



# Spatial community turnover of pollinators is relaxed by semi-natural habitats, but not by mass-flowering crops in agricultural landscapes



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## ARTICLE INFO

### Keywords:

β-diversity  
Bees  
Canola  
Germany  
Landscape context  
Oil seed rape  
Species turnover  
Syrphids

## ABSTRACT

Understanding beta-diversity, i.e. species turnover in space and time, is essential for informing conservation actions. Soaring cultivation of mass flowering crops (e.g. oil seed rape OSR) and loss of semi-natural habitats (SNH) can strongly affect populations of native pollinators, yet it remains unclear how OSR and SNH affect spatial and temporal turnover of pollinator communities. Here, we examined how the landscape-scale proportions of OSR and SNH affect spatial and temporal community turnover in solitary bees and hoverflies, two key provider groups of pollination and pest control services in temperate agro-ecosystems. Using a novel grid-based landscape-wide sampling approach, we quantified pollinator communities within ten 1 km × 1 km landscapes representing independent gradients in OSR and SNH availability. We sampled during and after OSR flowering, in two subsequent years, yielding app. 8800 specimens representing 160 species. Spatial community turnover, measured as the slope of the dissimilarity-distance relationship, was not influenced by the proportion of OSR at any time. In contrast, SNH decreased community turnover for bees during OSR flowering and for hoverflies after flowering, likely caused by pollinator movement between land use types. This suggests that a high availability of SNH may help to promote an even distribution of native bees and hoverflies within temperate agricultural landscapes, hereby potentially stabilizing landscape-wide pollination services.

## 1. Introduction

Agricultural landscapes comprise 40% of the terrestrial surface of the Earth (Foley et al. 2005; Martin et al. 2012); maintaining biological diversity in such landscapes is therefore crucial for worldwide biodiversity conservation (Tscharntke et al. 2005; Fahrig et al. 2011). Semi-natural habitats (SNH) such as low-intensity grasslands are ecological key-elements for many species (e.g. Tscharntke et al. 2005; Kormann et al. 2015). Worldwide, SNH are increasingly lost through intensified agricultural practices, with strongly negative effects on local species richness (e.g. Kormann et al. 2015; Scherber 2015). In parallel, the global production of mass-flowering crops is expanding rapidly: The global harvest of oil seed rape (OSR) for example, Europe's most common biofuel crop, has increased by a factor 22.4 between 1961 and 2013 (FAOSTAT 2016).

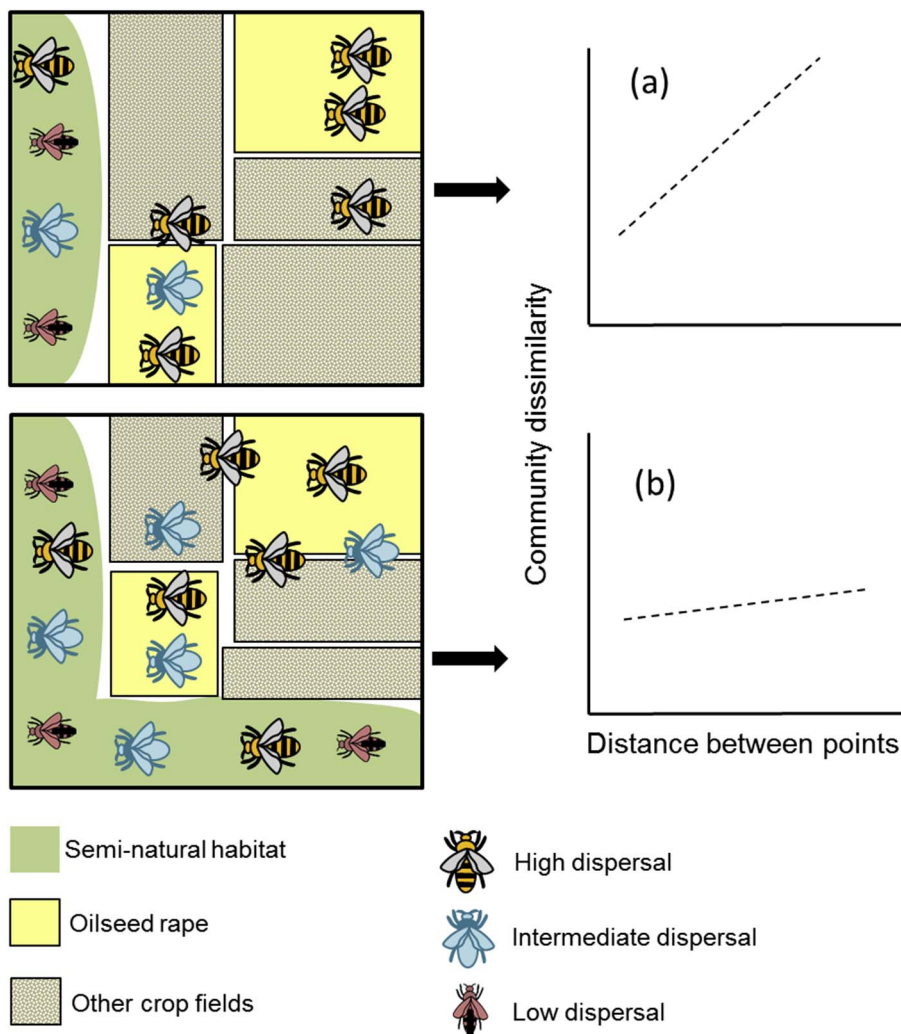
Although several recent studies have investigated the effect of SNH and OSR on biotic communities (e.g. Westphal et al. 2003; Gladbach et al. 2011; Diekötter et al. 2014; Holzschuh et al. 2016), it remains largely unknown how these two landcover types affect biotic

communities beyond simple descriptors of species richness and abundance. Importantly, local species richness or abundance may be inappropriate descriptors for changes in community composition, and only weakly, if at all, reflect patterns of species identities in space and time (Tscharntke et al. 2012; Gámez-Virués et al. 2015; Socolar et al. 2016). This is particularly the case for agro-ecosystems, which are characterized by heterogeneous habitat patches and rapid changes in composition in response to harvest and crop rotation (Wissinger 1997; Thies et al. 2005; Thies et al. 2008). Thus, to understand the processes that shape biodiversity in agricultural landscapes, scientists must explicitly investigate the organization of species assemblages in space and time (Socolar et al. 2016). For example, the few studies that assess the relationship between agricultural intensification and community structure at landscape scales often ignore spatial community turnover, focusing only on alpha or gamma diversity and disregarding the spatial distance between communities in their analyses (Liebhold and Gurevitch 2002; Soininen et al. 2007). This may be risky, as high spatial turnover in species identities (high β-diversity) has been associated with high levels of ecosystem functions and services (Van Der Plas et al.

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**Fig. 1.** Hypothesized relationships between geographical distance and community dissimilarity. (a) Example of a landscape with low proportion of semi-natural habitats (meadows, pastures or forest margins). In this scenario, bees with low or intermediate dispersal abilities (as central place foragers) forage in proximity to semi-natural habitats but cannot access distant resources. This generates a steeper slope for the community dissimilarity-distance relationship. (b) Example of a landscape with high proportion of semi-natural habitats. In this case, there are more resources in arable fields within the foraging distance of bees with low or intermediate dispersal abilities, and thus, a higher proportion of the landscape can be used by those bees for foraging. This generates a shallower slope for the community dissimilarity-distance relationship. Because hoverflies generally disperse over longer distances, and their resources are not habitat-restricted, we predict that they will be characterized by shallower slopes than bees, regardless of the proportion of semi-natural habitats.

2016), which are very important for increasing productivity in agricultural land, reducing the need for further arable land. Moreover, examining spatial patterns of species turnover, in contrast to alpha or gamma diversity, can provide valuable information on how biological communities respond to climate and environmental change (Wiersma and Urban 2005). This information is crucial to understand how the edges of species' ranges are delineated and to help in the planning of conservation areas (Wiersma and Urban 2005; Holt et al. 2005).

Pollinators are critically important for crop production (Klein et al. 2007) and the sexual reproduction of most wild plants (Ollerton et al. 2011). Yet, pollinator populations are known to be highly variable across space and time (Williams et al. 2001), and a diverse set of species can guarantee pollination for a broader suite of plants (Kremen et al. 2002). Similarly, the stability of pollination services in space and time is crucial for agriculture, and has been shown to often increase with the number of pollinator species present in a landscape (McCann 2000; Garibaldi et al. 2011). Diverse pollinator communities can further meet the pollination requirements of a greater number of crops, and provide insurance in the event of shortages of individual species (Kremen et al. 2002; Winfree and Kremen 2009; Garibaldi et al. 2013).

Spatial dispersal processes have been shown to considerably affect community composition and turnover (Cottenie 2005). Communities in agricultural landscapes often consist of species adapted to frequent disturbance events, with dispersal-related traits positively selected for (Harrison and Taylor 1997; Leibold et al. 2004). While (semi-) natural habitats provide spatiotemporally stable resources (Duelli and Obrist 2003) in rather low abundance or quality, temporary cropland habitats,

such as oilseed rape, often contain larger amounts of resources (Tschamntke et al. 2012), generating source-sink dynamics in agricultural landscapes and spillover of organisms among crops and other habitats. Cross-habitat spillover is a function of the movement ability of the species and tends to be restricted for organisms with limited dispersal capacity (Tschamntke and Brandl 2004; Tschamntke et al. 2012).

In this study, we use a novel landscape-wide grid-based sampling scheme (Beduschi et al. 2015; Scherber et al. 2012) to sample mobile pollinating insects across ten 1-km<sup>2</sup> landscapes. We focus on the spatial turnover of solitary bees and hoverflies, two groups that have been shown to respond differentially to landscape structure as a result of distinct resource requirements and dispersal abilities (i.e., foraging ranges) (Gathmann and Tschamntke 2002; Steffan-Dewenter et al. 2002; Holzschuh et al. 2008). For example, solitary bees have a small foraging range of only up to 600 m in agricultural landscapes (Gathmann and Tschamntke 2002). Given that they commute between nesting and feeding sites in order to collect pollen for their offspring, they require small distances between nesting and foraging sites (Gathmann and Tschamntke 2002; Steffan-Dewenter et al. 2002). Hoverflies, on the other hand, have no need to return to their oviposition sites and are able to disperse over greater distances (Jauker et al. 2009; Raymond et al. 2013). Additionally, hoverflies are often more generalist flower-feeders than bees (Biesmeijer et al. 2006), and predatory species often find their prey in arable fields (Meyer et al. 2009). Consequently, hoverflies tend to be less severely affected by agricultural intensification or may even benefit from it (Jauker et al. 2009). Thus, even though bees are considered to be more efficient pollinators (Jauker et al. 2012),

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