



Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands



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ABSTRACT

Pollinator communities exhibit variable responses to changing landscape composition. A general expectation is that a decreasing cover of semi-natural habitats negatively affects pollinator reproduction, population size and pollination services, but few studies have investigated the simultaneous effects of landscape complexity on different aspects of pollinator communities and functioning.

In 20 agricultural landscape plots the size of an average Dutch farm, we studied how changing landscape complexity affected wild bee abundance, species richness and reproduction. To measure pollination, we placed potted strawberry plants as phytometers in landscapes. Landscape complexity was characterized as the area of semi-natural habitats. In addition, we estimated floral resource abundance in each landscape plot. We expected that i) bee species richness, reproduction and pollination would be positively related to area of semi-natural habitats and flower abundance, and that ii) species richness and reproduction would be positively related to pollination.

An increase in semi-natural habitats in landscapes increased both the abundance of cavity-nesting bees colonizing trap nests, and the growth rates of experimental *Bombus terrestris* L. colonies, but not the species richness of wild bees measured by pan traps. There was only a tendency for higher pollination levels of strawberry plants with higher cover of semi-natural habitats. There was no relationship between species richness and bee reproduction in a landscape and the pollination services. Estimated flower abundance in landscape had a positive effect on bumblebee colony growth only and not on the other variables.

Our results suggest that, by improving habitat quality on their farms through establishing more semi-natural habitats or enhancing the flower availability in semi-natural habitats, farmers can promote reproduction of a number of functionally important bee species and the pollination services they provide. Bee species richness, however, seems to be more difficult to enhance and requires more than just creating more of the same type of habitats or flowers.

1. Introduction

The decline of wild pollinators and associated pollination services is largely related to habitat destruction and agricultural intensification, which both reduce the availability of essential floral resources and nesting substrates (Kohler et al., 2008; Winfree et al., 2011; Le Feon et al., 2010). Initiatives to mitigate pollinator loss are currently taken

on a large scale in many countries, inspired by concerns for loss of pollination services and a decline of threatened pollinator species (Pywell et al., 2012; Carvell et al., 2004, 2007; Batáry et al., 2010). The most effective way to mitigate the negative impact of current intensive agricultural practices is to establish new semi-natural habitats targeted to the needs of pollinators, such as wildflower strips or hedgerows (Carvell et al., 2007; Morandin and Kremen, 2013; Scheper et al.,

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2013). Numerous studies have demonstrated that cover of semi-natural habitats is positively related to abundance and diversity of wild bee communities and the services they deliver in agro-ecosystems (Steffan-Dewenter et al., 2002; Tschamtko and Brandl, 2003; Kohler et al., 2008; Loyola and Martins, 2008; Garibaldi et al., 2011).

A general assumption is that a decreasing cover of semi-natural habitats negatively affects reproduction of pollinators which in turn negatively affects population size and subsequently pollination services (Petersen and Nault, 2014). Most studies however, look at descriptors of pollinator communities and pollination services in isolation and provide little or no information on the mechanisms producing the observed patterns. Few studies have examined the relationship between landscape complexity and reproduction of pollinators (but see Holzschuh et al., 2010; Williams et al., 2012). Recent papers show that pollinator species vary markedly in their response to changing landscape complexity, with dominant pollinators showing less response to change in land use than rarer species and pollination services can sometimes be subject to only few, highly dominant pollinator species (Cariveau et al., 2013; Kleijn et al., 2015; Winfree et al., 2015). A likely consequence of such variation in pollinator responses to land use is the finding that pollination is less related to landscape complexity than pollinator diversity (e.g. Garibaldi et al., 2011). Studies that concurrently examine the relations between landscape complexity and pollinator diversity, reproductive success and pollination could provide mechanistic insight.

On the landscape side, a general assumption is that decreasing the cover of semi-natural habitats results in a decline of critical resources such as host plants, pollen, nectar and nesting sites (Potts et al., 2005). Semi-natural habitats may consist of a variety of different habitats (e.g. extensive grasslands, fallows, field margin strips, woodlots, roadside verges and ditch banks) that may differ markedly in the type and amount of resources they offer. Furthermore, resources such as pollen and nectar may also be available outside semi-natural habitats, for example in insect-pollinated crops (Holzschuh et al., 2013). Analyses that compare relations between pollinators, cover of semi-natural habitats and the availability of specific resources required by pollinators could help us explain patterns between landscape complexity and pollinator diversity.

Most studies relate pollinator communities at a single location to the amount of semi-natural habitats in the surrounding landscape (e.g. Steffan-Dewenter et al., 2002). While this facilitates accurate estimates of landscape complexity, it does not necessarily give good estimates of the bee communities inhabiting the landscape because community variables acquired at a single site will be influenced by the specific characteristics of that site (e.g. plant species composition, exposition, soil type). In many parts of the world, management units (i.e. farms, nature reserves) are much smaller than the foraging range of the more mobile pollinator species. As semi-natural habitats in intensive agro-ecosystems are rarely contain enough resources to sustain viable populations of the target species group, pollinators need to repeatedly traverse across using both crop and non-crop habitat types (Westrich, 1996; Osborne et al., 1999; Tschamtko et al., 2012). Measuring the effects semi-natural habitats on pollinator communities at the farm or reserve level may help the implementation of mitigation measures independent of neighbouring land users.

Here we studied wild bee communities in 20 agricultural landscapes in the Netherlands. We quantified and compared the effects of changing landscape complexity on bee species richness, reproductive output and pollination services. We characterized landscape complexity on 50 ha farmlands, as either the area (in ha) covered by semi-natural habitats or as the availability of floral resources. We tested whether bee species richness, reproductive output and delivery of pollination services, measured at the landscape scale, were significantly related to landscape complexity. We also examined whether species richness, reproductive output and pollination were more strongly related to the availability of floral resources than to cover of semi-natural habitats and discuss

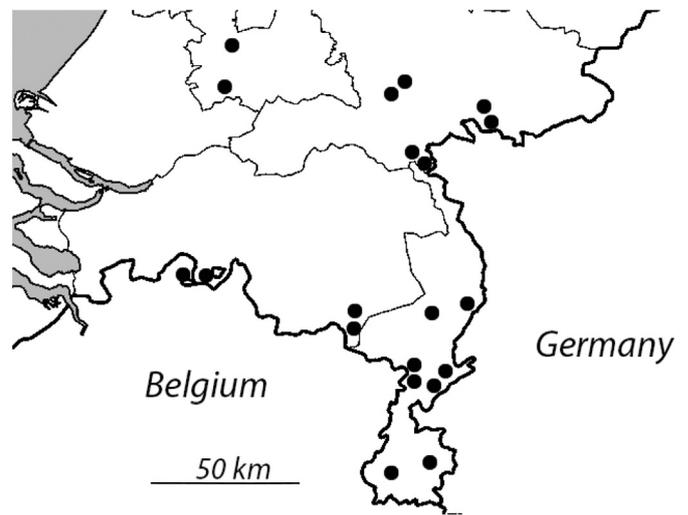


Fig. 1. Map with locations of the 20 experimental landscapes in the Southern and Central part of the Netherlands.

implications for the processes underlying the observed relationships.

2. Materials & methods

2.1. Study sites

In 2012, we selected twenty rectangular 50 ha landscape plots in agricultural areas in the southern and central parts of The Netherlands, scattered across a ca. 10,500 km² large area (Fig. 1; Supplementary Table S2) and located along a landscape complexity gradient. The size and shape of the study area was roughly based on the average size of a Dutch farm (42 ha; CBS, 2015) and therefore the management unit in which measures to mitigate pollinator loss can be independently implemented in the landscape. In each landscape we quantified the cover of different land use types by means of a topographic reference geodataset (Top10NL) in ArcGIS 10.0. We selected landscapes that contained predominantly agricultural land, with high-input or regularly mowed grasslands, arable land, forests and woodlots dominated by a small number of deciduous or coniferous trees and open semi-natural habitats (extensive grasslands, fallows, field boundaries, road verges, and ditch banks). Landscape plots contained little or no buildings and domestic areas (3.1% ± 0.67 S.E.). Our study sites contained the occasional field of spring flowering croplands, such as early sweet cherry and apple (0.8% ± 0.6 SE), two sites contained blueberry and winter oil seed rape was present on a single site. As our study focused on bee communities and pollination in summer time, these crops contained no flowers and were not likely to influence our response variables and thus were not included in our estimates of flower availability.

2.2. Flower availability in landscapes

Flower availability in landscape plots was quantified using a stratified random sampling method similar to that described in Rundlöf et al. (2014) and Scheper et al. (2015). In each landscape plot we mapped the land use types that contained flowers, such as grasslands, road verges, ditch banks and occasionally cereal fields. We subsequently grouped these in eight different habitat classes for which we collected information on flower cover between the end of June to end of August, when the study was carried out. Because we considered our sample size of flower cover in 2012 too low to obtain reliable estimates for the different habitat classes we collected additional information on flower cover in the summer months of 2013. To estimate flower abundance in a landscape, we randomly selected 4–12 transects of 100 m² in each of the eight habitat classes. Transects in each habitat

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