Original Article

The value of small arable habitats in the agricultural landscape: Importance for vascular plants and the provisioning of floral resources for bees

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Abstract

Small remnants of non-arable habitat within the farmland mosaic are considered important for the conservation of farmland biodiversity, but their contribution to landscape-scale species richness is poorly understood. In the present study, we examined the relative contributions of different habitat types to the landscape-scale species richness of vascular plants within farmland of varying landscape complexity. We also analysed pollen collected by bees to examine the extent to which the different habitat types contributed towards the provisioning of floral resources for three taxa (Bombus terrestris, Megachile sp. and Osmia bicornis). We found that plant species richness increased with landscape complexity (defined as the proportion of semi-natural habitats). The relative contribution of small fragments of non-arable habitat to total plant species richness was high within all landscape types, especially in relation to the small area they covered. The importance of small non-arable fragments for the provisioning of floral resources to bees varied over time and between taxa. Bombus terrestris used the different habitat types differently during different parts of the growing season: arable fields were important early in the season, leys late in the season, and small non-arable habitat fragments during the mid-season when no mass-flowering crops were in bloom. In contrast, Megachile sp. and O. bicornis mainly foraged on plants occurring within grasslands. We conclude that small fragments of non-arable habitat are important for plant species richness at the landscape-scale and that their importance for plants may cascade to the bees that use them as foraging resources. Consequently, it is important to consider the entire landscape mosaic when taking actions to conserve farmland species.

1. Introduction

Whereas traditional agricultural landscapes contain a mosaic of different habitats that support a wide range of vascular plant species (Storkey et al., 2012; Wuczyński et al., 2014; Loos et al., 2015), arable expansion at the expense of more permanent, semi-natural habitats has eroded plant species richness (Robinson and Sutherland, 2002; Firbank et al., 2008; Meyer et al., 2013). Intensified management and fragmentation have reduced the habitat quality of the remaining grasslands (Plantureux et al., 2005; Kleijn et al., 2009; Gaujour et al., 2012). In addition, agricultural intensification, including the increased use of fertilizers and herbicides as well as subsurface drainage and simplified crop rotations, has resulted in the loss of many arable plant species (Storkey et al., 2012; Meyer et al., 2013; Richner et al., 2015). The insect pollinators of wild plants, in particular bees, have also declined in response to agricultural intensification and landscape simplification (Biesmeijer et al., 2006; Le Feon et al., 2010; Dupont et al., 2011). Loss and fragmentation of foraging resources, loss of nest sites and the negative impact of pesticides are all factors that have contributed to the decline of wild bees within agricultural landscapes (Potts et al., 2010). Because plants and bees have a mutualistic relationship, the declines in the numbers of plant and bee species may reinforce each other (Kearns et al., 1998; Dupont et al., 2011; Thomann et al., 2013; Clough et al., 2014).

The long-term persistence of populations of many plant species is likely to depend on the maintenance of a landscape mosaic containing a wide range of different habitats (cf. Duelli, 1997; Tscharntke et al., 2005; Bennett et al., 2006; Firbank et al., 2008). In agricultural landscapes, fragments of forest and permanent meadows and pastures may support viable populations of vascular plants (Pykälä et al., 2005; Cousins and Lindborg, 2008). However, many contemporary agricultural landscapes contain only small, more-or-less disjunct fragments...
of such non-arable habitats (Ilse, 1995; Tscharntke et al., 2005). These habitat fragments include midfield inlets, ditches, road verges and non-arable field boundaries (hereafter collectively referred to as “small biotopes”). Small biotopes can reduce the negative effects of habitat loss by providing refugia for many of the organisms that depend on non-arable habitats (Marshall and Moonen, 2002; Duelli and Obrist, 2003; Croxton et al., 2005). For example, while many plant species cannot maintain viable populations in arable fields alone, forest species can persist in hedgerows (Särövä Herlin and Fry, 2000; de Blois et al., 2002; Aavik et al., 2008), grassland species in fragments of permanent vegetation (Smart et al., 2002; Cousins, 2006; Lindborg et al., 2014), and wetland species in open ditches (Avik et al., 2008; Herzon and Helenius, 2008), within agricultural landscapes. Small biotopes may also provide refugia for arable weeds that are adversely affected by in-field intensification (Fried et al., 2009). Despite the presumed importance of small biotopes for the maintenance of species diversity, the contribution of these incidental habitats to landscape-scale species richness in intensively farmed landscapes is still poorly understood.

Levels of plant species richness are not only affected by local conditions, but also by the composition of the surrounding landscape and, in particular, plant species richness is expected to increase with increasing ecological complexity (e.g. Tscharntke et al., 2005; Gaujour et al., 2012). Large areas of non-arable habitat within the landscape are likely to have an overall positive influence on the local richness of plant species within small biotopes (Avik and Liira, 2009; Lindborg et al., 2014; Irminger Street et al., 2015), which could suggest that small biotopes harbour higher biodiversity in complex landscapes. However, the conservation value of a particular patch of habitat will not only depend on the local species richness but also on the composition of the surrounding landscape. For example, woodland species are less likely to depend on hedgerows for their survival in landscapes where patches of forest are present than in landscapes where they are not. Within agricultural landscapes, a high proportion of a particular non-arable habitat in the surroundings may reduce the contribution of smaller fragments of that habitat to the overall species diversity at a landscape scale (cf. Tscharntke et al., 2005), suggesting that the conservation value of small biotopes may be higher in simple landscapes than in more complex landscapes.

The relative importance of different habitat types for overall biodiversity is usually assessed by comparing their local species richness (Grashof-Bokdam and van Langevelde, 2004; Biller et al., 2008). One of the main limitations of this approach is that the degree of habitat specialization is not taken into consideration (Lande, 1996). Plant communities may have similar levels of species richness but differ in their species composition and, therefore, in their functional diversity and degree of habitat-specialization. The habitat specificity measure proposed by Wagner and Edwards (2001) instead considers both the number of species within a habitat and the degree to which those species are ecologically dependent on that particular habitat. Habitat specificity is calculated on the basis of the relative abundance of each species within a given habitat type and on the proportion of the total area of the landscape that is covered by that habitat type. The habitat specificity measure provides an estimate of the relative contribution made by a habitat type to the total species richness within a landscape and can consequently be used to extrapolate from data collected at a patch scale to a landscape-scale (Wagner and Edwards, 2001).

As central-place foragers, bees depend on a supply of pollen and nectar in the vicinity of their nests, and the potential foraging distances vary between species from a few 100 m to several km (Gathmann and Tscharntke, 2002; Steffan-Dewenter et al., 2002; Zurbucher et al., 2010). In structurally simplified agricultural landscapes, the distance between potential nest sites and high quality habitat may be large, compelling bees to also use less-preferred foraging habitats, such as small biotopes (Osgathorpe et al., 2011), in order to maximize the amount of food they bring back to the nest (Olsson et al., 2015). In addition, the more far-reaching social bumble bees require a constant supply of pollen and nectar to sustain their offspring (Benton, 2006). To reduce the spatio-temporal variation in forage availability, many bee species therefore use flowers in multiple habitats (Bronstein, 1995; Williams and Kremen, 2007) and track available resources throughout the landscape over the season (Westphal et al., 2009; Mandelik et al., 2012; Williams et al., 2012). For example, mass-flowering crops such as oilseed rape (Brassica napus) and red clover (Trifolium pratense) may provide forage at least to some bee species (see e.g. Lindström et al., 2016), but then only during restricted periods (Westphal et al., 2003a; Rundlöf et al., 2014). When those crops are not available, other flowerrich habitats such as semi-natural grasslands or small biotopes may provide alternative floral resources (Jha et al., 2013). Bees may, therefore, use mass-flowering crops and flower-rich non-arable habitats alternately over the season (Hanley et al., 2011; Holzschuh et al., 2011; Mandelik et al., 2012; Rundlöf et al., 2014), and the relative importance of different habitat types as providers of floral resources may change over the season (Mandelik et al., 2012). In intensively farmed landscapes, floral resources provided by natural habitats, including small biotopes, may be important also for species able to utilize mass-flowering crops during the part of the season when mass-flowering crops are not in bloom (Williams and Kremen, 2007; Persson and Smith, 2013). For species less able to utilize mass-flowering crops, the value of small biotopes may show less seasonal dependence. However, the contribution made by small biotopes to the foraging patterns, provisioning and persistence of bee populations across the season are poorly understood.

The aim of the present study was to investigate whether small biotopes serve the dual function of maintaining plant species richness at landscape-scales and benefitting the pollinators that may be important for the long-term persistence of the plant populations. We evaluated the relative contributions of small biotopes to the landscape-scale species richness of (i) all vascular plants and (ii) of plant species that provide pollen and nectar resources for bees. We also (iii) evaluated the extent to which bees use small biotopes as pollen resources and how the use of small biotopes varied across the season. We expected that the relative contribution of small biotopes to plant species richness would depend on landscape complexity. We also predicted that the extent to which small biotopes were used as foraging habitat would differ between solitary and social bees.

2. Methods

2.1. Study area

The study was carried out in the province of Scania, south Sweden. As a first step towards determining the importance of small biotopes for plants and pollinators, in the context of varying levels of landscape complexity, we divided the province into 2.5 × 2.5 km landscape squares and assigned those that fulfilled relevant criteria to one of three landscape types. Following Irminger Street et al. (2015), the three landscape types were defined in terms of the proportions of arable fields and pastures out of the total land-cover, as well as the total length of uncultivated field boundaries (Table 1). Non-arable habitats were largely absent within “simple agricultural landscapes”. The “complex agricultural landscapes” were also dominated by arable fields but, because of smaller field sizes, they contained a significant proportion of small biotopes in the form of field boundaries. Finally, the “pasture

<table>
<thead>
<tr>
<th>Field boundaries (km)</th>
<th>54.9 ± 10.4</th>
<th>100.0 ± 10.9</th>
<th>98.4 ± 20.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pastures (%)</td>
<td>0.9 ± 1.5</td>
<td>2.4 ± 1.1</td>
<td>17.5 ± 4.2</td>
</tr>
<tr>
<td>Arable fields (%)</td>
<td>86.7 ± 7.5</td>
<td>85.4 ± 3.3</td>
<td>36.5 ± 7.0</td>
</tr>
<tr>
<td>Simple</td>
<td>Complex</td>
<td>Pasture</td>
<td></td>
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</tbody>
</table>

Table 1 The extents of arable fields and pastures, and field boundary length (mean ± SD) within the 10 selected landscape squares within each of the three defined landscape types.
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