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Landscape features are a better correlate of wild plant pollination than agricultural practices in an intensive cropping system

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ABSTRACT

Organic farming is commonly associated with increased pollinator diversity and abundance, but the net effects on pollination rates are less documented. Besides, organic farms are often surrounded by more diverse landscapes than conventional farms, such that the contributions of landscape diversity vs. farming practices to pollination rates are often confounded with each other. Here, the roles of local vs. landscape scale variables on pollination rates of experimental plants are examined in agricultural landscapes. To this end, fruit set and seed production were measured in the obligate insect-pollinated *Lotus corniculatus*. Plants were located in pairs of neighboring organic vs. conventional farms, which were characterized by contrasting landscape structures and compositions. Fruit set, a proxy for pollinator visitation rates, was significantly related to landscape variables: fruit set was higher in farms close to a patch of semi-natural habitat, but lower in landscapes with a high cover of semi-natural habitats. Fruit set also correlated with local variables, such as habitat type, but not with farming type. Identical pollination rates in conventional and organic farms are likely due to similar diversities of habitats, crops and weeds in both farming types of the study area. These results therefore confirm that habitat diversity prevails over pesticide-free practices to explain the higher pollinator abundances usually observed in organic vs. conventional farms.

1. Introduction

The ongoing loss of biodiversity in agricultural landscapes (e.g., Robinson and Sutherland, 2002) is believed to alter animal pollination, an ecosystem service essential for food production (Deguines et al., 2014; Klein et al., 2007) and for the sexual reproduction of many wild plants (Kearns et al., 1998; Ollerton et al., 2011). Beyond the simple effect of reduced numbers of pollinators, the pollination crisis may also be related to declines in the functional diversity of pollination networks, which can lower reproductive success and community persistence (Fontaine et al., 2006). Pollinator declines have been reported numerous times (Potts et al., 2010; Steffan-Dewenter et al., 2005; Winfree et al., 2009 for reviews), particularly in intensive agricultural landscapes, and the expected parallel declines of insect-pollinated plants are already observed at large scales in Europe (Biesmeijer et al., 2006). Plants provide food and habitats for many animal species involved in biological control for example, so that pollinator-induced changes in plant communities and their diversity could also have cascading effects on other ecosystem services (Scherber et al., 2010).

The design of efficient conservation schemes to reverse the loss of pollinators and pollination services in agroecosystems requires a complete understanding of the mechanisms responsible for this downward trend. Positive effects of organic farming on pollinator species richness and abundance have been documented numerous times (Clough et al., 2007; Holzschuh et al., 2010, 2008; Holzschuh et al., 2007 Kennedy et al., 2013; Kremen et al., 2002,b; Rundlöf et al., 2008a,b; Rundlöf and Smith, 2006), which suggests that agricultural practices in conventional fields are partly responsible for pollinator loss. Pesticide-free practices, together with abundant and diverse floral resources, likely provide higher quality crop and non-crop habitats and food sources in organic vs. conventional farms. Organic farms could therefore sometimes sustain populations of wild pollinators without requiring semi-natural habitats, thanks to high-quality foraging and nesting sites (Williams and Kremen, 2007).

However, the effective impact of organic farming on pollinators and pollination is still open to discussion. First, the actual effects of

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organic farming often depend on the landscape context, with higher benefits in intensive landscapes (Rundlöf and Smith, 2006; Holzschuh et al., 2007; Rundlöf and Smith, 2006). Second, organic farms often encompass a larger proportion of semi-natural habitats (e.g., grassland, field boundaries or hedgerows) than conventional farms (Feber et al., 2007; Fuller et al., 2005; Gibson et al., 2007; Norton et al., 2009). Pollinator abundance and diversity are known to depend on the presence and proximity of semi-natural habitats (reviewed in Ricketts et al., 2008), which provide both nesting sites and foraging resources, so that the observed positive effects of organic farming on pollinators could be mostly attributable to a landscape effect, which has considerable implications to design conservation schemes. Finally, most studies of the impact of agricultural practices have focused on pollinator diversity and abundance (Andersson et al., 2012 but see e.g., Brittain et al., 2010b; Carvalheiro et al., 2010), whereas pollinator abundance and pollination efficiency are sometimes only weakly correlated (Ricketts et al., 2008). There is thus a need to (1) further disentangle the relative effects of in-field agricultural practices (influencing the quality of the agricultural matrix as a foraging and nesting resource) vs. landscape features (isolation from semi-natural habitat) on pollination, and (2) measure actual pollination efficiency as a necessary complement to pollinator abundance.

Here, the pollination rate of potted birdsfoot trefoil plants (*Lotus corniculatus* L., Fabaceae), estimated in terms of fruit and seed set, was compared across contrasting landscapes using a paired design (eight pairs of organic/conventional farms) in an intensive agricultural region in France. The following questions were specifically addressed: (1) Is wild plant pollination higher in organic vs. conventional farms regardless of landscape features? If organic practices favor pollinator survival and reproduction in the agricultural matrix, a positive effect of organic farming is expected irrespective of the distance to or proportion of semi-natural habitats in the surroundings. (2) How do semi-natural habitats influence pollination rates in farms? An increase in pollination rates is expected closer to semi-natural habitats (if the latter act as sources of pollinators) or with larger proportions of semi-natural habitats (as providers of food resources), at least in conventional farms.

2. Material and methods

The pollination of experimental plants was monitored in eight pairs of crop farms in the intensive agricultural region surrounding Paris, France. Each pair consisted of one conventional and one organic farm located close to each other (Supplementary Fig. 1, mean distance between paired farms 2915 m; range: 490–6000 m). A farm is defined as a collection of fields managed by the same person, hence under identical practices. Organic farms are rare in the study region, such that their fields are often interspersed with conventional fields. To avoid confounding effects of neighboring agricultural practices (e.g., contamination by pesticides from an adjacent conventional field) eight organic farms consisting of clustered fields were sampled first. A conventional farm of similar size was then selected within five kilometers of each organic farm (Supplementary Fig. 1). The eight pairs of farms were located in contrasting landscapes, which were described a posteriori by the quantity and proximity of semi-natural habitats (see Section 2.2).

All farms grew mainly cereals, the dominant crops in the study region, except one organic farm that also included a few grasslands and a small sheep herd. Organic farms grew a significantly larger number of crops than conventional farms (Supplementary Table 1; mean ± SD: 9 ± 2.4 in organic farms vs. 5.6 ± 1.1 in conventional farms, Student's test, $P = 0.005$). Some of the supernumerary crops grown in organic farms are pollinator-attractive plants, so that one may expect higher pollinator visitation rates in organic farms. Note however that pollinator-attractive crops represented a small proportion of arable land in both farming systems, and that conventional farms also grew pollinator-attractive crops (e.g., oilseed rape, Supplementary Table 1).

In each farm two experimental sites were selected in each of two habitats: set-asides and margins of cereal fields. One conventional farm (C6) contained no set-aside that year; all sites were thus located in margins of cereal fields. Set-asides contain numerous pollinator-attractive flowers in contrast to margins of cereal fields; the two habitats can be compared to evaluate the influence of local resource availability on pollination rates. Within a farm, experimental sites were chosen so that they were widely distributed over the farm area, yet never adjacent to a conventional field in organic farms (and vice versa) or to mass-flowering crops such as oilseed rape or buckwheat. No managed honeybee hive was present within the studied farms. The mean distance between two sites within a farm was 750 m (range: 175–2040 m).

2.1. Measurement of pollination efficiency

The self-compatible, strictly entomogamous (Ollerton and Lack, 1998) birdsfoot trefoil was used to quantify pollination by several *Bombus* species, which are abundant in the study area. The cultivated forage crop varieties Leo and Baco were chosen to minimize individual variation in morphological traits such as number of flowers per inflorescence. Wild *L. corniculatus* is common in the study region (although it was not found in the direct vicinity of the experimental sites, see below) but was not cultivated as a crop in the study area.

All plants were first grown together in an insect-proof greenhouse from April to June 2009. A total of 256 pots, each containing three to five individuals of either variety (Leo 128 pots; Baco; 128 pots) were used for this experiment. Just before flowering, potted plants were moved to experimental sites, with four individual pots per site (two pots of each variety to prevent potential self-incompatibility among individuals of the same variety). No native *L. corniculatus* plants were found in the close vicinity of the sites. After two weeks in the field, i.e., just before farmers started harvesting fields and mowing set-asides, plants were brought back to the insect-free greenhouse. Every inflorescence was labeled and the number of flowers counted. At pod maturity, fruits of each inflorescence were counted, harvested and opened to count seeds.

A substantial number of plants were lost in the field, due either to water deprivation or to the destruction of pots by farmers or wild boars: only 93 pots from 51 (instead of 64) sites were retrieved. This loss created two imbalances in the dataset: there were many more pots of the Baco than of the Leo variety (78 vs. 15) and data were available for one habitat only in two farms (C5 and C8, see Supplementary Fig. 1), in addition to farm C6. However, discarding the Leo variety or the farm pairs 5, 6 and 8 did not modify our main results. Results presented here are therefore based on the full dataset.

During the experiment, positive and negative controls were grown outside and inside the greenhouse. The negative controls consisted of 12 pots of each variety kept in the insect-free greenhouse during the flowering period. Inflorescences were labeled and flowers counted (total: 694 flowers on 200 inflorescences). At the end of the experiment, no fruit was found on any of the marked branches. The positive controls consisted of three sites of four pots (two of each variety, as in the farms) located in a grassland nearby the greenhouse, surrounded by natural habitats. In the positive controls, the number of fruits and seeds per fruit was counted on each inflorescence. The between-variety difference in fruit and seed production was tested using generalized linear mixed-effects models (glmer, R package lme4), with the