2
Veronica sp	1	0
Vicia sp	14	1
Viola sp	1	0

Table S4. Full and minimum adequate models for network specialization (H2) and network connectance selected with likelihood ratio tests (via "drop1"). Significance levels: ***p<0.001. **p<0.01, *p<0.05

Response variable	**Model**	**Fixed effects**	**LRT (F)**	***P***
H2 standardized	Full	Network type	11.25	0.0024**
		Landscape diversity (350 m)	11.96	0.0020**
		(log) Fragment area	0.43	0.52
		(log) Connectivity Index	0.12	0.73
H2 standardized	Min	Network type	11.33	0.0023**
		Landscape diversity (350 m)	13.58	0.0011**
Connectance standardized	Full	Network type	0.99	0.33
		Landscape diversity (200 m)	0.63	0.44
		(log) Fragment area	1.34	0.25
		(log) Connectivity Index	0.55	0.47

Table S5. Interactions occurring in both, the visitation and pollen transport datasets

Interaction
Ajuga reptans Bombus pascuorum
Anthyllis vulneraria Bombus pascuorum
Aquilegia vulgaris Bombus hortorum
Aquilegia vulgaris Bombus pratorum
Astragalus glycyphyllos Bombus pascuorum
Campanula sp Bombus lapidarius
Carduus nutans Bombus pascuorum
Carduus nutans Bombus terrestris
Carlina vulgaris Bombus pascuorum
Centaurea jacea Bombus bohemicus
Centaurea jacea Bombus lapidarius
Centaurea jacea Bombus pascuorum
Centaurea jacea Bombus pratorum
Centaurea jacea Bombus terrestris
Centaurea jacea Halictus rubicundus
Centaurea jacea Halictus scabiosae
Centaurea jacea Halictus simplex
Centaurea jacea Megachile versicolor
Centaurea scabiosa Bombus bohemicus
Centaurea scabiosa Bombus campestris
Centaurea scabiosa Bombus hortorum
Centaurea scabiosa Bombus hypnorum
Centaurea scabiosa Bombus lapidarius
Centaurea scabiosa Bombus pascuorum
Centaurea scabiosa Bombus pratorum
Centaurea scabiosa Bombus rupestris
Centaurea scabiosa Bombus terrestris
Centaurea scabiosa Ceratina cyanea
Centaurea scabiosa Halictus scabiosae
Centaurea scabiosa Halictus simplex
Centaurea scabiosa Lasioglossum pauxillum
Centaurea scabiosa Megachile versicolor

Interaction
Cerinthe minor Bombus pascuorum
Cirsium sp Bombus bohemicus
Cirsium sp Bombus lapidarius
Cirsium sp Bombus pascuorum
Cirsium sp Megachile versicolor
Crepis sp Lasioglossum albipes
Crepis sp Lasioglossum villosulum
Daucus carota Bombus terrestris
Echium vulgare Bombus pascuorum
Fragaria vesca Andrena flavipes
Fragaria vesca Andrena minutuloides
Fragaria vesca Halictus tumulorum
Fragaria vesca Lasioglossum fulvicorne
Fragaria vesca Osmia bicolor
Genista tinctoria Bombus lapidarius
Genista tinctoria Bombus pascuorum
Genista tinctoria Megachile ericetorum
Genista tinctoria Megachile willughbiella
Helianthemum nummularium Bombus pascuorum
Helianthemum nummularium Bombus pratorum
Hieracium cymosum Bombus hortorum
Hieracium pilosella Lasioglossum brevicorne
Hieracium pilosella Lasioglossum leucozonium
Hieracium pilosella Lasioglossum villosulum
Hippocrepis comosa Andrena gravida
Hippocrepis comosa Andrena ovatula
Hippocrepis comosa Andrena similis
Hippocrepis comosa Bombus hortorum
Hippocrepis comosa Bombus lapidarius
Hippocrepis comosa Bombus pascuorum
Hippocrepis comosa Halictus rubicundus
Hippocrepis comosa Megachile ericetorum
Hippocrepis comosa Osmia aurulenta
Hippocrepis comosa Osmia bicolor

Interaction
Knautia arvensis Bombus bohemicus
Knautia arvensis Bombus campestris
Knautia arvensis Bombus pascuorum
Leucanthemum vulgare Andrena gravida
Lotus corniculatus Bombus lapidarius
Lotus corniculatus Bombus pascuorum
Lotus corniculatus Halictus rubicundus
Medicago falcata Bombus pascuorum
Myosotis arvensis Andrena subopaca
Onobrychis viciifolia Bombus hypnorum
Onobrychis viciifolia Bombus lapidarius
Onobrychis viciifolia Bombus pascuorum
Onobrychis viciifolia Bombus pratorum
Onobrychis viciifolia Bombus terrestris
Onobrychis viciifolia Osmia aurulenta
Onobrychis viciifolia Osmia leucomelana
Ononis sp Anthidium manicatum
Ononis sp Bombus lapidarius
Ononis sp Bombus pascuorum
Ononis sp Bombus terrestris
Ononis sp Megachile versicolor
Plantago lanceolata Bombus terrestris
Plantago lanceolata Lasioglossum pauxillum
Plantago media Bombus pascuorum
Potentilla sp Andrena minutuloides
Potentilla sp Halictus tumulorum
Potentilla sp Osmia bicolor
Primula veris Anthophora plumipes
Primula veris Bombus hortorum
Prunella grandiflora Bombus pascuorum
Ranunculus bulbosus Andrena gravida
Ranunculus bulbosus Andrena strohmella
Ranunculus bulbosus Andrena subopaca
Ranunculus bulbosus Bombus hortorum

Interaction
Ranunculus bulbosus Chelostoma florisomne
Ranunculus bulbosus Halictus confusus
Ranunculus bulbosus Halictus tumulorum
Ranunculus bulbosus Osmia bicolor
Ranunculus bulbosus Osmia bicornis
Ranunculus repens Osmia bicornis
Salvia pratensis Bombus hortorum
Salvia pratensis Bombus lapidarius
Salvia pratensis Bombus pascuorum
Senecio sp Bombus bohemicus
Silene dioica Bombus bohemicus
Stellaria holostea Nomada flavoguttata
Stellaria holostea Nomada lathburiana
Taraxacum officinale Nomada lathburiana
Taraxacum officinale Osmia bicolor
Trifolium pratense Bombus hortorum
Trifolium pratense Bombus lapidarius
Trifolium pratense Bombus pascuorum
Trifolium repens Bombus pascuorum
Veronica austriaca Bombus hortorum
Veronica austriaca Bombus pratorum
Veronica chamaedrys Andrena labiata
Veronica chamaedrys Andrena subopaca
Veronica chamaedrys Bombus pascuorum
Vicia sp Bombus hortorum
Vicia sp Bombus pascuorum
Vicia sp Bombus pratorum

Table S6. Interactions exclusive to the pollen transport dataset

Interaction
Ajuga reptans Anthophora plumipes
Anthriscus sylvestris Bombus pascuorum
Anthriscus sylvestris Bombus terrestris
Astragalus glycyphyllos Bombus lapidarius
Campanula sp Bombus terrestris
Campanula sp Megachile ericetorum
Campanula sp Megachile willughbiella
Carlina vulgaris Bombus lapidarius
Centaurea jacea Bombus campestris
Centaurea jacea Lasioglossum costulatum
Centaurea jacobea Bombus bohemicus
Centaurea scabiosa Bombus sylvestris
Cerastium arvense Andrena strohmella
Cerinthe minor Anthophora plumipes
Cirsium sp Bombus campestris
Cotoneaster interregimus Andrena fulva
Crepis sp Andrena flavipes
Crepis sp Bombus lapidarius
Crepis sp Bombus pascuorum
Crepis sp Bombus terrestris
Crepis sp Halictus scabiosae
Crepis sp Halictus simplex
Crepis sp Lasioglossum costulatum
Crepis sp Megachile versicolor
Crepis sp Osmia bicolor
Filipendula vulgaris Megachile willughbiella
Fragaria vesca Andrena strohmella
Fragaria vesca Bombus pascuorum
Galium sp Anthophora plumipes
Galium sp Bombus campestris
Galium sp Bombus pascuorum
Galium sp Bombus terrestris

Interaction
Geum urbanum Bombus terrestris
Geum urbanum Osmia bicolor
Helianthemum nummularium Bombus hortorum
Helianthemum nummularium Bombus lapidarius
Helianthemum nummularium Osmia aurulenta
Hippocrepis comosa Bombus rupestris
Hippocrepis comosa Osmia leucomelana
Knautia arvensis Bombus hortorum
Lotus corniculatus Bombus rupestris
Melampyrum pratense Bombus pascuorum
Mentha type Bombus lapidarius
Ononis sp Bombus pratorum
Ononis sp Halictus simplex
Plantago lanceolata Bombus campestris
Plantago lanceolata Bombus pascuorum
Plantago lanceolata Bombus rupestris
Plantago lanceolata Megachile willughbiella
Plantago media Bombus pratorum
Plantago media Lasioglossum pauxillum
Potentilla sp Anthophora plumipes
Pulmonaria sp Bombus pascuorum
Ranunculus acris Andrena subopaca
Ranunculus acris Bombus lapidarius
Ranunculus acris Bombus sylvestris
Ranunculus acris Bombus terrestris
Ranunculus acris Halictus tumulorum
Ranunculus acris Osmia bicolor
Ranunculus acris Osmia bicornis
Ranunculus bulbosus Bombus lapidarius
Ranunculus bulbosus Bombus pascuorum
Rumex obtusifolius Bombus hortorum
Salvia pratensis Bombus pratorum
Sanguisorba minor Andrena minutuloides
Sanguisorba minor Anthophora plumipes

Interaction
Sanguisorba minor Chelostoma florisomne
Sanguisorba minor Osmia bicolor
Saxifraga sp Andrena subopaca
Saxifraga sp Bombus hortorum
Saxifraga sp Bombus pascuorum
Saxifraga sp Bombus pratorum
Saxifraga sp Osmia bicolor
Scabiosa columbaria Andrena gravida
Scabiosa columbaria Bombus rupestris
Senecio sp Bombus campestris
Senecio sp Megachile versicolor
Silene vulgaris Andrena gravida
Stellaria holostea Andrena strohmella
Stellaria holostea Lasioglossum punctatissimum
Taraxacum officinale Anthophora plumipes
Taraxacum officinale Halictus tumulorum
Taraxacum officinale Lasioglossum punctatissimum
Trifolium pratense Andrena gravida
Trifolium pratense Andrena similis
Trifolium pratense Halictus rubicundus
Trifolium repens Bombus lapidarius
Trifolium repens Osmia bicolor
Trifolium sp Andrena ovatula
Trifolium sp Bombus lapidarius
Trifolium sp Bombus pascuorum
Valeriana officinalis Bombus bohemicus
Veronica chamaedrys Bombus hortorum
Veronica sp Bombus terrestris
Viola sp Bombus lapidarius

Table S7. Interactions exclusive to the visitation dataset

Interaction
Ajuga reptans Bombus hortorum
Alliaria petiolata Lasioglossum calceatum
Anemone sylvestris Bombus pratorum
Anemone sylvestris Bombus terrestris
Anthyllis vulneraria Bombus hortorum
Aquilegia vulgaris Osmia aurulenta
Carlina vulgaris Bombus terrestris
Centaurea jacea Ceratina cyanea
Centaurea jacea Halictus quadricinctus
Centaurea jacea Lasioglossum albipes
Centaurea jacea Lasioglossum calceatum
Centaurea jacea Lasioglossum morio
Centaurea scabiosa Halictus quadricinctus
Centaurea scabiosa Halictus rubicundus
Centaurea scabiosa Hylaeus communis
Centaurea scabiosa Lasioglossum costulatum
Centaurea scabiosa Lasioglossum fulvicorne
Cerastium arvense Bombus pascuorum
Cirsium sp Lasioglossum morio
Cirsium vulgare Bombus bohemicus
Cirsium vulgare Bombus rupestris
Clinopodium acinos Bombus pratorum
Clinopodium vulgare Bombus pascuorum
Cotoneaster integerrimus Andrena fulva
Cotoneaster integerrimus Bombus hypnorum
Cotoneaster integerrimus Bombus pratorum
Crataegus monogyna Andrena chrysosceles
Crataegus monogyna Bombus pratorum
Crataegus monogyna Bombus terrestris
Dactylorhiza fuchsii Bombus pascuorum
Dictamnus albus Bombus pratorum
Euphorbia cyparissias Andrena subopaca

Interaction
Euphorbia cyparissias Nomada flavoguttata
Filipendula vulgaris Andrena nitida
Fragaria vesca Nomada flavoguttata
Genista tinctoria Bombus terrestris
Genista tinctoria Megachile nigriventris
Geum urbanum Andrena subopaca
Helianthemum nummularium Anthidium punctatum
Hieracium lachenalii Lasioglossum villosulum
Hieracium murorum Bombus bohemicus
Hieracium umbellatum Bombus pascuorum
Hieracium umbellatum Bombus terrestris
Hippocrepis comosa Andrena nigroaenea
Hippocrepis comosa Andrena subopaca
Hippocrepis comosa Anthidium punctatum
Hippocrepis comosa Bombus terrestris
Hippocrepis comosa Lasioglossum punctatissimum
Hippocrepis comosa Megachile nigriventris
Hippocrepis comosa Megachile versicolor
Hippocrepis comosa Megachile willughbiella
Hippocrepis comosa Sphecodes niger
Hypericum perforatum Bombus pascuorum
Hypericum perforatum Bombus terrestris
Knautia arvensis Bombus hypnorum
Knautia arvensis Bombus lapidarius
Knautia arvensis Bombus pratorum
Knautia arvensis Bombus rupestris
Knautia arvensis Bombus sylvestris
Knautia arvensis Bombus terrestris
Knautia arvensis Ceratina cyanea
Knautia arvensis Coelioxys elongata
Knautia arvensis Halictus rubicundus
Knautia arvensis Halictus scabiosae
Knautia arvensis Halictus simplex
Knautia arvensis Lasioglossum albipes

Interaction
Knautia arvensis Lasioglossum calceatum
Knautia arvensis Lasioglossum morio
Knautia arvensis Lasioglossum pauxillum
Knautia arvensis Megachile versicolor
Lathyrus sylvestris Megachile ericetorum
Leontodon hispidus Anthidium punctatum
Leontodon hispidus Ceratina cyanea
Leucanthemum vulgare Andrena nigroaenea
Leucanthemum vulgare Andrena subopaca
Leucanthemum vulgare Andrena wilkella
Leucanthemum vulgare Bombus hortorum
Leucanthemum vulgare Sphecodes rubicundus
Lotus corniculatus Coelioxys inermis
Lotus corniculatus Halictus tumulorum
Lotus corniculatus Megachile ericetorum
Lotus corniculatus Megachile ligniseca
Medicago lupulina Osmia bicolor
Medicago sativa Bombus pascuorum
Medicago sativa Halictus tumulorum
Melampyrum arvense Bombus hortorum
Myosotis arvensis Bombus pratorum
Ononis sp Anthidium punctatum
Origanum vulgare Halictus rubicundus
Origanum vulgare Halictus tumulorum
Origanum vulgare Lasioglossum morio
Orobanche rapum-genistae Lasioglossum fulvicorne
Polygala comosa Bombus pascuorum
Potentilla sp Lasioglossum pauxillum
Primula veris Andrena nitida
Primula veris Anthophora furcata
Primula veris Bombus pascuorum
Primula veris Lasioglossum pauxillum
Primula veris Osmia bicolor
Prunella grandiflora Bombus hortorum

Interaction
Ranunculus bulbosus Andrena scotica
Ranunculus bulbosus Lasioglossum pauxillum
Ranunculus bulbosus Nomada flavoguttata
Ranunculus bulbosus Osmia aurulenta
Ranunculus repens Andrena subopaca
Rhinanthus minor Bombus hortorum
Rhinanthus minor Bombus pratorum
Sanguisorba minor Bombus pratorum
Senecio sp Halictus tumulorum
Senecio sp Lasioglossum calceatum
Senecio sp Lasioglossum morio
Taraxacum officinale Eucera nigrescens
Trifolium pratense Bombus bohemicus
Veronica austriaca Andrena labiata
Veronica austriaca Bombus terrestris
Veronica austriaca Hylaeus confusus
Veronica austriaca Osmia bicolor
Veronica chamaedrys Andrena viridescens
Veronica chamaedrys Lasioglossum pauxillum
Veronica chamaedrys Osmia bicolor
Vicia sp Bombus sylvarum
Vicia sp Eucera longicornis
Vicia sp Eucera nigrescens

Table S8. Richness of flower visitors (Degree) per plant species in the visitation dataset.

Plant	Degree
Ajuga reptans	2
Alliaria petiolata	1
Anemone sylvestris	2
Anthyllis vulneraria	2
Aquilegia vulgaris	3
Astragalus glycyphyllos	1
Campanula sp	1
Carduus nutans	2
Carlina vulgaris	2
Centaurea jacea	14
Centaurea scabiosa	19
Cerastium arvense	1
Cerinthe minor	1
Cirsium sp	5
Cirsium vulgare	2
Clinopodium acinos	1
Clinopodium vulgare	1
Cotoneaster integerrimus	3
Crataegus monogyna	3
Crepis sp	2
Dactylorhiza fuchsii	1
Daucus carota	1
Dictamnus albus	1
Echium vulgare	1
Euphorbia cyparissias	2
Filipendula vulgaris	1
Fragaria vesca	6
Genista tinctoria	6
Geum urbanum	1
Helianthemum nummularium	3
Hieracium cymosum	1
Hieracium lachenalii	1

Plant	Degree
Hieracium murorum	1
Hieracium pilosella	3
Hieracium umbellatum	2
Hippocrepis comosa	19
Hypericum perforatum	2
Knautia arvensis	19
Lathyrus sylvestris	1
Leontodon hispidus	2
Leucanthemum vulgare	6
Lotus corniculatus	7
Medicago falcata	1
Medicago lupulina	1
Medicago sativa	2
Melampyrum arvense	1
Myosotis arvensis	2
Onobrychis viciifolia	7
Ononis sp	6
Origanum vulgare	3
Orobanche rapum-genistae	1
Plantago lanceolata	2
Plantago media	1
Polygala comosa	1
Potentilla sp	4
Primula veris	7
Prunella grandiflora	2
Ranunculus bulbosus	13
Ranunculus repens	2
Rhinanthus minor	2
Salvia pratensis	3
Sanguisorba minor	1
Senecio sp	4
Silene dioica	1
Stellaria holostea	2
Taraxacum officinale	3

Plant	Degree
Trifolium pratense	4
Trifolium repens	1
Veronica austriaca	6
Veronica chamaedrys	6
Vicia sp	6

Table S9. Richness of flower visitors (Degree) per plant species in the pollen transport dataset.

Plant	Degree
Ajuga reptans	2
Anthriscus sylvestris	2
Anthyllis vulneraria	1
Aquilegia vulgaris	2
Astragalus glycyphyllos	2
Campanula sp	4
Carduus nutans	2
Carlina vulgaris	2
Centaurea jacea	11
Centaurea jacobea	1
Centaurea scabiosa	15
Cerastium arvense	1
Cerinthe minor	2
Cirsium sp	5
Cotoneaster interregimus	1
Crepis sp	11
Daucus carota	1
Echium vulgare	1
Filipendula vulgaris	1
Fragaria vesca	7
Galium sp	4
Genista tinctoria	4
Geum urbanum	2
Helianthemum nummularium	5
Hieracium cymosum	1
Hieracium pilosella	3
Hippocrepis comosa	12
Knautia arvensis	4
Leucanthemum vulgare	1
Lotus corniculatus	4
Medicago falcata	1
Melampyrum pratense	1

Plant	Degree
Mentha type	1
Myosotis arvensis	1
Onobrychis viciifolia	7
Ononis sp	7
Plantago lanceolata	6
Plantago media	3
Potentilla sp	4
Primula veris	2
Prunella grandiflora	1
Pulmonaria sp	1
Ranunculus acris	7
Ranunculus bulbosus	11
Ranunculus repens	1
Rumex obtusifolius	1
Salvia pratensis	4
Sanguisorba minor	4
Saxifraga sp	5
Scabiosa columbaria	2
Senecio sp	3
Silene dioica	1
Silene vulgaris	1
Stellaria holostea	4
Taraxacum officinale	5
Trifolium pratense	6
Trifolium repens	3
Trifolium sp	3
Valeriana officinalis	1
Veronica austriaca	2
Veronica chamaedrys	4
Veronica sp	1
Vicia sp	3
Viola sp	1

Table S10. Full and minimum adequate models for unique interactions and unique interactions' proportion in the visitation and pollen transport datasets. Minimum adequate models were selected with likelihood ratio tests (via "drop1"). Significance levels: ***p<0.001. **p<0.01, *p<0.05

Response variable	Model	Fixed effects	LRT	*P*
Unique interactions	Full visitation	Landscape diversity (150 m) (log) Fragment area (log) Connectivity Index	4.06 0.11 0.018	0.044* 0.74 0.89
Unique interactions	Min visitation	Landscape diversity (150 m)	4.59	0.032*
Unique interactions	Full transport	Landscape diversity (500 m) (log) Fragment area (log) Connectivity Index	4.07 2.35 0.24	0.044* 0.13 0.62
Unique interactions	Min transport	Landscape diversity (500 m)	5.96	0.015*
Unique interactions' proportion	Full visitation	Landscape diversity (150 m) (log) Fragment area (log) Connectivity Index	0.94 0.38 0.64	0.20 0.71 0.53
Unique interactions' proportion	Full transport	Landscape diversity (500 m) (log) Fragment area (log) Connectivity Index	2.79 1.55 0.014	0.11 0.22 0.91
Unique interactions' proportion	Min transport	Landscape diversity (500 m)	5.26	0.030*

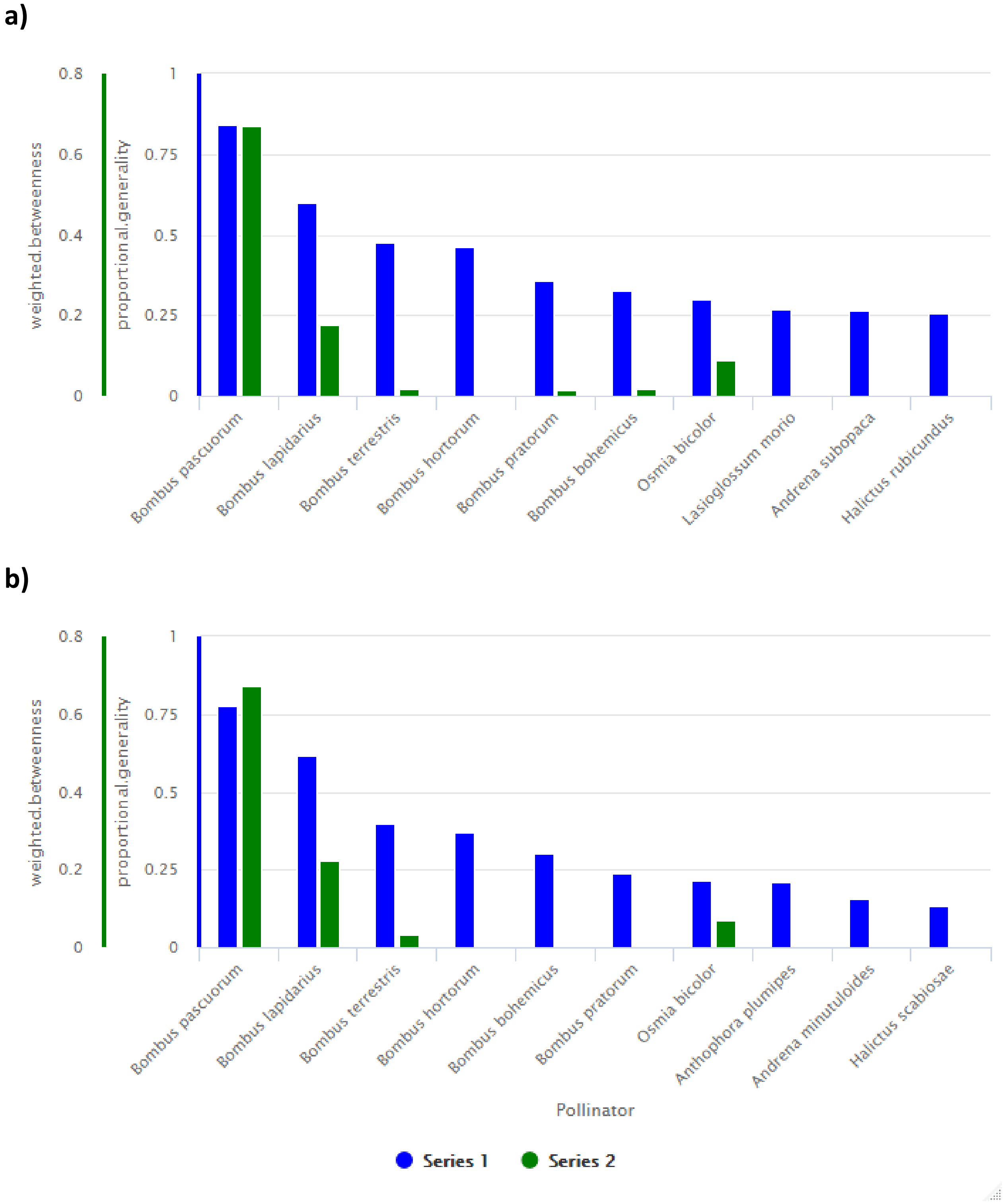
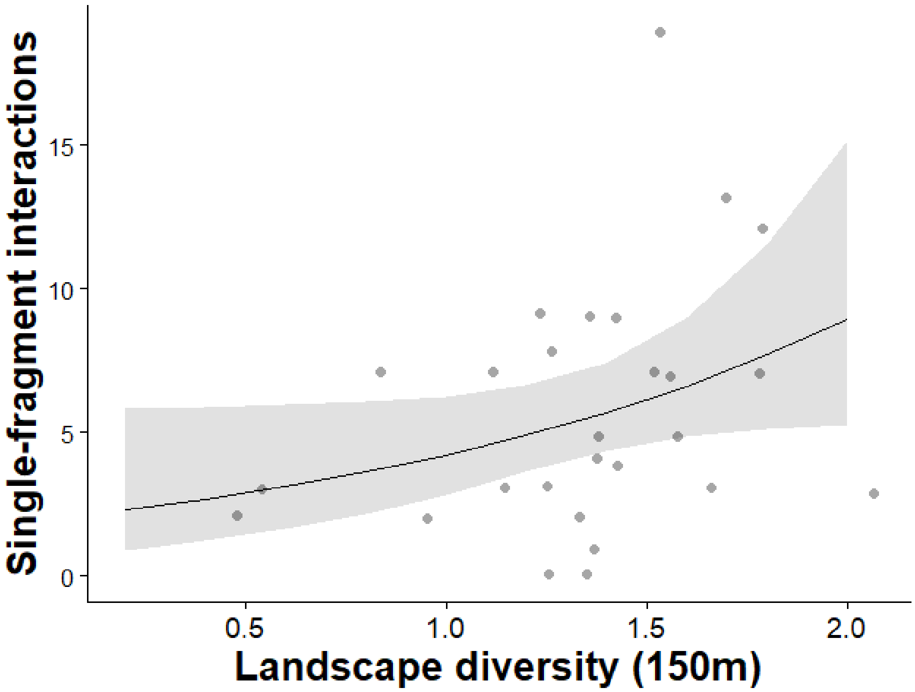


Figure S1. The 10 most central pollinator species based on proportional generality in a) the visitation metanetwork and b) the pollen transport metanetwork.

a)



b)

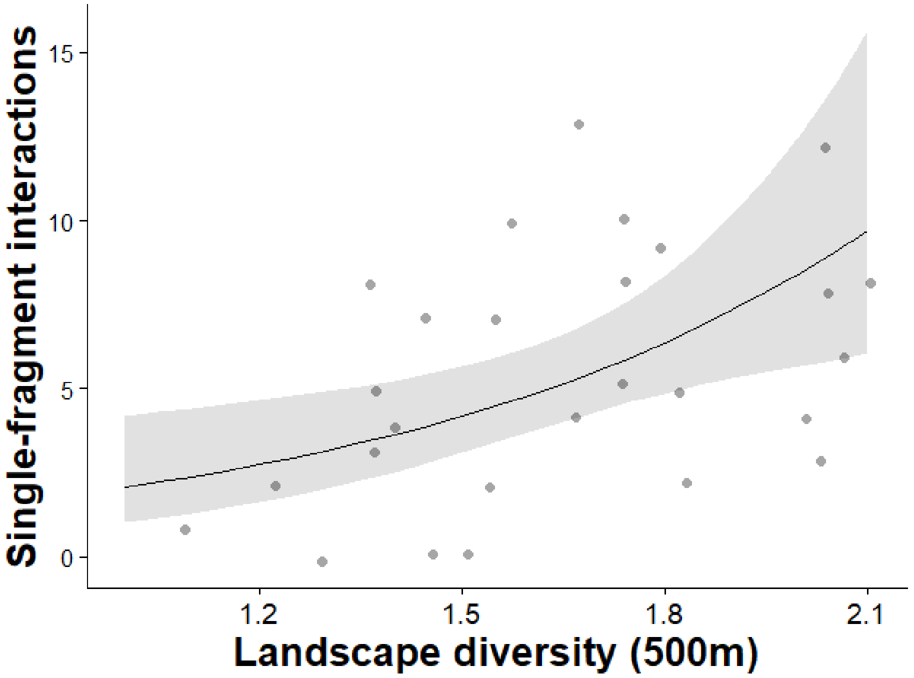


Figure S2. Effect of landscape diversity on the number of single-fragment interactions in local networks in a) the visitation dataset and b) the pollen transport dataset.

CV

Felipe Miguel Librán Embid

Curriculum Vitae

Personal Details

Born: 01/03/1989 - Montevideo/ - Uruguay

Nationality: Uruguayan and Spanish

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E-mail: feliem3@gmail.com

Education

2016 - 2020 PhD student in Agricultural Sciences
Georg-August-University Göttingen, Göttingen, Germany
Title: Plant-pollinator networks in fragmented calcareous grasslands.
Supervisor: Prof. Dr. Teja Tscharntke

2013 - 2015 Master in Ecology (Mestrado em Ecologia)
Universidade de São Paulo, USP, São Paulo, Brasil
Title: Landscape structure effects on the biological control of the coffee-leaf-miner (*Leucoptera coffeella,* Lepidoptera: Lyonetiidae) provided by birds and bats.
Supervisor: Prof. Dr. Jean Paul Walter Metzger

2007 - 2011 BSc in Biological Sciences (Licenciatura en Ciencias Biológicas)
Universidad de la República, UdelaR, Montevideo, Uruguay
Title: Reproductive behaviour in *Austrolebias affinis*, Amato 1986
Supervisor: Dra. Bettina Tassino

Scholarships

1. Georg-August-University Göttingen
    - 2016 – 2019 PhD scholarship by the German Science Foundation (DFG)

2. Universidade de São Paulo – USP
    - 2013 - 2015 MSc scholarship by the PAEC-OEA-GCUB program

3. Universidad de la República- UdelaR
    - 2010 - 2011 Initiation to research scholarship by PEDECIBA (Program for the development of basic sciences)

Field of study

1. Landscape Ecology/ Ecological networks / Ecosystem Services

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Projects

Research projects

2016 - 2020 Plant-pollinator networks in fragmented calcareous grasslands. Financially supported by the German Research Foundation (DFG) through the RTG 1644-“Scaling problems in statistics".

2013 - 2015 Landscape structure effects on the biological control of the coffee-leaf-miner (*Leucoptera coffeella*) provided by birds and bats.
Financed by the University of São Paulo (USP) and the Foundation for research support of the state of São Paulo (FAPESP)

Personal skills and competences

Native tongue

1) **Spanish / Castilian**

Other languages

	Understanding				**Speaking**				**Writing**	
European level (*)	Listening		Reading		Spoken interaction		Spoken production			
2) English	C2	Proficient user	C2	Proficient user	C1	Proficient user	C2	Proficient user	C1	Proficient user
3) Portuguese	C2	Proficient user	C2	Proficient user	C2	Proficient user	C2	Proficient user	C2	Proficient user
4) Italian	B2	Independent user	B1	Independent user	A2	Basic user	A2	Basic user	A1	Basic user
5) German	B2	Independent user	B1	Independent user	B1	Independent user	B1	Independent user	A2	Basic user

(*) Common European Framework of Reference for Languages - Self-assessment grid

Computer skills R language, ArcGis, QGis

Other skills Member of the youth (2006, 2007) and junior (2008) Uruguayan national handball teams

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Relevant graduate courses

- Ecosystem services and landscape planning – Grade A
- Landscape Ecology, concepts and research methods – Grade A
- Advanced statistical methods in Ecology and Evolution – Score 12/12

Awards

- 6th highest GPA of the 2007 biological sciences class (UdelaR, Uruguay).
- Best ecology thesis of 2015 (USP, Brasil).
- “Summa cum laude” grade in PhD dissertation and disputation

Author Publications

Published in peer reviewed journals

1. LIBRÁN-EMBID, F., DE COSTER, G., METZGER, JP.

Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. *Landscape Ecology* **32,** 1907–1920 (2017). https://doi.org/10.1007/s10980-017-0555-2

2. GRASS, I., LOOS, J., BAENSCH, S., BATÁRY, P., **LIBRÁN-EMBID, F.**, FICICIYAN, A., KLAUS, F., RIECHERS, M., ROSA, J., TIEDE, J., UDY, K., WESTPHAL, C., WURZ, A., TSCHARNTKE, T.

Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature* 1: 262– 272 (2019). https://doi.org/10.1002/pan3.21

3. METZGER, JP., BUSTAMENTE, M., FERREIRA, J., FERNANDES GW., **LIBRÁN-EMBID, F.**, PILLAR, V., PRIST, P., RIBEIRO RODRIGUEZ, R., VIEIRA, IC., OVERBECK, G.

Why Brazil needs its Legal Reserves. *Perspectives in Ecology and Conservation*, 17(3), 91-103 (2019). https://doi.org/10.1016/j.pecon.2019.07.002

4. LIBRÁN-EMBID, F., KLAUS, F., TSCHARNTKE, T., GRASS, I.

Unmanned aerial vehicles (UAVs) for biodiversity-friendly agricultural landscapes – a systematic review. *Science of the total Environment.* 732, 139204 (2020). https://doi.org/10.1016/j.scitotenv.2020.139204

In preparation

LIBRÁN-EMBID, F., GRASS, I., GANUZA, C., EMER, C., TSCHARNTKE, T.

A plant-pollinator metanetwork along a habitat fragmentation gradient

LIBRÁN-EMBID, F., GRASS, I., ALARCÓN, V., HERMANN, B., BIAGIONI, S., C., EMER, C., GANUZA, C., HERRERA-KRINGS, C., SETYANINGSIH, CA., TSCHARNTKE, T.

Pollination networks in fragmented landscapes are more specialized for pollen transport than flower visitation

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A PhD thesis demands years of dedication, perseverance and commitment. Also, as plant-pollinator interactions, it makes little sense to be analyzed in isolation. Many people have contributed in this path in direct and indirect ways. Therefore, in the next lines, I will take the liberty of not skimping on words.

My grandmother was a fantastic woman that I had the pleasure to enjoy 19 years of my life. Her name was Esperanza ("hope" in spanish); a name tightly related to what she taught me in life through words and example. One of her most brilliant phrases was "*la matemática es la materia más sencilla que hay, el problema es que padece de muy malos profesores… La materia más difícil son las relaciones humanas"* (i.e. "math is the easiest subject there is, the problem is that lacks good teachers…The toughest subject are the human relationships"). Coming from one of the first female engineers of Uruguay (graduated in the 1950 class) these words had a special meaning and sticked deeply in my head. As usual, I would confirm the truth behind her words over time.

Indeed, mathematical rules are immutable through space and time and a solid ground to base our hypotheses and knowledge. When these logical rules, patterns and relationships are correctly explained then math becomes easy. Human relationships, on the other hand, are an intrinsic part of the human biology as social beings, that are not possible to solve through mathematical rules. Actually, they involve large amounts of variables, which interact with each other and are abruptly changing in space and time. Furthermore, their solution involves many other areas from the brain not related to mathematical thinking, but to emotion and empathy, among others. Clearly Esperanza was right, differently from the common belief, human relationships are far harder than math.

Human relationships permeate every single aspect of our lives and form complex interaction networks and metanetworks shaping our lives, our happiness and our miseries.

The process of learning and the search of knowledge and understanding has always been the motor os my passion and the main sense of my existence. Learning and knowledge have helped me to overcome challenges from a very young age and to see the beauty in life.

A very common trait in Latin Americans is our smiling and cheerful mood. In science and in Germany I can see how surprising and misleading that is. A smile and kind treat might be seen as an unnecessary (non-mathematical) trait related to a lack of consciousness on the severity or importance of certain events. Also, it is often unconsciously associated to a low responsibility and seriousness that could impare a person from dealing with tough or complicated situations/problems. All these being very important skills that a scientist and a person should "theoretically" have.

Independently of our cultural differences, humans from all corners of the world need love and support in their lives and most especially during childhood. For many different reasons, love and support are not guaranteed for many Latin American kids. The ghosts of violence, inequality, food scarcity and educational shortages deny a healthy development for most Latin American kids and are abominations that need to be faced and palliated. Those of us who do survive and reach adulthood develop a set of skills that we used to overcome those challenges, namely smiles and kindness. Kindness to the suffering of other human beings and smiles to face the complex and sometimes almost unbearable events in life. Our smiles are the scars of what we have seen and experienced and our choice on how to deal with life in its beauty and misery. Therefore, far from a weakness, is our best skill to face every single challenge no matter how big and complex.

In this huge network of human interactions that we live in, I like to believe that the artificial modularity that has been imposed to us can be overcome. I dream that humanity can be saved by promoting a higher connectance among us and the planet we all share. I hope that through this amazing network, my kindness can spread beyond the limits of my physical frontiers and reach, in remote places, the souls of those in need.

Having said the above I want to give tailored acknowledgements:

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To my grandparents Esperanza and Aurelio for the gifts of love, beauty, intelligence, sensibility and hope that guided me through dark times and were the very reason to keep fighting.

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To Dr. Carine Emer for all the amazing support, good humor and great discussions. Vc foi um anjo que apareceu do nada para me ajudar! Muuuitíssimo obrigado pelos scripts, as dicas, por me ajudar até final de semana e também me escutar nas horas de dessespero. Não tenho como agradecer!

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La primavera está en
todo su esplendor brillante
la luz del sol
El jardín ~~presenta~~ se estrena do sus
nuevos vestidos verdes
y entre ~~las~~ unas matas erguidas y frondosas
todos los años en ~~este mismo~~ día
surge brillante ~~bajo la~~
~~luz del sol~~ una hermosa.
y cautivante flor.
La flor de la Esperanza.
para mí
Esa flor eres tú

Declaration

I hereby declare that I have written this doctoral thesis entitled “Plant-pollinator networks in fragmented calcareous grasslands” independently, that I have not used other sources or facilities other than the ones mentioned, that I have not used unauthorized assistance and that I have not submitted this thesis previously in any form for another degree at any university or institution.

Göttingen, June 2020

Felipe

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