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Disentangling multiple drivers of pollination in a landscape-scale experiment

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Animal pollination is essential for the reproductive success of many wild and crop plants. Loss and isolation of (semi-)natural habitats in agricultural landscapes can cause declines of plants and pollinators and endanger pollination services. We investigated the independent effects of these drivers on pollination of young cherry trees in a landscape-scale experiment. We included (i) isolation of study trees from other cherry trees (up to 350 m), (ii) the amount of cherry trees in the landscape, (iii) the isolation from other woody habitats (up to 200 m) and (iv) the amount of woody habitats providing nesting and floral resources for pollinators. At the local scale, we considered effects of (v) cherry flower density and (vi) heterospecific flower density. Pollinators visited flowers more often in landscapes with high amount of woody habitat and at sites with lower isolation from the next cherry tree. Fruit set was reduced by isolation from the next cherry tree and by a high local density of heterospecific flowers but did not directly depend on pollinator visitation. These results reveal the importance of considering the plant's need for conspecific pollen and its pollen competition with co-flowering species rather than focusing only on pollinators' habitat requirements and flower visitation. It proved to be important to disentangle habitat isolation from habitat loss, local from landscape-scale effects, and direct effects of pollen availability on fruit set from indirect effects via pollinator visitation to understand the delivery of an agriculturally important ecosystem service.

1. Introduction

Effective animal pollination is an extremely important ecosystem service. It directly benefits humans through higher fruit set and crop yield [1–3]. About 75% of crop species and 35% of crop production worldwide depend at least partly on animal pollination [1], and the area cultivated with pollinator-dependent crops has disproportionately increased in the last decades [4]. Pollinator-mediated sexual reproduction also supports global wild plant biodiversity through increased fecundity and gene flow [5–7].

Expansion of agricultural land leads to loss and fragmentation of (semi-) natural habitats, two key factors threatening biodiversity and ecosystem services, for example pollination [8,9]. The effects of fragmentation on pollination are especially strong in self-incompatible plants where the presence of conspecific plants as pollen donors within foraging distance of pollinators is essential for reproductive success [5]. Historically, habitat fragmentation *per se* was rarely separated from habitat loss [10–14]. Knowledge on the independent effects of habitat loss and fragmentation is necessary for an effective landscape management for biodiversity and ecosystem services [12,15,16]. The amount of suitable habitat determines the pool of available organisms in a given landscape [14]. By contrast, habitat isolation is a measure of fragmentation *per se* (here expressed as the distance between a focal habitat and its nearest neighbour) and determines to what extent a habitat patch is accessible for organisms of this pool [14]. This access might be especially important in landscapes with low amount of suitable habitat where local biodiversity is primarily determined by landscape-wide

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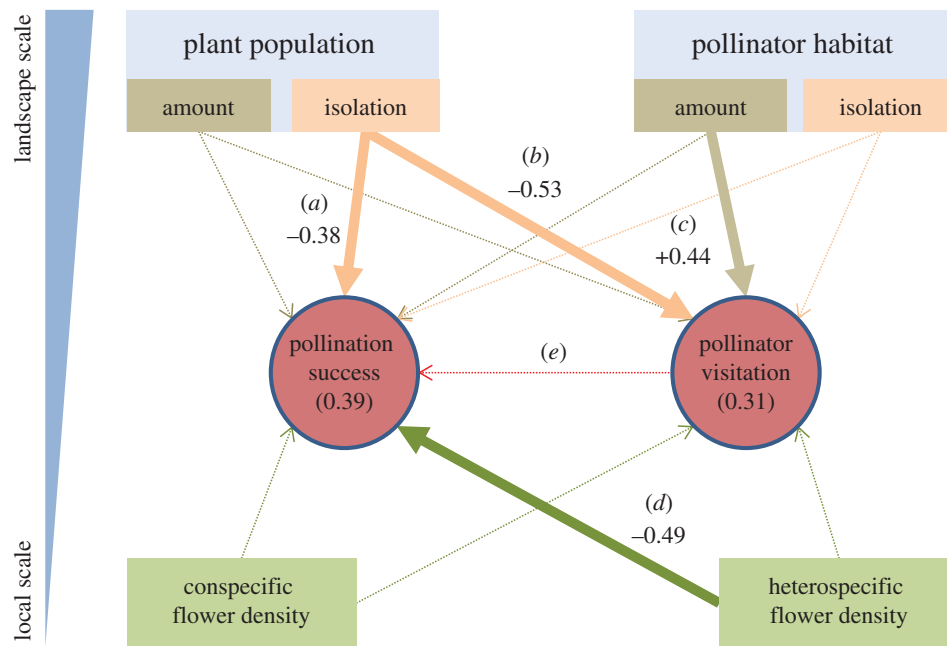
Figure 1. Disentangling key drivers of pollination in fragmented landscapes. Separation of the spatial distribution of target plant population *versus* pollinator habitat, habitat amount *versus* isolation (as a measure of fragmentation), local (50 m buffer) *versus* landscape scale (100–350 m for isolation and 500 m buffer for amount) and beneficial densities (pollinator visitation) *versus* provision of ecosystem service (pollination success). Dotted arrows show hypothesized impacts, bold arrows significant impacts derived from GLM and SEM (see Results for details). Increased isolation of cherry trees, but not the amount of cherry trees in the landscape, was associated with (*a*) lower fruit set and (*b*) decreased number of flower visits. (*c*) High amount of woody habitat (pollinator habitat) at the landscape scale, but not isolation from the next woody habitat, was associated with a high number of flower visits. Pollinator habitat amount and isolation did not impact pollination success. (*d*) Increased number of heterospecific shrubs in bloom on the local scale, but not the density of conspecific flowers, was directly associated with lower fruit set without changing rates of flower visitation. (*e*) Increased number of flower visits did not lead to higher fruit set. The numbers next to bold arrows indicate standardized regression weights (slope of relationship between standardized predictor and response) from SEM. Explained variation of response variables (sum of squared standardized regression weights) is shown in parentheses. Figure based on ideas from reference [12]. (Online version in colour.)

remnant communities compared with rich landscape where the species pool is high everywhere [8,14,17].

The effect of habitat isolation on pollination can be mediated through lower access to pollen donors (i.e. isolation of the plant population), through lowered pollinator density (caused by isolation of pollinator habitat) and through changes in pollinator movement [12]. Isolated plant populations can show lower pollination success independent of pollinator visitation because of a lack of compatible donor plants [18]. In turn, the absence of pollinators can decrease pollination success even in situations where the availability of donor plants is high [15]. Therefore, both habitat requirements of pollinators and the spatial distribution of plant populations have to be taken into account. Finally, visitation of pollinators and fruit set can be affected by pollinator movement [12]: high local flower density may positively affect visitation and fruit set by attracting more pollinators from the landscape pool (concentration effect), or may negatively affect visitation and fruit set by increasing intra- or interspecific competition for pollinators (dilution effect), resulting in lower visitation per flower at sites with more flowers [14,15,19,20]. Furthermore, direct negative effects of local heterospecific flower resources on fruit set can arise independent of visitation because of lower quality of pollen mix transported by pollinators (mix with less conspecific pollen) [15].

We used a landscape-scale experiment with systematically planted young cherry trees, as an insect-pollinated, self-incompatible model plant, to test the following predictions for pollination services in fragmented agricultural landscapes (figure 1).

(i) Visitation of pollinators and pollination success (fruit set) are higher in landscapes with high amount

of woody habitat and low isolation from the next woody habitat (pollinator habitat). Woody habitats were considered as main habitats providing nesting and floral resources for pollinators in our landscapes [21–29] but we also controlled for possible effects of open (non-woody) semi-natural habitats [30].

(ii) Effects of isolation from woody habitat are stronger in landscapes with low amounts than in landscapes with high amounts of woody habitats (interacting effects of isolation and amount of woody habitat).

(iii) Visitation and pollination success are influenced by the spatial distribution of cherry trees (plant population) in the landscape. Visitation and pollination success increase in landscapes with higher amount of cherry trees and in study sites less isolated from conspecifics because of better outcross pollen availability.

(iv) Local heterospecific flower resources, both on the ground and in shrubs, as well as conspecific flower density affect pollinator visitation and pollination success.

2. Material and methods

(a) Experimental design and landscape variables

The study was conducted in 2011 in the Swiss plateau between the cities of Bern, Solothurn and Fribourg, where agricultural areas are interspersed with forest. We used 30 separate landscape sectors distributed over an area of 23 × 32 km. Experimental sites in the centre of each landscape sector consisted of 18-m-long rows of seven 7-year-old wild cherry trees (*Prunus avium* L.) on permanent grassland. The sites were selected systematically to cover a gradient in

the percentage of woody habitat in a 500 m buffer (from 4 to 74%) and to differ in their level of local isolation from woody habitat independently of the percentage of woody habitat ($F_{2,27} = 0.004$, $p > 0.9$; electronic supplementary material, figure S1). Woody habitats comprised hedgerows, traditional high-stem orchards, single-standing trees on field margins and in gardens, treelines and all types of forest occurring in the landscapes, whereby the majority of forest was dominated by *Fagus sylvatica* L. Relative shares of different woody elements are indicated in the electronic supplementary material, table S1. Woody habitat isolation had three levels: (i) 10 sites were located at the edge of dense and tall-growing forest representing no isolation from woody habitat ('adjacent'). The remaining 20 sites were located in a distance of 100–200 m from the next forest, (ii) half of them connected by small-sized woody habitats such as hedgerows or trees ('connected') and (iii) the other half isolated from any woody habitat by 100–200 m ('isolated'; electronic supplementary material, figure S1). The studied distances of isolation are lower than the expected maximal foraging ranges of some flower visitors. Nevertheless, only few individuals have the capability to cover the maximal foraging distances [31] and effects of isolation have previously been detected at scales of 200 m or lower [30,32]. 'Connected' sites were included to test whether small woody habitats can mitigate the isolation from forest edge [23]. To assess isolation and amount of target plant populations, we measured the distance of each study site to the next wild or cultivated cherry tree taller than 3 m (cherry isolation) and the number of wild or cultivated cherry trees within each landscape sector (cherry amount). To test possible effects of open (non-woody) semi-natural habitats on pollinator visitation and pollination success, we assessed the percentage of low-intensity grasslands and sown wildflower strips per landscape. Landscape variables were derived from national digital land-use maps (vector25, swisstopo, Wabern), official records of ecological compensation areas (GEOPORTAL, Kanton Bern), aerial photographs and field inspections. Because of low tree vigour and lack of sufficient flowering, we omitted two sites for the analysis of fruit set and three sites for the analysis of flower visitation.

(b) Local flower densities

Local conspecific flower density was estimated by counting the fully open cherry flowers (stigma and anthers visible) on all seven cherry trees per site (number of cherry flowers). Local heterospecific flower density was estimated by counting the number of flowering shrubs (mostly *Prunus spinosa*) within 50 m buffer around the focal cherry tree line (no. of shrubs in bloom) and counting the number of flowers or inflorescences (in Asteraceae) on the ground in four 1 m^2 plots per site (ground flower cover). Flower cover of ground vegetation did not influence pollinators on cherry trees in another study [33]. Nevertheless, we included ground flower density as covariable to control for potential influence. All local variables were measured three times during the flowering period and averaged per site for analysis.

(c) Flower visitation

We used high-definition handycams (Sony HDR-CX115E/B) to assess flower visitors on cherry trees. At each site, we filmed a group of two to three flowers (rarely one or four, mean = 2.37, s.d. = 0.75) for 30 min on three different days during bloom, resulting in recordings of approx. 225 flower-minutes per site. Each of the three films per site was recorded at a different daytime (10.00–12.00, 12.00–14.00 and 14.00–16.00). During each video, maximal wind speed (m s^{-1}) was assessed by measuring wind speed three times for 2 min (start, middle and end of video) with hand anemometers (PCE-A 420, PCE Deutschland GmbH). Maximal wind speed was assessed for each video, and then averaged per site for analysis. As the number of flowers filmed slightly differed between sites, we calculated the mean number

of flowers filmed per site (flower per video) to control for in our analysis (included as covariable in full models). Based on videos, we derived the number of insect visitors to flowers (visitation rate), the species richness of visitors, the mean duration per insect visit (duration) and the behaviour of the visitor on the flower. According to the behaviour of the visitor, each visit was assigned to one of three categories: visitors touching stigma and anthers (score 3), only anthers (score 2) or only petals (score 1). We separated visitor groups that are potential pollinators, i.e. consistently touched stigma and anthers, from those only rarely and hazardously touching stigma or anthers. We only used potential pollinator groups (with a mean visit score greater than or equal to 2.5) in analysis of flower visitation (see electronic supplementary material, table S2). With the help of a specialist (see Acknowledgements) and a reference collection, all bee visitors were determined to species level. Other flower visitors were determined to family or superfamily level.

(d) Fruit set

At half of the sites ($N = 15$), 16 groups of flower buds were marked on four different trees per site and randomly assigned to four treatments: open pollination ('open'), bagged flowers ('control'), self-pollination by hand ('self') or cross-pollination by hand ('cross'). At the remaining sites, only eight groups were marked and randomly assigned to 'open' and 'control' treatments. Treatments were applied approximately one week before bloom. In treatment 'open', groups were freely exposed to pollinators. In treatment 'control', 'self' and 'cross', flower groups were bagged with polyethylene bags (mesh size 0.4 mm; Sefar AG, Switzerland) to prevent access of pollinating insects, but permitting access of pollen transported by wind [34]. During the bloom, in treatment 'self' all flowers were hand pollinated by paintbrush two to three times (on different days) with pollen obtained from unmarked flowers of the same tree. In treatment 'cross', marked flowers were cross-pollinated with pollen obtained from at least three different wild cherry trees from forest edges in our study area. The 'control' treatment did not receive any additional handlings apart of being bagged. Immediately after the bloom (petal abscission), all bags were removed to avoid climatic impacts on developing fruits. We had to exclude 78 of the 344 marked groups from our analysis because of broken twigs, herbivores eating flowers or buds not developing into fertile flowers. Fruit set (pollination success) per treatment was calculated as the percentage of intact marked flowers (not damaged by herbivores) that developed into swollen green fruits approximately three weeks after pollination per site. This measure is highly correlated with the final fruit set in cherry trees [33].

(e) Statistical analyses

We performed a generalized linear mixed-effects model (GLMER) with binomial error distribution to assess the effects of pollination treatments (fixed effect) on fruit set. Marked flowers nested within trees and trees nested within sites were included as random effects. Inference was based on model comparison (ANOVA). Pairwise differences between treatments are based on z-values from GLMER model summary. To test the effect of visitation rate (square root-transformed to obtain homoscedasticity) on fruit set of the 'open' pollination treatment, we used a generalized linear model (GLM) with quasi-binomial error distribution. To test the effects of landscape and local variables on visitation rate, duration per visit, and fruit set of 'open' and 'control' treatments (all variables pooled per site), we performed GLM with Poisson error distribution for visitation (count data) and GLM with binomial error distribution for fruit set (proportion data). Flower visitor species richness was not used in the models because it was highly positively correlated with visitation rate (Pearson's correlation, $r = 0.84$, $n = 25$, $p < 0.001$). We used quasi-distributions if

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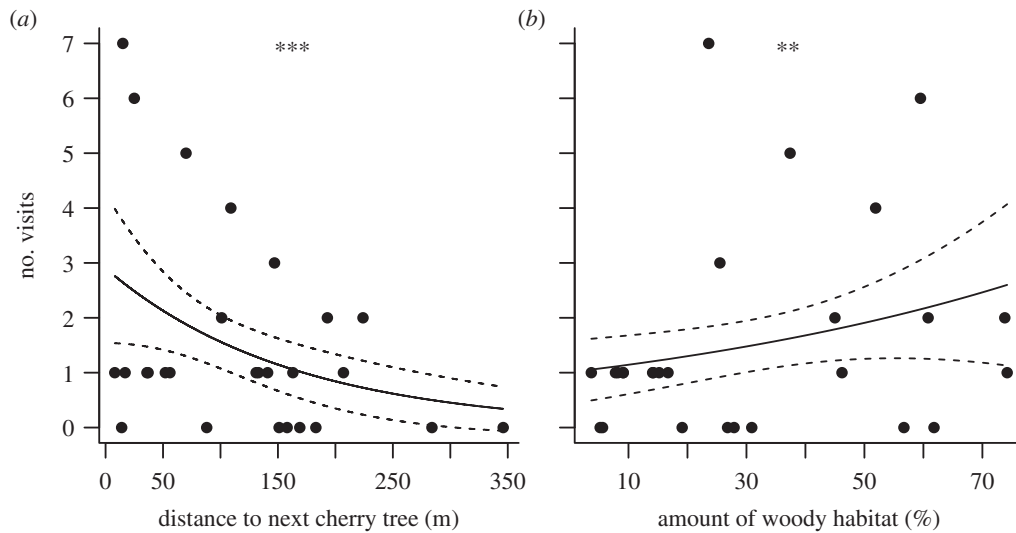
Figure 2. Pollinator visitation. Number of insect visits to cherry flowers during 90 min of video observation in relation to (a) distance to next wild or cultivated cherry tree and (b) amount of woody habitat in the landscape (500 m buffer around study site). Results are based on GLM (Poisson error distribution). Solid lines show predicted values, dashed lines are estimated 95% confidence intervals. Dispersion parameter = 1.3, residual d.f. = 24, significance levels: ***$p < 0.001$, **$p < 0.01$, explained deviance = 35%.

dispersion parameter was more than 1.5 (overdispersion) and removed outliers with Cook's distance more than 1.

To disentangle variables with and without relevance for pollination, we performed automated model selection (dredge function [35]) based on Akaike's information criterion for small samples sizes (AICc, or QAICc in case of overdispersion). Variables were considered as relevant (r_1) if they were present in all models with δ-(Q)AICc < 3. Variables were considered as irrelevant (r_2) if they were absent in the best model and if the δ-(Q)AIC between the best model and the first model containing r_2 instead of r_1 was more than 3 (see electronic supplementary material, tables S3 and S4). Some of the explanatory variables were significantly correlated with each other (see electronic supplementary material, table S5). If a variable (x_1) included in the best model was correlated with any other variable (x_2) not contained in the best model, we report δ-(Q)AICc values between the best model and the best alternative model in which x_2 appears in place of x_1. We accepted a correlated variable in the best model if δ-(Q)AICc of the alternative model was more than 3 (see electronic supplementary material, tables S3 and S4). Linear models and model selection were performed in R v. 2.15.0 [36] using the packages lme4 [37] and MuMIn [35].

Additionally, we performed a structural equation model (SEM) in IBM SPSS AMOS v. 21 to disentangle direct effects of drivers on pollination success from indirect effects via flower visitation. From an overall model with all hypothesized effects, as depicted in figure 1, we selected the best model with AIC selection, using the specification search function.

Full data used in this study are available in the electronic supplementary material.

3. Results

(a) Flower visitation

In total, 127 insect visits to cherry flowers were filmed (Hymenoptera: 54; Diptera: 51; Coleoptera: 21; Heteroptera: 1). Honeybees were only observed at one site. Bees (Apiformes) and two families of flies (Empididae and Syrphidae) showed a mean visit behaviour score greater than or equal to 2.5 and were therefore considered as potential pollinators and used for modelling flower visitation. Wild bee visitors comprised *Andrena haemorrhoa*, *Andrena* cf. *gravida*, *Andrena nitida* and *Osmia bicornis* (see electronic supplementary material, table
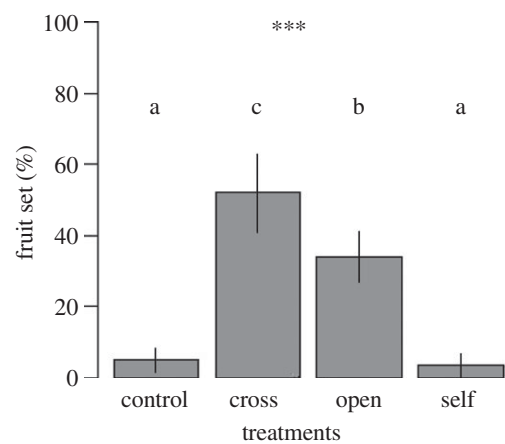
Figure 3. Pollen limitation. Mean fruit set (% of flowers that developed into fruits) per pollination treatment. 'Control' flowers were bagged, 'cross' flowers were bagged and pollinated by hand with pollen from other trees, 'open' flowers had no treatment and 'self' flowers were bagged and pollinated by hand with pollen from the same tree. Results are based on GLMER (binomial error distribution). Error bars indicate standard error of the mean. Overall significance of treatments on fruit set indicated with ***$p < 0.001$. Different letters above bars indicate significant differences between treatments at $p < 0.01$.

S2). Visitation rate was best explained by cherry isolation and wood amount. Alternative models containing local variables, cherry amount or wood isolation instead of cherry isolation or wood amount had substantially less support (δ-AICc > 8.2; electronic supplementary material, table S3). Visitation rate increased with decreasing isolation from the next cherry tree ($z = -3.58$, d.f. = 24, $p < 0.001$) and with increasing amount of woody habitat in the landscape ($z = 3.15$, d.f. = 24, $p = 0.002$; figures 1 and 2). Cherry isolation and woody habitat amount explained together 35% of the total model deviance and were present in all models with δ-AICc < 4.7 (see electronic supplementary material, table S3). Excluding the few visits by honeybees did not change the variables retained in the best model. Duration per visit was only explained by wind: higher wind speed was associated with increased visitation time ($t = 2.53$, d.f. = 25, $p = 0.024$, explained deviance by wind: 26%).

(b) Fruit set

In total, 266 groups of flowers were included in our experiment. Fruit set was strongly affected by the different pollination treatments (figure 3): 52% of 'cross' flowers, 34% of 'open' flowers, 5% of 'control' flowers and 4% of 'self' flowers set fruit ($\chi^2 = 178$, $p < 0.001$). 'Control' and 'self' treatments had a significantly lower fruit set than 'open' and 'bagged' treatments ($z = 7.95$, $p < 0.001$). 'Cross' treatment had a significantly higher fruit set than 'open' flowers ($z = 2.99$, $p = 0.003$). 'Control' and 'self' treatments did not differ ($z = 0.24$, $p = 0.8$).

When testing effects of landscape and local variables on fruit set of 'open' flowers, fruit set was best explained by cherry isolation and the number of heterospecific shrubs in bloom. Alternative models containing the number of cherry flowers, wood amount, wood isolation or cherry amount instead of cherry isolation or heterospecific shrubs had substantially less support (δ-QAICc > 4.8; electronic supplementary material, table S4). Fruit set increased with decreasing isolation from the next cherry tree ($t = -3.27$, d.f. = 25, $p = 0.003$) and decreased with increasing numbers of heterospecific shrubs in bloom within a 50 m buffer around studied trees ($t = 2.67$, d.f. = 25, $p = 0.013$; figures 1 and 4). Cherry isolation and number of shrubs explained 37% of the total model deviance and were present in all models with δ-QAICc < 3.8 (see electronic supplementary material, table S4). Fruit set of 'control' flowers was best explained by wind, cherry isolation and isolation from woody habitat but wind was the only significant variable increasing fruit set of 'control' flowers ($t = 2.23$, d.f. = 22, $p = 0.037$). Wind, cherry isolation and isolation from woody habitat explained 45% of the total model deviance.

Fruit set of 'open' flowers was significantly related to visitation rate ($t = 2.13$, d.f. = 25, $p = 0.043$). Nevertheless, results from SEM indicate that fruit set was not directly related to visitation rate but that both variables were independently affected by cherry isolation: the best SEM after AIC model selection did not contain a direct effect of visitation rate on fruit set (figure 1).

4. Discussion

We show how local and landscape management can affect the delivery of pollination services (figure 1). The amount of pollinator habitat in the landscape, but not isolation from the next habitat patch, increased the number of visits to cherry flowers. Isolation of studied cherry trees from conspecifics decreased visitation rates and fruit set. At the local scale, heterospecific flower density decreased pollination success but not visitation rates.

(a) Pollinator habitat amount

The amount of suitable habitat in the landscape determines the pool of available species and individuals and increases the chance of local populations to persist [14]. In accordance with this prediction (hypothesis 1), we found higher visitation rates in landscapes with higher amount of woody habitats (figure 2b). Woody habitats comprised different elements (forest, orchards, hedgerows, single trees, etc.) but forest made up by far the largest amount (see electronic supplementary material, table S1). In contrast to the frequent expectation that flower-rich open (non-woody) semi-natural habitats favour pollinator communities [30], visitation rates

did not correlate with higher amount of open semi-natural habitats. In our study landscapes, open semi-natural habitats were relatively rare (below 8%, except one site with 12%). A minimal threshold of 20% of semi-natural habitats was suggested to ensure meaningful protection of biodiversity and ecosystem services [14]. Thus, open semi-natural habitats may have been too rare in the studied landscapes to have a strong effect on pollinator activity. By contrast, woody habitats covered more than 20% of the area in 15 out of 30 studied landscapes. Woody habitats including forests provide nesting cavities for bees [27]. Additionally, in spring these habitats provide favourable conditions for ground nesting bees (most wild bee species observed on cherry flowers; electronic supplementary material, table S2) because of a combination of relatively undisturbed and sunny ground before the appearance of canopy foliage [25,27]. Pollinators nesting in the forests are known to enter open landscape for foraging trips [25]. Furthermore, woody habitats provide abundant food resources in spring in the form of vernal blooms of trees, shrubs and ground flowering plants [24,26,38]. The concentration of these resources in spring may explain why woody habitats were less important for bee communities sampled in the same landscapes but over the entire vegetation period [23]. In contrast to a study in almonds [39], the positive effect of amount of suitable pollinator habitat on visitation did not translate into higher fruit set, showing that the availability of pollinators is not always limiting pollination success [12]. The effectiveness of pollen transfer may rather depend on the availability of outcross pollen (see section 4c). This may be a reason why fruit set is generally decreasing less steeply with distance from semi-natural habitats than visitation [40,41].

(b) Pollinator habitat isolation

Isolation from woody habitats, as a measure of fragmentation *per se*, was not relevant for pollinators at the investigated scale (100–200 m), showing the importance of separating isolation and habitat amount [10–14]. The scale of isolation we used was less than the maximal foraging ranges of most solitary bees [42,43]. However, only few individuals have the capability to cover the maximal foraging distances [31] and effects of isolation on abundance, richness and fitness have previously been detected at scales of 200 m or lower [30,32]. The concept of mobile link compensation (discussed in [38]) would predict that the absence of isolation effects is caused by pollinators compensating isolation with longer foraging distances. In this study, this remains speculative as we did not test foraging duration per site, a measure expected to increase in isolated populations because of higher movement costs [15]. Furthermore, pollinators may not perceive the open agricultural matrix as a resource depleted barrier [7]. The absence of an interaction between habitat amount and isolation (hypothesis 2) gives no support for the prediction that isolation becomes more important in simplified landscapes with lower amount of semi-natural habitats [14].

(c) Spatial distribution of plant population

In accordance with our predictions (hypothesis 3), we found a strong reduction of pollination success with isolation from cherry trees (figure 4a). Further, we proved pollen limitation in our study system by showing a significantly higher fruit set when pollination was artificially maximized by
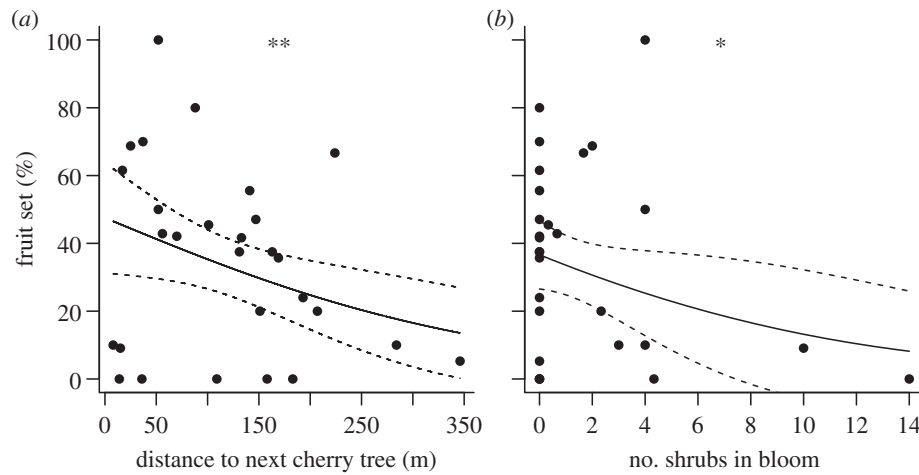
Figure 4. Pollination success. Mean fruit set of 'open' flowers per study site in relation to (*a*) distance to the next wild or cultivated cherry tree and (*b*) the number of shrubs in bloom around the study site (50 m buffer). Results are based on GLM (quasi-binomial error distribution). Solid lines show predicted values, dashed lines are estimated 95% confidence intervals. Dispersion parameter = 2.1, residual d.f. = 24, significance levels: **$p < 0.01$, *$p < 0.05$, explained deviance = 37%.

supplementing compatible pollen by hand ('cross' treatment) compared with insect-pollinated flowers ('open'; figure 3). Pollen limitation in self-incompatible plants can be explained by a lack of pollinators or by a lack of compatible pollen in the vicinity of the focal plant [7]. Here, fruit set was correlated with visitation rate. However, the results from SEM (figure 1) suggest that this relationship is not causal but that both variables are independently affected by isolation from cherry trees. This suggests that pollen limitation is caused by the lack of compatible pollen sources rather than by the number of visiting pollinators. Effects of isolation from the next conspecific plant on fruit set have been reported earlier [6], and human disturbance is known to disrupt plant–pollinator interactions causing outcross pollen limitation [44,45].

As visitation rates declined with cherry tree isolation (figure 2*a*), we suspect flower consistency of wild pollinators to cherry. All bee visitors were flower generalists (polylectic) [46] but generalist pollinators may temporally switch strategy and become specialized in times of low flower availability [12]. Alternatively, higher visitation at less isolated sites can be explained by a spill over from concentrated pollinator communities around cherry trees. Both visitation rates and fruit set dropped by approximately 75% along 350 m of cherry isolation (figures 2*a* and 4*a*). Declines in visitation and fruit set are commonly not parallel [40,41] but may be observed if first, local plant populations are so small that compatible pollen has to come from outside the population or second, if isolation directly measures distance from nearest pollen donors. For example, isolation from woody habitat negatively affected fruit set of primroses (*Primula elatior*) in the same landscapes [22] possibly because distance to forest not only reflected isolation from suitable habitat for pollinators, but also from conspecific plant populations.

Surprisingly for an insect-pollinated plant, isolation from the next cherry tree and wind explained fruit set of bagged 'control' flowers best. This may be an indication that wind plays a role in cherry pollination when suitable pollen donors are close.

(d) Local flower densities

Because plant density can affect pollination at different spatial scales [12], we tested effects of target plant density not only at the landscape scale (cherry isolation and amount) but also at the local scale. In contrast to our predictions (hypothesis 4), we found no change in visitation or pollination success at sites with different local densities of cherry flowers. Higher number of cherry flowers on study trees (local conspecific flower density) neither attracted pollinators from the landscape (concentration effect) nor diluted them [14,19]. Furthermore, ground flowering plants seemed not to influence flower visitors on cherry trees, in agreement with findings from mature cherry trees in Germany [33]. Fruit set was negatively related to the number of heterospecific shrubs in bloom within a buffer of 50 m (figure 4*b*). This effect was not associated with decreasing visitation rates, contradicting the hypothesis of local dilution effects [14,19]. Instead, it suggests that the pollen mix of visiting insects contained a higher share of heterospecific pollen at sites with high heterospecific flower density [7]. The movement between con- and heterospecific flowers possibly led to the deposition of more heterospecific pollen on cherry stigmas causing pollen clogging (block of stamens) or chemical inhibition of pollen tube growth [7].

5. Conclusion

Our study demonstrates how local and landscape management can affect the delivery of an agriculturally important ecosystem service. The amount of woody habitat but not isolation (up to 200 m) influenced insect visitation rates to cherry flowers. This extends the understanding of independent effects of habitat isolation (as a measure of fragmentation) and habitat loss. Surprisingly, pollination success did not directly depend on pollinator visitation. Instead, both appeared to be independently reduced by isolation from conspecific trees. These results underline the importance of considering the plant's need for conspecific pollen rather than focusing only on pollinators' habitat requirements and flower visitation. In accordance with the relevance of conspecific pollen availability, pollen competition with co-flowering species at the local scale decreased pollination success but not visitation, suggesting that movements of pollinators between different species reduce the quality of pollen mix transported. Our study

underlines the importance of disentangling local from landscape-scale effects, and direct effects of pollen availability on fruit set from indirect effects via pollinator visitation to understand animal pollination services.

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