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Effects of landscape complexity on pollinators are moderated by pollinators' association with mass-flowering crops

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Conserving and restoring semi-natural habitat, i.e. enhancing landscape complexity, is one of the main strategies to mitigate pollinator decline in agricultural landscapes. However, we still have limited understanding of how landscape complexity shapes pollinator communities in both crop and non-crop habitat, and whether pollinator responses to landscape complexity vary with their association with mass-flowering crops. Here, we surveyed pollinator communities on mass-flowering leek crops and in nearby semi-natural habitat in landscapes of varying complexity. Surveys were done before and during crop bloom and distinguished between pollinators that visit the crop frequently (dominant), occasionally (opportunistic), or not at all (non-crop). Forty-seven per cent of the species in the wider landscape were also observed on leek flowers. Crop pollinator richness increased with local pollinator community size and increasing landscape complexity, but relationships were stronger for opportunistic than for dominant crop pollinators. Relationships between pollinator richness in semi-natural habitats and landscape complexity differed between groups with the most pronounced positive effects on non-crop pollinators. Our results indicate that while dominant crop pollinators are core components of crop pollinator communities in all agricultural landscapes, opportunistic crop pollinators largely determine species-richness responses and complex landscapes are local hotspots for both biodiversity conservation and potential ecosystem service provision.

1. Background

Biodiversity in agricultural landscapes is rapidly declining [1] along with the ecosystem services it provides [2]. Loss of semi-natural habitat, or landscape simplification, is generally considered to be one of the main drivers underlying these declines [3]. Insect pollinators of crops are among the best examined species groups and show a particularly consistent decline with reductions in the proportion of semi-natural habitat in the landscape (i.e. landscape complexity [3,4]). Ecological intensification has been proposed as an approach to maintain high yield levels while at the same time promoting biodiversity in agricultural landscapes [5,6], in particular by conserving and restoring semi-natural habitats in agricultural landscapes [6,7]. However, we still lack the knowledge of how landscape complexity modifies the crop and non-crop pollinator communities in agricultural landscapes, and how pollinator responses differ depending on their association with mass-flowering crops. Elucidating these patterns may help us to design effective management strategies that unite the goals of enhancing and protecting crop pollination services with wider biodiversity conservation.

Pollinator species differ in the extent to which they use crops as a food source, which can be used to classify them into different functional groups. Crop flower visitation is generally dominated by a relatively small number of species that are particularly able to exploit mass-flowering crops and thereby contribute most to crop yield (dominant crop pollinators; [8]). Other pollinator species may only make opportunistically use of crop flowers, as they are only occasionally observed on crops and usually in small numbers (henceforth referred to as opportunistic crop pollinators). Recent studies have shown that these species can make a significant contribution to crop pollination that is additional to that of the dominant crop pollinators [9,10]. However, the majority of all the species that occur in agricultural landscapes within flying distance of a crop may never be encountered on crop flowers because they for example do not collect pollen (cuckoo bees), or are specialized on other plant species [11]. The proportion of the three different functional groups (dominant, opportunistic and non-crop pollinators) of pollinator species in the local species pool (i.e. the species in the semi-natural habitat) is unknown and may furthermore change with the size of the local species pool (figure 1). In turn, this is generally related to the proportion of semi-natural habitat in the landscape (figure 1) because agricultural fields rarely provide all the resources required by pollinators to complete their life cycle [3,4].

It may be expected that the relationship with landscape complexity is stronger for non-crop pollinators than for species that can use crop resources because non-crop pollinators rely on semi-natural habitats for provision of all their resources, while crop visitors can obtain part of their floral resources outside semi-natural habitats. For similar reasons we may expect relationships with semi-natural habitat cover to be stronger for opportunistic crop pollinators than for dominant crop pollinators. With larger complexity of the landscape, not only the local species pool size may differ but also the relative contribution of the three groups of pollinators to that local species pool. Furthermore, these relationships are probably influenced by whether the crop is flowering or not. During crop flowering, part of the local species pool, i.e. the species that forage on crops, will be concentrated on the crop fields [4], potentially freeing up floral resources for the pollinators remaining behind in the semi-natural habitats. Whether this strengthens or weakens relationships between landscape complexity and the species pools of the three groups of pollinators has yet to be determined.

Abundance, rather than diversity, of crop pollinators is the main contributor to crop pollination service delivery [8,12]. A final issue that therefore needs to be considered is whether the relationships between local pollinator species pool size and landscape complexity are indicative of the relationships between pollinator abundance and landscape complexity. This is not necessarily the case because in agricultural landscapes dominant crop pollinators species may make a small contribution to the local species pool but often make up the majority of all pollinators in the crop [8]. In the crop, abundances of these dominant crop pollinators usually increase with increasing landscape complexity because with increasing cover of semi-natural habitat surrounding crop fields more individuals can move into these fields when they start to flower [13–15]. We can only speculate how the migration of large numbers of pollinators out of the semi-natural habitats affects the abundances of the individuals that remain in the semi-natural habitats during crop flowering [15].

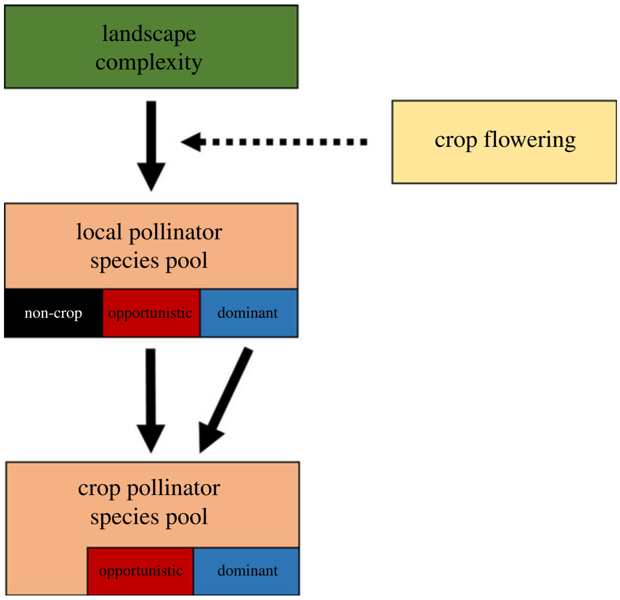

Figure 1. The local pollinator species pool (i.e. species pool in nearby semi-natural habitats) in agricultural landscapes is expected to be related to landscape complexity, but this relationship may differ between functional groups of pollinators depending on their association with crops, and this relationship may be moderated by crop flowering. The size of the local pollinator species pool is likely to be related to the crop pollinator species pool, but may differ for functional groups that differ in their association with crops. (Online version in colour.)

Here we study whether pollinator communities on crop fields (crop pollinator species pool) are related to the pollinator communities in semi-natural habitats (local pollinator species pool) in landscapes of varying structural complexity, and whether this relationship differs with the association of pollinator species with crops (figure 1). We surveyed pollinators in the landscape and in the mass-flowering, hybrid leek-seed production fields in 18 agricultural landscapes in Italy both prior and during crop flowering (see [10] for the pollination effects on crop yield). We examined what proportion of the local pollinator species pool size contributes to crop pollination and examined whether the size of the local species pool was related to the number of species observed on crop flowers. We subsequently tested how the species pool size and abundance of pollinators are related to landscape complexity, and whether this was moderated by crop flowering, and by functional groups based on pollinators' association with crops. Our results provide important insights into whether and how landscape-scale management can simultaneously benefit biodiversity conservation and ecosystem service delivery objectives.

2. Methods

(a) Study system and landscape selection

Our study area is situated in southern Italy in a Mediterranean agricultural landscape spanning about 615 km^2. The main cultivated crop in this area is wheat, but several other crops are cultivated as well such as tomato, field bean, asparagus, and our focal crop leek (*Allium porrum*) for hybrid seed production. Flowering leek is an attractive crop for insect pollinators, and high abundances and a high diversity of species have been found on leek in earlier studies [10,16]. Depending on the altitude, leek flowers for approximately four to six weeks in June and July.

In autumn 2015 we selected 18 leek fields (0.5–2 ha) along a gradient of semi-natural habitat cover (%) to examine relationships between landscape complexity and species richness and abundance of pollinators in the landscape as well as in the crop [10]. Because altitude was generally positively correlated with the cover of semi-natural habitat, we took special care to select sites with lower altitude and high semi-natural cover and vice versa. After selection, landscape complexity ranged from 0.4% to 55.4% semi-natural habitat cover (mean = 20.30% ± 18.4 s.d.). The field sites were usually located 2000 m or more from each other, so that there was no overlap in landscape cover. Because the average flight distance of most bees, the majority of leek pollinators [10], is less than 1000 m [17], the field sites can be considered independent of each other.

(b) Pollinator and flower surveys

In each landscape we surveyed pollinator abundance and species richness using standardized transect walks in the crop and in semi-natural habitats in the landscape surrounding the crop fields. Transects in the semi-natural habitat were located in flower rich herbaceous focal areas at on average 290 m ± 145 s.d. (range: 77–537 m) distance from the leek fields. Pollinators in the semi-natural habitat transects therefore had access to both the crop field and semi-natural habitats. On each observation day we walked one transect in semi-natural herbaceous habitat based on the most flower rich patches in the focal area, and one fixed transect in flowering leek fields. Transects in semi-natural habitats were visited five to seven times (mean 5.5 ± 0.8 s.e.) of which two to four times were before crop flowering (mean 2.6 ± 0.1 s.e.) and two to four times during crop flowering (mean 2.9 ± 0.1 s.e.). Crop transects were visited three to five times (mean 3.8 ± 0.7 s.e.). We visited each transect with a minimum of five days between subsequent visits between 19 May 2016 to 10 July 2016 and only under weather conditions that are favourable for pollinator activity [16].

Transects consisted of 150 m^2 of pollinator habitat, divided over three contiguous sub-transects of 50 m^2 to spread sampling time evenly over the transect [14,18]. Transect width was fixed to 1 m in crop fields, but varied from 1 to 3 m width in semi-natural habitat and length was adjusted accordingly. We observed each sub-transect for 5 min net collection time by slowly moving up and down alongside the transect boundary (15 min in total per transect), and recorded all bees and hoverflies that were clearly associated with flowers (i.e. excluded flybys) [14,18]. Pollinators were identified on the wing whenever possible. When this was not possible pollinators were collected for later identification to the lowest taxonomic level possible. Directly after surveying the pollinators in each transect in semi-natural habitat, we visually estimated the flower cover (%) of each plant species for each sub-transect with increasing accuracy with decreasing flower cover (i.e. 10% cover with 1% accuracy, and 1% cover with 0.1% accuracy). If the flower cover of a species was estimated to be lower than 0.05% (250 cm^2 per sub-transect), we set the flower cover for that species at 0.025%. We summed the flower covers of each plant species to obtain total flower cover estimates (%).

(c) Landscape complexity

We quantified landscape complexity as the cover (%) of semi-natural habitat such as woodland, semi-natural grassland, fallow arable fields, and road verges in a radius of 1000 m around the centre of the leek fields. To estimate total cover of roadside verges we first determined the total road length and then multiplied this with an assumed standard 1 m width of road verge on each side of the road. The delineations and classifications were based on aerial imagery and ground-truthed by visual inspection of the fields and by using up-to-date RGB satellite imagery of 22 July 2016 (10 m spatial resolution, source: Sentinel 2, processing level 1C). The main mass-flowering crops other than leek were field bean (mean 3.7% cover), tomato (1.8%) and asparagus (0.4%). Field bean flowered well before the sampling period of this study and in this study area is visited mainly by species that were no longer active during the current study (*Eucera* spp., *Anthophora plumipes*, *Xylocopa violacea* and *Bombus hortorum*; T. Fijen 2018, personal observation). We considered the temporal overlap and/or range in cover of mass-flowering crops to be insufficient for producing meaningful results and therefore did not consider this factor in our analyses.

(d) Analysis

Before analysis, we first assigned each encountered pollinator species to one of the functional groups: dominant, opportunistic or non-crop pollinators. Kleijn *et al.* [8] define dominant crop pollinators as bee species that comprise at least 5% of all crop pollinators in a single study. If we would use this criterion based on the data from our own survey, the maximum possible dominant crop pollinator species would be 20. Because the number of opportunistic pollinator species is not bound by such an upper limit this could inherently lead to opportunistic pollinators being more responsive to explanatory variables than dominant crop pollinators. We therefore classified pollinators as dominant crop pollinators if they were listed as dominant crop pollinators in any of the European crops by Kleijn *et al.* [8]. Unfortunately, such a database does not exist for hoverflies and we therefore chose to define hoverfly species as being dominant if they comprised at least 5% of all crop pollinators counted in our own crop fields. To check whether the use of different classification criteria affected the results we also ran two sets of analyses using alternative classifications: dominant crop pollinators based on our own survey data, or based on Kleijn *et al.* [8] but excluding hoverflies. These different classifications resulted in the same overall patterns (electronic supplementary material, figures S1–S8) except for the densities of opportunistic crop pollinators in the semi-natural habitats before crop flowering when excluding hoverflies (electronic supplementary material, figure S8, see results). All other pollinators found in our crop fields were classified as opportunistic crop pollinators. Species that were only encountered in semi-natural habitat were classified as non-crop pollinators. Honeybees (*Apis mellifera*) are common in the area, and because we are interested in the patterns of wild pollinators, we excluded honeybees from all analyses. However, analyses including honeybees as a dominant crop pollinator yielded qualitatively similar results (electronic supplementary material, figures S9–S12), and mean abundances of honeybees were not related to landscape complexity (electronic supplementary material, figure S13). Because the sampling effort between field sites differed, we used bootstrapping to estimate the average cumulative number of species per functional group, standardized to the minimum number of transects walked (n = 2, 2, 4 and 3 for landscape before, during, and before and during crop flowering, and in the crop, respectively). For example, in a field site where we walked three transects in semi-natural habitat before crop flowering, we made 1000 random combinations of two observation dates, with replacement, and calculated average cumulative species richness for each combination. Pollinator abundance was averaged over all transects and was log-transformed before analyses to improve normality of residuals; flower cover and cover of semi-natural habitat were respectively log- and square root-transformed to reduce positive skew. We included the average flower cover in analyses in the semi-natural habitats, as this was highly variable between sites and may cause an attraction effect [4], while this was not the case for the crop transects.

To test the relationship between the local pollinator species pool (i.e. the number of pollinator species in semi-natural habitat, before and during crop flowering) and the crop pollinator species pool, we first used linear regressions for richness and abundance. Subsequently, to test whether this relationship was different for the dominant and opportunistic crop pollinator species pool (i.e. in the crop field) we used mixed effects models with site as random factor using the function 'lmer' in R-package *lme4*. Significance of effects was assessed using likelihood-ratio tests. Response variables were the number of pollinator species and abundance of pollinator species encountered in the crop fields. Explanatory variables were the total number of species encountered in the semi-natural habitat (before and during crop flowering), functional group and their interaction to test if the relationship between local and crop species pool differed between dominant and opportunistic crop pollinators.

To examine the relationship between landscape complexity and pollinator species richness, we first performed separate linear regressions between landscape complexity and pollinator species richness, respectively measured in the semi-natural habitats and crop fields. To test how this relationship was moderated by crop flowering and functional group, we used mixed effect models with site as random factor in separate analyses for pollinator richness in the crop and semi-natural habitat. For the response of species richness in the semi-natural habitat transects we included the three-way interaction of landscape complexity, functional group and crop flowering as fixed factors, and we included the average flower cover as this was highly variable between sites and may cause an attraction effect [4], while this was not the case for the crop transects. Patterns of species richness in crop transects were analysed with a similar model except that only the effects of landscape complexity, functional group and their interaction were included as factors. In case of significant interactions, we further explored observed patterns by performing *post hoc* analyses for each pollinator group separately.

Similar to analysis with species richness, we first tested whether overall abundance in the semi-natural habitat transects and in the crop transects was related to landscape complexity in simple linear regressions. To test the relationship between landscape complexity and pollinator abundance for each functional group and whether this was moderated by crop flowering, we distinguished between the pollinator abundances before crop flowering and during crop flowering, resulting in a total of eight different abundances. As the abundances could differ two orders of magnitude between different locations or periods, we used separate linear regressions to test the relationship of each of the eight abundances to semi-natural habitat cover.

Finally, to test if average pollinator abundances in nearby semi-natural habitats differed between before and during crop flowering periods, and to test if pollinator abundances differed between the semi-natural and crop transects, we compared the average abundances for each of the functional groups using mixed effect models with site as random factor. As explanatory variables we included period of sampling (before or during crop flowering), functional group and their interaction for the first model, and habitat type, functional group and their interaction for the second model. All statistical analyses were performed in R, version 3.5.1 [19].

3. Results

We counted 7578 pollinator individuals in leek transects and 4047 individuals in semi-natural habitat transects, comprising a total of 171 species of wild bees ($n = 8278$ individuals, $n = 133$ species) and hoverflies ($n = 3347$ individuals, $n = 38$ species). Eighteen species (10.5% of all species; mean 310 ± 482 s.d. individuals per species) were classified as dominant crop pollinators, with the five most dominant species being *Bombus lapidarius* ($n = 1480$), *Andrena flavipes* ($n = 1448$), *Bombus terrestris/lucorum* ($n = 1112$), *Lasioglossum malachurum* ($n = 692$) and *Syritta pipiens* ($n = 520$). A total of 62 species (36.3%; mean 80 ± 237 s.d. individuals species^{-1}) were encountered only occasionally in crops and the remaining 91 species (53.2%; mean 12 ± 30 s.d. individuals species^{-1}) were only found in the semi-natural habitat transects. Eighteen species were only encountered in the crop fields (10.5%; mean 7 ± 11 s.d. individuals species^{-1}).

(a) Local pollinator species pool size

The total crop pollinator species pool size was significantly positively related with the local species pool size in the semi-natural habitat transects ($F_{1,16} = 14.68$, $p = 0.001$), but this relationship was stronger for the opportunistic crop pollinators than for the dominant crop pollinators (significant interaction effect local species pool × functional group: $\chi^2_1 = 4.68$, $p = 0.03$; figure 2*a*). In the most species-poor landscapes, the crop species pool was approximately as large as the local species pool, while in the species-rich landscapes the crop species pool comprised 71% of the local species pool size (figure 2*a*). With an increasing local species pool in the landscape, the abundance of pollinators in crop fields increased ($\chi^2_1 = 5.24$, $p = 0.02$; figure 2*b*) similarly for both dominant and opportunistic crop pollinators (i.e. no significant interaction effect local species pool × functional group: $\chi^2_1 = 0.80$, $p = 0.37$; figure 2*b*). Dominant crop pollinators were more abundant in crop fields than opportunistic crop pollinators ($\chi^2_1 = 13.64$, $p = 0.003$; figure 2*b*), and made up approximately 63% of all crop visitors across the entire gradient in local species pool.

(b) Landscape complexity

The total size of the local species pool did not significantly increase with increasing landscape complexity ($F_{2,15} = 2.17$, $p = 0.11$). There was only marginal support for a three-way interaction between functional group, period of sampling and landscape complexity (three-way interaction: $\chi^2_2 = 5.30$, $p = 0.07$; figure 3*a*), but both the two-way interactions between functional group and period ($\chi^2_2 = 9.82$, $p = 0.007$), as well as between functional group and landscape complexity ($\chi^2_2 = 6.22$, $p = 0.04$) were significant. There were no strong effects of landscape complexity before crop flowering, whereas during crop flowering, non-crop pollinators responded positively to semi-natural habitat cover ($F_{2,15} = 3.48$, $p = 0.03$). Total pollinator species richness in the crop fields increased significantly with landscape complexity ($F_{1,16} = 8.93$, $p = 0.008$). Both the species richness of dominant ($F_{1,16} = 8.93$, $p = 0.02$) and opportunistic crop pollinators ($F_{1,16} = 8.93$, $p = 0.01$) increased with increasing landscape complexity, and this effect was stronger for opportunistic crop pollinators ($\chi^2_2 = 4.87$, $p = 0.03$; figure 3*b*).

In the semi-natural habitats surrounding leek fields, the total average abundance of pollinators was not related to semi-natural habitat cover ($F_{2,15} = 4.85$, $p = 0.83$), nor was one of the functional groups, both before and during leek

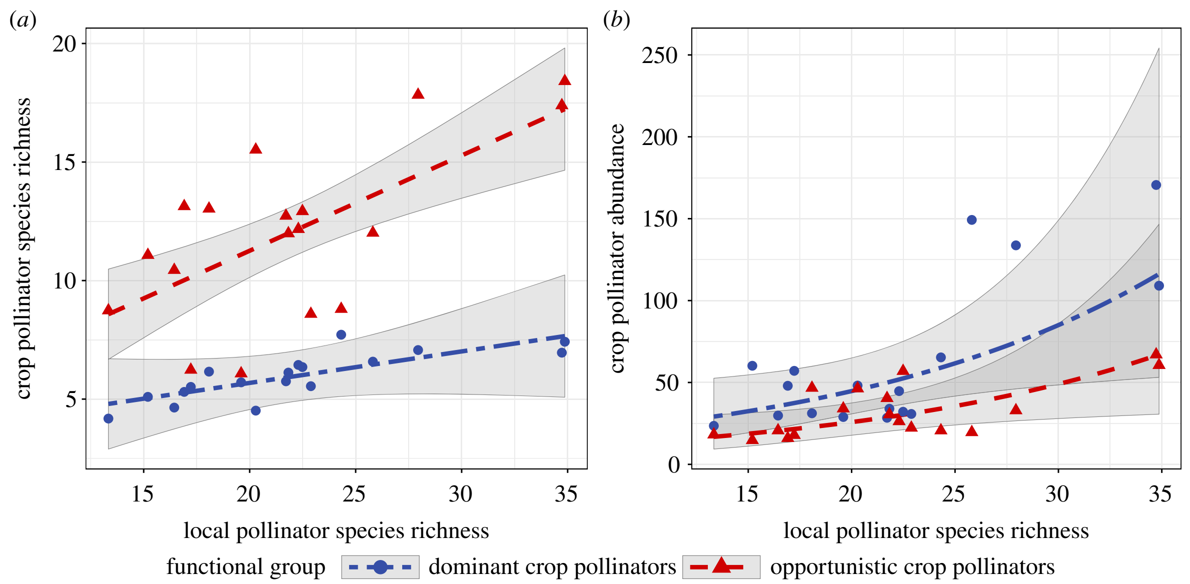

Figure 2. Relationships between the local pollinator species richness and the pollinator species richness (*a*) and abundance (*b*) in crops. Local pollinator species richness is based on transects in semi-natural habitat (both before and during crop flowering), while crop abundances and richness are based on transects in crop fields. Separate regressions are indicated for dominant crop species (blue circles) and opportunistic crop species (red triangles), and 95% confidence intervals are indicated with grey. Results are back-transformed partial residuals. (Online version in colour.)

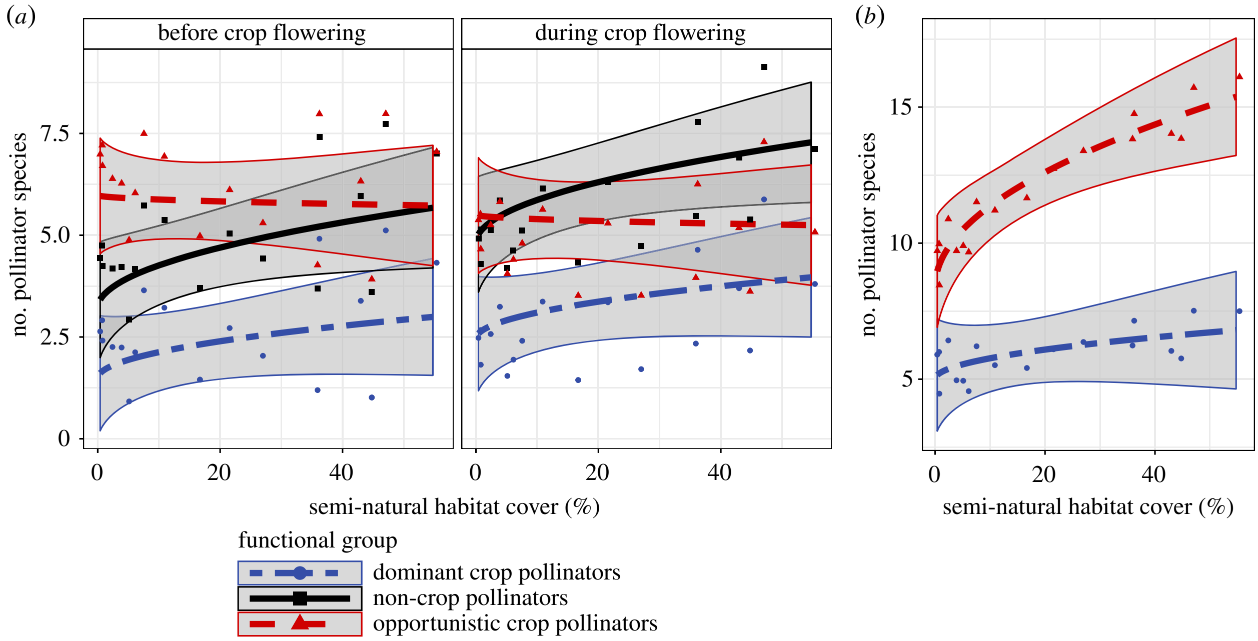

Figure 3. Relationships between cover of semi-natural habitat (%) and pollinator species richness. Separate panels are given for (*a*) semi-natural habitat transects before and during crop flowering and (*b*) crop transects during crop flowering. Back-transformed regressions and predicted species richness are indicated for dominant crop pollinator species (blue circles), opportunistic crop pollinator species (red triangles), and non-crop pollinator species in the landscape (black squares); 95% confidence intervals are indicated with grey. (Online version in colour.)

flowering ($p > 0.35$, figure 4*a–f*). Abundances in the crop were generally related to semi-natural habitat cover ($F_{1,16} = 8.17$, $p = 0.01$), but this was largely caused by the dominant crop pollinator abundance ($F_{1,16} = 14.74$, $\beta = 0.12$, $p = 0.001$; figure 4*g*), as the abundance of opportunistic crop pollinators was not related to semi-natural habitat cover ($F_{1,16} = 0.77$, $\beta = 0.03$, $p = 0.39$; figure 4*h*).

(c) Crop flowering

Crop flowering did not alter the abundances of dominant crop pollinators in the landscape (mean log-difference $= 0.04 \pm 0.12$ s.e., $z = 0.30$, $p = 0.99$) or abundances of non-crop pollinators in the landscape (mean log-difference $= 0.06 \pm 0.12$ s.e., $z = 0.454$, $p = 0.99$). However, the opportunistic crop pollinators showed a 60% decline in abundances in the landscape when the nearby crop was flowering (mean log-difference $= 0.45 \pm 0.12$ s.e., $z = 3.596$, $p = 0.004$; figure 5*a*). This pattern may be largely explained by hoverflies because analyses without hoverflies showed no difference in abundance of opportunistic pollinators before and during crop flowering (electronic supplementary material, figure S8). Abundances of dominant crop pollinators were about 10 times higher in the crop than in the semi-natural habitat

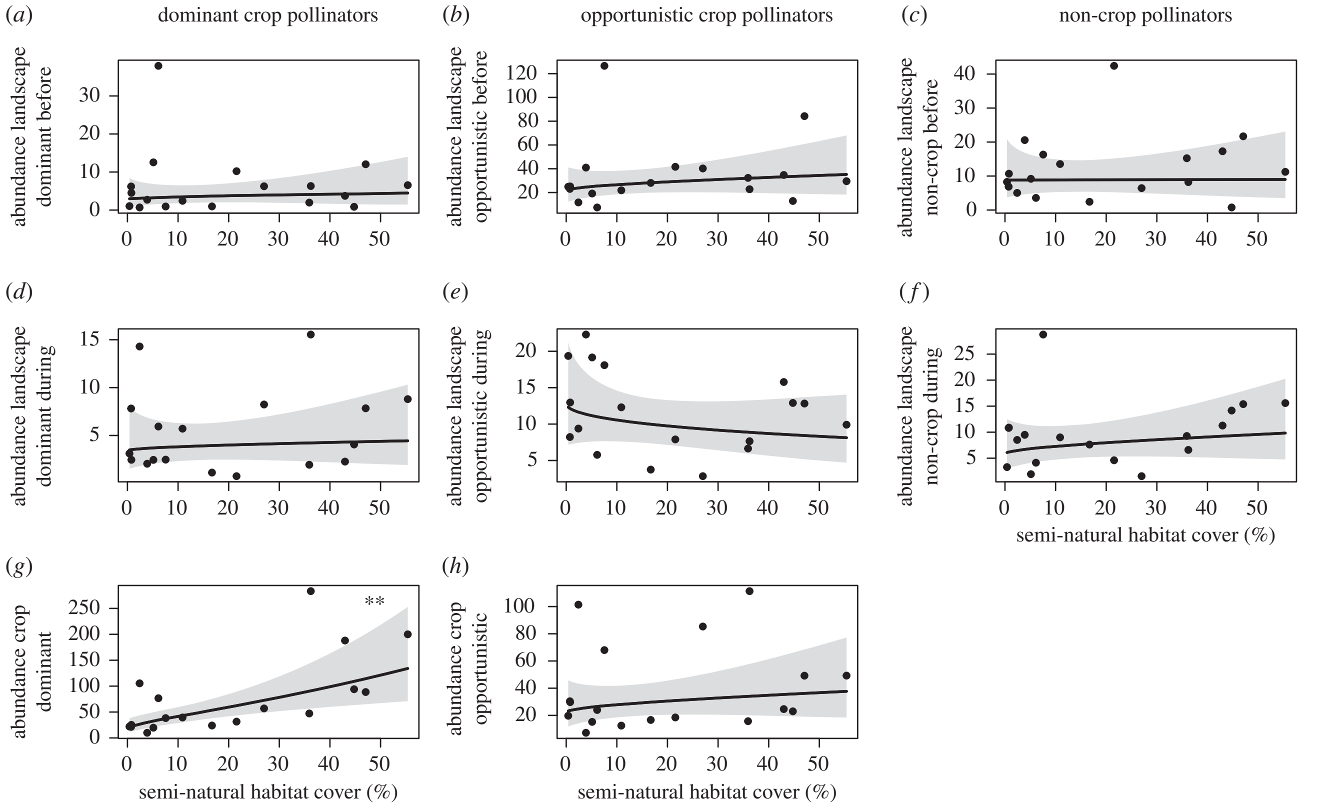

Figure 4. Relationships of pollinator abundances with semi-natural habitat cover (%). Abundances were separated in (*a–c*) semi-natural habitat transects before crop flowering, (*d–f*) semi-natural habitat transects during crop flowering and (*g*,*h*) crop transects. Panels (*a*, *d* and *g*) reflect dominant crop pollinator abundances, (*b*, *e* and *h*) opportunistic crop pollinator abundances and (*c* and *f*) non-crop pollinator abundances. Results are back-transformed partial residuals corrected for flower cover. Panels (*a–f*) and (*h*) show no significant relationship, while (*g*) is significant ($p < 0.01$, indicated with **); 95% confidence intervals are indicated with grey.

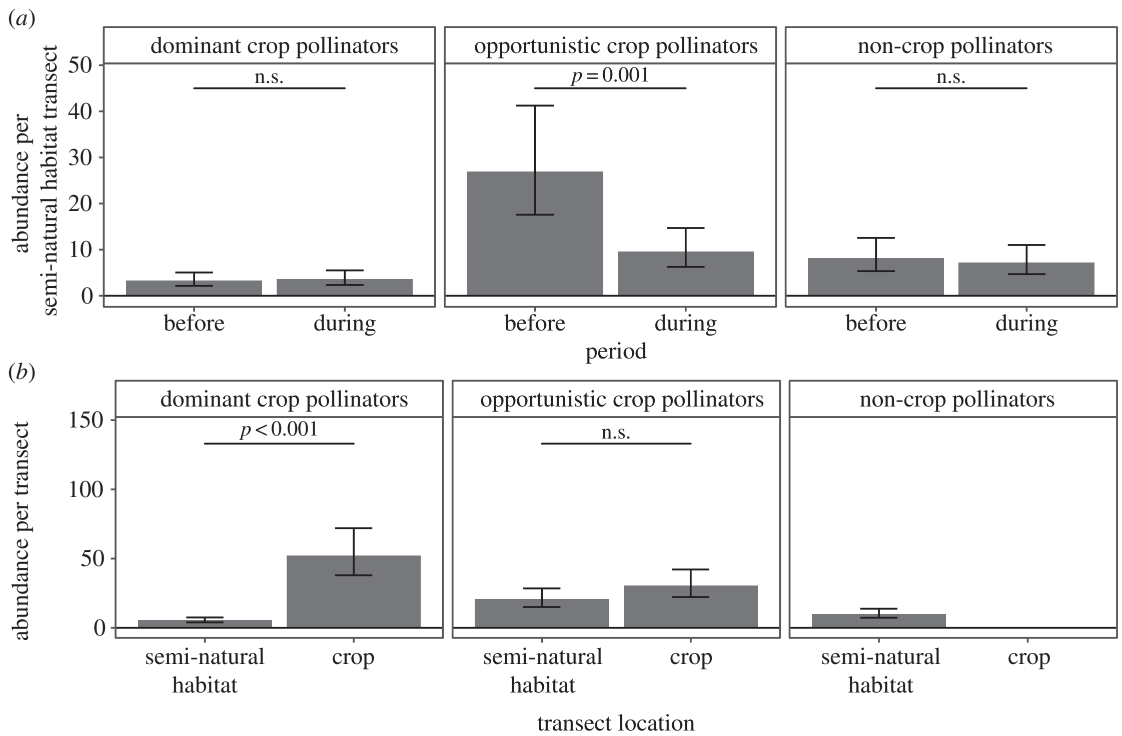

Figure 5. (*a*) Back-transformed mean abundances of dominant, opportunistic and non-crop pollinators in the landscape, before and during crop flowering. (*b*) Back-transformed mean abundances of dominant and opportunistic in the landscape (before and during crop flowering together) and in the crop, and mean abundances of non-crop pollinators in the semi-natural habitat for comparison. Error-bars are 95% confidence intervals. Pairwise significance values are indicated on top (n.s. = not significant).

in the surrounding landscape (mean log-difference = 0.98 ± 0.08 s.e., $z = 11.577$, $p < 0.001$; figure 5*b*). This was mainly caused by surprisingly low abundances of dominant crop pollinators in the landscape even before crop flowering. In semi-natural habitats surrounding leek fields, dominant crop pollinator abundances were almost four times lower than abundances of opportunistic crop pollinators (mean log-difference = 0.58 ± 0.08 s.e., $z = 6.834$, $p < 0.001$) and 1.8 times lower than abundances of non-crop pollinators (mean log-difference = 0.26 ± 0.08 s.e., $z = 3.121$, $p < 0.02$). Abundances of non-crop pollinators in the landscape were around half of the abundances of opportunistic crop pollinators (mean log-difference = 0.32 ± 0.08 s.e., $z = 3.713$, $p = 0.001$). Perhaps surprisingly, abundances of opportunistic crop pollinators in the crop were comparable to those in the landscape (mean log-difference = 0.17 ± 0.08 s.e., $z = 2.005$, $p = 0.26$).

4. Discussion

Ecological theory predicts that the species richness of pollinators on crops is determined by the size of the local pollinator species pool which, in turn, depends mainly on the quantity of resources that is available in semi-natural habitats [4,15,20]. However, the empirical evidence to date is scarce. Here we provide partial support for these relationships by showing that the abundance and species richness of pollinators in crops is directly and positively related to the size of the local species pool in the surrounding landscape. This relationship differs, however, between functional groups, with dominant crop pollinators showing weaker relationships than opportunistic crop pollinators (figure 2). Surprisingly, significant relationships with landscape complexity, a proxy for overall resource availability, were restricted to species richness and abundance of pollinators on crop flowers, and to non-crop pollinators in semi-natural habitats during crop flowering. Landscape complexity did not explain species richness or abundance of crop pollinators in transects in the wider landscape at any time, and dominant crop pollinators were virtually absent in the semi-natural habitats surrounding crop fields, even before bloom of the crop.

Our results indicate that it is important to distinguish between different functional groups when considering crop pollination or pollinator conservation. The species richness of opportunistic crop pollinators was much more strongly related to the local species pool than that of dominant crop pollinators, which could explain why in species-poor landscapes dominant crop pollinators make up a much larger proportion of the crop-visiting pollinator communities than in species-rich landscapes [8]. This makes dominant crop pollinator species a relatively constant component of crop pollinator communities [21], and variation in the overall species richness of pollinators on crops seems to be primarily determined by the larger number of less common species that use crop flowers opportunistically. Interestingly, the higher species richness of opportunistic species compensated for their lower abundance per species, as the relative abundance on crop flowers of the two functional groups remained fairly constant along the gradient of local species pool size (figure 2*b*). The species that were not encountered on crops were even less abundant than the opportunistic crop pollinators in the semi-natural habitat, but as a group, the non-crop pollinators did make up more than half of the total number of observed pollinator species across all study sites. Although non-crop pollinators were also observed in species-poor landscapes (figure 3*a*,*b*) the majority of the non-crop pollinator species was probably restricted to species-rich landscapes where 30% of the local pollinator species pool was never observed on the crop, a pattern which is in line with other studies [22,23]. In contrast to the crop pollinators, hardly any of the species that relied solely on semi-natural habitats were observed in large numbers. Potential reasons for this could be that non-crop pollinators may have restricted or specialized pollen diet requirements [24], or that in semi-natural habitats resource availability was too low and scattered to maintain species with larger populations for the duration of their activity period.

Surprisingly, species-richness and abundance of pollinators in the wider landscape was generally not related to landscape complexity. At first glance this would indicate that the hypothesized positive relationship between landscape complexity and local species pool size is not supported. However, we think the lack of response in both abundance and richness was caused by the pollinators spreading out evenly over the available pollinator habitat up to a certain carrying capacity [4]. Other studies examining pollinators inside semi-natural habitat likewise fail to find relationships with landscape complexity [25,26]. Estimating pollinator population sizes requires taking into account the total area of pollinator habitat as well as the density per unit area [27]. Complex landscapes by definition contain larger surface areas of pollinator habitat. Equal pollinator densities in simple and complex landscapes then translate into larger population sizes in complex landscapes. Species richness does not show linear relationships with surface area [26], but the surveyed transects were relatively small and did not exhaustively represent all available semi-natural habitat types in the landscapes. The same process may largely explain why also here we failed to observe relationships with landscape complexity. The only exception were the non-crop pollinators, whose species richness in semi-natural habitats was positively related to landscape complexity during crop flowering. This can be explained by crop flowering temporally alleviating competition between the non-crop pollinator species and the crop pollinators in the wider landscape [28,29], which may have had more pronounced effects on resource availability in complex than in simple landscapes. Other studies have found honeybees to influence wild bee densities through competition for floral resources [28]. Although, resource competition between managed and wild bees probably also occurred in this study it is unlikely to explain the observed relationships between wild bees and landscape complexity because honeybee densities, both in the crop and in semi-natural habitats, were constant across the landscape complexity gradient.

In contrast to effects in the semi-natural habitats, we did find clear positive relationships of landscape complexity on species richness and abundance of pollinators on crop flowers. Mass-flowering crops like leek generally concentrate pollinators that are within flight range of the field [14] as indicated by the general higher abundance and richness of, in particular, the dominant crop pollinators in crop fields than in the semi-natural habitat. When the surrounding landscape contains a lot of pollinator habitat, more pollinators may be attracted onto the crop field than when these landscapes contain little of such habitats [3]. Crop fields thus magnify relationships between pollinators and the proportion of semi-natural habitats in the landscape, and because opportunistic crop pollinators are more reliant on semi-natural habitats than dominant crop pollinators [30], the relationship with opportunistic pollinator species richness may have been more pronounced than the relationship with dominant crop pollinators. In summary, these findings support that complex landscapes have larger pollinator species pools of all three functional groups even though this is not always reflected in higher species richness or abundance per transect in semi-natural habitats. Moreover, it shows that the crop pollinator species pool in mass-flowering crops is mostly limited by the available pollinator habitat cover in the landscape surrounding the crop fields.

Opportunistic crop pollinators were on average as abundant in the semi-natural habitat as in the flowering crop, but before crop flowering their abundances in the landscape were much higher. This probably reflects that opportunistic crop pollinators generally use crop fields as a useful additional food source when it starts flowering, but the reduced and still relatively high abundance of opportunistic crop pollinators in semi-natural habitats suggests that they require additional floral resources from the semi-natural habitats as well [13,15]. Unexpectedly, we found no evidence for such spill-over effects for dominant crop pollinators, despite the fact that most dominant crop pollinators were eusocial or multivoltine bees and must have large populations in the area. In fact, we hardly found dominant crop pollinators in the landscape at all, even though the abundances of dominant crop pollinators in the crop were about five times higher than those of opportunistic crop pollinators. This suggests that most dominant crop pollinators foraged in habitats that were not part of our sampling design. It is possible that these species were foraging in other mass-flowering crops that were flowering before the leek crop. Dominant crop pollinators may consist of species that preferentially exploit mass-flowering crops, as it may provide fitness advantages to collect large amounts of resources in a short period of time. In natural systems this mechanism may have evolved in response to abundant mass-flowering wild species such as some canopy trees [31], or certain species of Brassicaceae and Rosaceae [32], of which many crops in Europe have derived (e.g. *Brassica napus* and *Rubus fruticosus* [30,32]). In agricultural landscapes these dominant crop pollinators may simply hop from one mass-flowering crop to another mass-flowering crop for their food sources [33]. Although this would make these crop hoppers less dependent on semi-natural habitats for food availability, they nevertheless depend on these habitats for nesting [34] or food sources when there is no mass-flowering crop flowering [20,21], which probably underlies the relationship between dominant pollinators on crops and landscape complexity. Insights in the whereabouts of this key group of crop pollinators before flowering of the focal crop can help better understand the contribution of wild pollinators to crop pollination, and to identify effective pollinator-supporting strategies.

Recent studies suggest that pollinator abundance and species richness have significant complementary effects on crop pollination [9,10,35]. While pollinator abundance is strongly determined by dominant crop pollinators, species richness is more strongly determined by opportunistic crop pollinators. Our study shows that the relationship with landscape complexity, and therefore dependence on semi-natural habitats, differs between these different functional groups of pollinators, with opportunistic crop pollinators being more dependent on semi-natural habitats than dominant crop pollinators. Dependence of non-crop pollinators on semi-natural habitats was even higher than of opportunistic crop pollinators. However, all three groups seem to increase with increasing complexity of the landscape, resulting in the largest local pollinator species pool in the wider landscape as well as the largest pollinator species pool on the mass-flowering crop in the most complex landscapes. Because in this cropping system higher pollinator abundance and species richness is directly related to higher marketable seed yield [10], this suggests that complex landscapes are local hotspots for biodiversity conservation as well as ecosystem service provision. In addition to the intrinsic value of biodiversity and aesthetics, this may provide an important argument for the preservation of semi-natural habitats in times of land-use change.

Data accessibility. Data and the R-script supporting the results of this article can be found online at the Dryad Digital Repository: https://doi.org/10.5061/dryad.cb74s0q [36].

Competing interests. We declare we have no competing interests.

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