Effects of habitat amount and fragmentation on reproductive success of insect-pollinated plants in a Swiss vineyard landscape

Master thesis

Faculty of Science, University of Bern

Handed in by

Elisabeth Klaus

2018

Supervisors

Dr. A. Jacot, Prof. R. Arlettaz

EFFECTS OF HABITAT AMOUNT AND FRAGMENTATION ON REPRODUCTIVE SUCCESS OF INSECT-POLLINATED PLANTS IN A SWISS VINEYARD LANDSCAPE

E. Klaus[1], L. Bosco[1,2], C. Maurer[1], B. Schranz[1], F. Arnold[1], R. Arlettaz[1,2], A. Jacot[1,2]

[1] Division of Conservation Biology, University of Bern, Switzerland

[2] Swiss Ornithological Institute, Valais Field Station, Switzerland

Abstract

The ongoing intensification of agriculture has led to habitat loss, degradation and fragmentation with their concomitant negative effects on biodiversity. For plant species relying on pollination those processes are expected to have severe effects on individual fitness due to reduced number of pollinators. Intensively managed vineyards represent an ideal study system due to their near-binary division into vegetated and bare vineyards and their high variation in habitat amount and configuration on a landscape-scale. Here we investigated the separate effects of habitat amount and the degree of fragmentation on fitness-related variables in three plant species (*Lotus corniculatus, Centaurea jacea* and *Sinapis alba*) and the relationships with pollinator abundance. Habitat amount and fragmentation significantly affected pollinator visitation rate and reproductive success of plants. Plant reproduction was affected congruently and positively by habitat amount while fragmentation effects were found exclusively for *S. alba*. Pollinators responded differently to both variables, most likely due to changes in behavior and species composition according to plant specialization. Overall our results indicate that reproductive success of plants is mainly determined by habitat amount rather than fragmentation, while for pollinator abundance effects are potentially more variable due to divergent habitat requirements between pollinators. To enhance conditions for plant-pollinator interactions we recommend vineyard management with flower-rich ground vegetation enhancing habitat amount and to preserve patchiness of different managements for intermediate levels of habitat fragmentation.

Keywords

Plant reproductive success, pollinator visitation rate, habitat fragmentation, habitat amount, landscape scale, ground vegetation, vineyards

Introduction

The ongoing intensification of agricultural land has led to landscape modifications resulting in loss, degradation and fragmentation of natural habitat with major impacts on global biodiversity and ecosystem services such as pollination (Andrén 1994; Fischer & Lindenmayer 2007). The process of habitat fragmentation is usually defined as "a large expanse of habitat being transformed into a number of smaller patches of smaller total area, isolated from each other by matrix of habitats unlike the original" (Wilcove, McLellan & Dobson 1986). This definition of habitat fragmentation implies four effects: reduction in habitat amount, increase in number of patches, decrease in size of habitat patches and increase in isolation of patches (Fahrig 2003). Several studies have stressed the importance of separating the effects of habitat amount and fragmentation as these processes potentially have divergent effects on biodiversity (McGarigal & Cushman 2002; Fahrig 2003; Hadley & Betts 2012). Habitat loss is known to be a main driver of global biodiversity decline (Potts *et al.* 2010; Haddad *et al.* 2015) and to impair functions such as breeding, foraging and dispersal success or predation rates (reviewed in Fahrig 2003). Regarding fragmentation *per se*, the answer is often less clear. It has been suggested that fragmentation effects could be mediated by the amount of habitat available (Rybicki & Hanski 2013). If habitat amount is high, effects of fragmentation can become less pronounced or even positive, e.g. by offering different kinds of habitat structures improving overall landscape heterogeneity (Fahrig *et al.* 2011; Mallinger, Gibbs & Gratton 2016). However, at low habitat amounts within the landscape, the spatial arrangement becomes more important and fragmentation is expected to have negative effects (Andrén 1994).

Interactions between plants and animals are of particular interest for fragmentation research because of their importance for ecosystem functioning (Klein *et al.* 2007; Papanikolaou *et al.* 2017). Mutualistic interactions include those between plants and pollinators, antagonistic those between plants and herbivores or predators (Kearns, Inouye & Waser 1998; Mack *et al.* 2000). The pollination services are needed for almost 90% of all flowering wild plants and crops leading to a considerable economic value (Klein *et al.* 2007; Papanikolaou *et al.* 2017). Pollinators are at risk globally (Potts *et al.* 2010) and outcrossing plant species are decreasing suggesting a causal connection between these two processes (Biesmeijer *et al.* 2006). There is growing concern that these parallel declines might ultimately lead to a demographic collapse of plant populations (Aizen, Ashworth & Galetto 2002).

A factor that only recently drew increased attention is the effect of connectivity between fragments on pollination and therefore on plant reproductive success (Matesanz *et al.* 2015). Studies have shown that a better connectivity increases pollen transfer (Townsend & Levey 2005) and is more important than fragment size (Matesanz *et al.* 2015; Gomez-Fernandez, Alcocer & Matesanz 2016).

Corridors between fragments can improve both pollinator and predator movement, supporting not only mutualistic but also antagonistic interactions with plants (Orrock & Damschen 2005; Menz *et al.* 2011). However, connectivity between fragments does not only depend on corridors but also on the type and quality of both habitat and matrix. Different land cover types surrounding habitat patches can be classified as hostile for some species but might be beneficial for others (Prugh *et al.* 2008). Furthermore, species differ in their ability to move through different matrix types which has been shown for different butterfly taxa and their resistance to either willow, conifer or meadow dominated matrices (Ricketts 2001). Therefore it is important to consider matrix quality instead of solely focusing on habitat patches for conservation efforts (Prugh *et al.* 2008; Franklin & Lindenmayer 2009). The presence of resource-rich sites within fragmented landscapes improves pollinator diversity and richness (Klein *et al.* 2007; Potts *et al.* 2016). Both bee abundance and species richness is higher in agricultural landscapes comprising more high-quality habitats (Kennedy *et al.* 2013). In landscapes dominated by only few different types of habitat, the effects of adding supplementary structures, i.e. heterogeneity, might have a stronger impact than within landscapes that already include more high-quality habitat (Kremen *et al.* 2007; Aguirre-Gutierrez *et al.* 2015).

For plant populations both habitat loss and fragmentation can have severe consequences such as reduced population sizes and viability due to variable reasons like decreased reproductive success and altered biotic interactions (Hobbs & Yates 2003; Haddad *et al.* 2017). Fragmentation can disrupt plant-pollinator interactions either as a result of decreased abundances or as a consequence of compositional or behavioral changes (Aguilar *et al.* 2006). If quality and quantity of transferred pollen (Aguilar *et al.* 2006; Aizen & Harder 2007; Kolb 2008) as well as efficiency of pollination services (Dauber *et al.* 2010) are reduced, reproductive success is limited with long term effects for the individual plant, the population and the plant community as a whole (Aizen, Ashworth & Galetto 2002; Matesanz *et al.* 2015). Several traits and trait guilds predispose plants to a higher susceptibility to fragmentation (Henle *et al.* 2004; Evju *et al.* 2015). Among them are reproductive potential, population size or ecological specialization (Henle *et al.* 2004). Reproductive potential can be limited if plant species depend exclusively on sexual reproduction mediated by pollinators, without the ability of vegetative propagation (Bond 1994; Bartlewicz *et al.* 2015). Pollinators are essential for sexually reproducing plants (Aguilar *et al.* 2006), hence plant reproduction can be interfered if lower numbers of pollinators visit small and isolated patches and if less conspecific plants for pollen exchange are available (Kolb 2008; Delmas *et al.* 2016). Besides the breeding system, fragmentation responses of plants can also differ depending on their compatibility system. Self-incompatible plants fully rely on animal vectors because only outcrossed pollen can be used for fertilization. In contrast, self-compatible plants have several possibilities for reproduction - they can either produce seeds

using pollen from conspecific plants or use their own pollen (Barrett & Harder 2017). Aguilar et al. (2006) concluded in a review that self-incompatible plants are more susceptible to pollen limitation caused by habitat fragmentation than self-compatible plants. Increased fragmentation reduces pollinator diversity and abundance as well as fitness of self-incompatible plants (Potts *et al.* 2016 and references within). Separate effects of habitat amount and fragmentation *per se* have been investigated on plant species richness (Haddad *et al.* 2017) and pollinators (Hopfenmüller, Steffan-Dewenter & Holzschuh 2014), but to our knowledge not on both mutualistic and antagonistic plant-insect interactions.

With our landscape-scale field experiment conducted in Swiss vineyards, we aimed to disentangle the effects of habitat amount and fragmentation on plant reproductive success and pollinator visitation rates. This vineyard landscape offers a near-binary system comprised of ground vegetated and bare vineyards. The majority (80%) of vineyards are bare due to intense herbicide applications, while only few wine growers allow ground vegetation to grow, providing increased foraging resources for pollinators and higher plant diversity and abundance. These vegetated fields vary in size and levels of isolation (i.e. connectedness to other vegetated fields) which possibly influences diversity, population sizes and reproductive success of plant populations. With a near-experimental set-up of three different plant species placed in areas varying in their degree of fragmentation (number of vegetated patches) and habitat amount (surface covered by vegetated patches), we sought to answer what the effects of habitat amount and fragmentation are on (i) reproductive success of exclusively insect-pollinated, self-incompatible plant species, (ii) overall pollinator visitations of these plant species and (iii) whether seed predation is affected by habitat amount and fragmentation.

Material & Methods

Study Sites

The study was carried out in July 2017 in the vineyards of Valais in south-western Switzerland (fig. S1). Vineyards are situated on the sun-exposed slopes along the Rhône valley with an elevation up to 900 m above sea level (Arlettaz *et al.* 2012). The average annual precipitation is around 580 mm, the average annual temperature 9.7 °C (for Sion, Anonymous 2017). Study sites were spread between the communities of Fully (46°8′N, 7°6′E) in the south-western part of the valley and Ausserberg (46°18′N, 7°51′E) in the north-eastern part. All but two study sites were located north of the Rhône, both in the plain and on hillsides. Vineyards in this region are very intensively managed with a high

amount of pesticide, mainly herbicide, inputs. Some vineyard areas are still interspersed by natural vegetation such as steppe or forest fragments, especially those situated on hillsides (Arlettaz *et al.* 2012).

Vineyard Field Characteristics & Fragmentation Classes

Vineyards were classified as either vegetated (> 40% ground vegetation cover) representing the 'habitat' or bare (< 40% ground vegetation cover), representing the 'matrix'. Ground vegetation percentage for each field was assessed using the Normalized Difference Vegetation Index (NDVI) derived from satellite pictures that were recorded before sprouting of the vine leaves (Sentinel-2, 10m resolution, recorded 11/3/2017). Habitat amount, as percentage of area covered by vegetated vineyard fields (PLAND, percentage of landscape), and fragmentation, measured as number of vegetated vineyard field patches per 100 ha (PD, patch density) were calculated using a moving window analysis with the statistical software FRAGSTATS (McGarigal, Cushman & Ene 2012). Both metrics were calculated within a radius of 250 m as studies have shown that most pollinators forage within this distance (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007; Wolf & Moritz 2008). Vineyard fields were selected according to a 2x2 factorial design as a combination of low or high habitat amount and low or high fragmentation, resulting in four classes. The matrix was included as a fifth class. Using the GIS software QGIS (QGIS Development Team 2017), we selected eight vineyard fields for each class with at least 200 m distance to each other. In total we had 40 fields distributed in a stratified random design to account for geographical variability and to avoid clumping of fields within classes (Fig S1).

Study Species

We selected the following three plant species as model organisms to measure plant reproductive success based on pollination activity: *Sinapis alba* (Abel, Wilson & Luhman 2003; Naumkin & Velkova 2013), *Lotus corniculatus* (McKersie, Tomes & Yamamoto 1981; Rasmussen & Brodsgaard 1992; Pellissier *et al.* 2012) and *Centaurea jacea* (Steffan-Dewenter, Munzenberg & Tscharntke 2001; Hegland & Totland 2008) (for more details see table 1). We selected these plant species because they fulfilled our three main criteria: they are (i) insect-pollinated; (ii) self-incompatible and (iii) reproduce sexually (based on the database BIOLFLOR, (Klotz, Kühn & Durka 2002)). These factors increase the sensitivity of plants to the impacts of fragmentation and reduced habitat amount (Rathcke & Jules 1993). By including five sites at which pollinators were excluded, we could test whether in fact all plant species depend on pollinator visitations to allow seed and fruit production. *C. jacea* and *L.*

corniculatus are relatively common in Valais vineyards, while *S. alba* does not occur naturally in this landscape and was included to detect possible differences of plant species that have no other conspecifics than our artificially placed plant individuals.

Experimental Design

Seeds of *S. alba*, *C. jacea* and *L. corniculatus* were purchased from Swiss seed growers and grown in a greenhouse. Seedlings were transplanted into 1 l - pots using standardized garden soil. To adapt to real weather conditions (especially to sun exposure), potted plants were put outside the greenhouse (six weeks for *C. jacea* and *L. corniculatus* and one week for *S. alba*), before we started the field-experiment. Since some plants had already started to bloom, open flowers were removed right before the transport to the study sites. At each location, 12 plants, i.e. four plant individuals per plant species, were randomly distributed and situated, in agreement with farmers, mostly at the margins of the vineyard fields to avoid incidents with farming activities (Steffan-Dewenter, Munzenberg & Tscharntke 2001). Within study fields, plants were placed in a manner to avoid having the same plant species next to each other. All plants were watered every three to five days depending on the weather conditions. To avoid lack of nutrients due to the rather small pot size, all plants were fertilized twice using a standard liquid fertilizer. To test for the degree of pollinator dependence of the three plant species, cages for pollinator exclusion (1x1.5x1.5 m) with white, fine-meshed (0.5x0.5 mm) cloth were installed in five of the 40 vineyard fields additionally (Steffan-Dewenter & Tscharntke 1999). Especially inside the cages aphid infestation was locally high which was treated either by manual comminution or by using a solution containing soft soap. After five weeks in the field, plants were re-collected and further seed ripening in the greenhouse was allowed. All flowers and buds were regularly removed to hinder ripening of fruits that were not pollinated during the field-experiment in the vineyards.

Plant Reproductive Success

To assess plant reproductive success, three proxy variables were used: seed number, seed weight and fruit number (Steffan-Dewenter & Tscharntke 1999; Van Rossum 2010; Pellissier *et al.* 2012). For all three plant species, fruits or capitulae (for *C. jacea*, hereafter called fruits) with seeds were collected. The leftover plants were cut right where the stem emerged from the soil. Both, fruits and plant biomass were separately stored in paper bags and dried in the oven at 80°C for at least 48 h. All fruits per plant were counted and the whole plant biomass weighed. Due to high amounts of fruits developed by *S. alba* (up to 351 fruits per plant) and the high amount of seeds per fruit for *C. jacea*

(up to 121 seeds per fruit), we selected a random subsample of six fruits per plant for all three plant species. For this subset, all seeds were counted and weighed after re-desiccation for at least 2 h at 80°C. Seed predation (holes in the seeds, larvae, pupae or adults) was assessed for *L. corniculatus* and *C. jacea*, but not for *S. alba* as there were not enough predated fruits available (Steffan-Dewenter, Munzenberg & Tscharntke 2001).

Flower-Visitor Observations

Flower-visitor observations were performed on days with suitable weather conditions (no rain, temperature above 20°C) between 08:30h and 17:30h (Steffan-Dewenter, Munzenberg & Tscharntke 2001; Gonzalez-Varo, Arroyo & Aparicio 2009; Fijen & Kleijn 2017). Every study site was visited twice (except for one) with pollinator observations lasting for 30 min (Fijen & Kleijn 2017). The amount of observers varied between one and four, adapted to the amount of flowers that had to be surveyed per study field. Prior to the census, open flowers or inflorescences were counted for each individual plant. All 12 plants per field were observed simultaneously. Flower-visitation rates were recorded on the plant level as it was impossible to count them per flower, especially so for flower-rich species as *S. alba* (Gonzalez-Varo, Arroyo & Aparicio 2009). Observers were either sitting or standing at least one meter away from the plants and kept calm for several minutes before and made minimal movements during the observation time (Dauber *et al.* 2010). Only insects that touched the reproductive parts of flowers to enable pollination were counted (Albrecht *et al.* 2007). During the observations, local temperature in the shade and wind speed were recorded (Peat & Goulson 2005) (see table 2).

Environmental Variables

Using QGIS (QGIS Development Team 2017), we calculated three topographical variables: NDVI, aspect and slope. To assess the impact of semi-natural habitats, we included the area and distance of those as a covariate, while we considered steppe, forest and meadows as semi-natural habitats. Also the number and distance of honey bee hives within a buffer of 250 m was included in the analysis. Presence of seed predation was used as a covariate, but only for *L. corniculatus* and *C. jacea* data was sufficient to be included in the analyses. Plant biomass of every study plant individual was measured after fruits and seeds had been removed. During pollinator observations, we counted all open flowers of the study plants and assessed wind speed, temperature, daytime (morning or afternoon) and weather conditions (sunny or cloudy, table 2).

Statistical Analysis

As our main interest lied in the effects of habitat amount and fragmentation, both of these variables entered all analyses as continuous effects. For both analyses, reproductive success and pollinator visitations, all continuous explanatory variables (see table 2) were tested for collinearity using the Spearman's correlation coefficient. If variables were correlated with $|r_s| > 0.7$, those variables that performed better based on lower AIC values in univariate models were retained (Sakamoto, Ishiguro & Kitagawa 1986; Dormann *et al.* 2013). Variables were transformed if necessary and standardized to facilitate comparison between estimates and improve model convergence. For count data we tested for over-dispersion using the function *dispersion_glmer* (R package blmeco, Korner-Nievergelt *et al.* 2015). If over-dispersed, we controlled for it by including an observation-level random effect in the model (Harrison 2014).

Plant Reproductive Success

Number of seeds, seed weight, number of fruits and seed predation were used as response variables in this study part (McKersie, Tomes & Yamamoto 1981; Steffan-Dewenter, Munzenberg & Tscharntke 2001; Van Rossum 2010; Pellissier *et al.* 2012). Data of predation on seeds was not sufficient for *S. alba.* For *L. corniculatus* few predation data was available but not sufficient to be used as response variable. Therefore responses to seed predation were only tested on *C. jacea*. However, for this plant species number of fruits was excluded, as it does not produce fruits but seeds develop in flower heads directly (capitulae) (Hardy & Vekemans 2001). For *S. alba*, we used linear mixed effect models with a Gaussian distribution (*lmer*, R package *lme4*, Bates *et al.* 2015) for number of seeds and 'site ID' as random factor. For the variable seed weight, a generalized linear mixed effect model (*glmer*, R package *lme4*, Bates *et al.* 2015) with Poisson distribution and 'site ID' and 'plant ID' as random factors as well as an observation-level random factor was built. Number of fruits was log-transformed and linear mixed effect models with a Gaussian distribution (*lmer*, R package *lme4*, Bates *et al.* 2015) and 'site ID' as random factor was applied. For all response variables of *L. corniculatus*, which are seed number, seed weight and fruit number, generalized linear mixed effect models (*glmer*, R package *lme4*, Bates *et al.* 2015) with a Poisson distribution and 'site ID' and 'plant ID' as random factors were used. For seed number and weight, we additionally included observation-level random factors to account for over-dispersion. For *C. jacea*, we applied generalized linear mixed effect models (*glmer*, R package *lme4*, Bates *et al.* 2015) with Poisson distribution with 'site ID', 'plant ID' and an observation-level random factor as random factors for number of seeds and seed weight. For the predation data of *C. jacea*, we used generalized linear mixed effect models (*glmer*, R

package *lme4*, Bates *et al.* 2015) with binomial distribution with 'site ID' and 'plant ID' as random factors. For all response variables, we also tested the interactive effects between habitat amount and fragmentation.

To test for the differences between pollinator exclusion and open plants, we applied a linear mixed effect model (*lmer*, R package *lme4*, Bates *et al.* 2015) with 'site ID' as random factor for seed number of S. alba. For all other variables (seed number, seed weight and fruit number) of the three plant species, we used generalized linear mixed effect models (*glmer*, R package *lme4*, Bates *et al.* 2015) with Poisson distribution with 'site ID' and 'plant ID' as random factors.

Pollinator Visitation Rate

For the analysis of pollinator visitations, data was checked for zero-inflation using the function *testZeroInflation* (R package *DHARMa*, Hartig 2018). Pollinator data for *S. alba* was zero-inflated which is why models were fitted using a generalized linear mixed effect model *glmer* with negative binomial distribution (*glmer.nb*, R package *lme4*, Bates *et al.* 2015). By using this model also over-dispersion could be controlled for. For *C. jacea* and *L. corniculatus,* generalized linear mixed effect models (*glmer*, R package *lme4*, Bates *et al.* 2015) with Poisson distribution accounting for over-dispersion were applied.

Results

Plant Reproductive Success

Sinapis alba

We collected data of 121 from originally 160 *S. alba* plants with in total 13'347 fruits and 49'494 seeds, extrapolated from the mean number of seeds and number of fruits per plant. For each plant we randomly selected up to six fruits, or less if fewer fruits were available, counted and weighed their seeds which resulted in a total amount of 2'291 for all plants together. Mean ± SD number of seeds per fruit was 3.71 ± 1.57, mean weight per seed 9.55 ± 9.31 mg and mean number of fruits per plant 109.62 ± 86.11. The difference between treatment and control (pollinator exclusion) was significant for number of seeds (*lmer*: estimate ± SE= 1.013 ± 0.434; t = 2.336; p = 0.019), but neither for seed weight nor for number of fruits (fig S2).

The best model for number of seeds included both habitat amount and fragmentation with their quadratic effects and NDVI (table 3), while habitat amount and fragmentation showed no significant

effects, NDVI was positively correlated (table 4, fig 1). In the best model for seed weight habitat amount and its quadratic effect, NDVI and plant biomass with its quadratic effect were included (table 3). Habitat amount had a quadratic positive effect, showing a minimum between 20 - 40%. Plant biomass had a significant negative effect with an optimum between 7 - 13 g, while NDVI had a linear positive effect (table 4, fig 2). For number of fruits, fragmentation and habitat amount with their quadratic effects, plant biomass, pollinator visits and distance to next natural habitat were all included in the best model (table 4). Fragmentation showed a quadratic negative effect with an optimum between 40 - 60 vegetated vineyard fields per 100 ha. Habitat amount had a significant positive quadratic effect with a minimum between 20 - 35%. Pollinator visits, distance to natural habitat and plant biomass all had significant positive effects (table 4, fig 3).

Lotus corniculatus

We re-collected 129 plants which had developed 5'844 fruits with a total of 58'577 seeds of which we counted and weighed 5'795 (of a subset six) fruits per plant. Mean ± SD number of seeds per fruit was 9.42 ± 6.11, mean seed weight 8.92 ± 6.89 mg and mean number of fruits per plant 56.04 ± 48.65. The treatment had significant positive effects on number of seeds (*glmer*: estimate ± SE = 2.728 ± 0.287; z = 9.508; p <0.001), seed weight (*glmer*: estimate ± SE = 2.665 ± 0.361; z = 7.381; p < 0.001) and number of fruits (*glmer*: estimate ± SE = 5.455 ± 0.553; z = 9.871; p < 0.001) (fig S3).

For number of seeds, the best model included habitat amount, plant biomass and distance to next honeybee hive with their quadratic terms and fragmentation (table 3). The quadratic term of plant biomass had a significant negative effect with an optimum between 25 - 35 g and distance to the next honeybee hive showed a positive quadratic effect with a minimum between 400 - 700 m (table 5, fig 4). For seed weight habitat amount and plant biomass with their quadratic effects were in the best model (table 3). Habitat amount had a significant positive quadratic effect with a minimum between 18 - 30% and plant biomass showed a negative quadratic effect with an optimum between 25 - 32 g. Seed weight was highly correlated with number of seeds (spearman correlation coefficient $|r_s|$ = 0.89), explaining the similar results (table 5, fig 5). Habitat amount, plant biomass and its quadratic term, pollinator visits and seed predation were retained in the best model for number of fruits (table 3). Habitat amount and seed predation had significant negative effects while pollinator visits showed a positive linear relationship and plant biomass a negative quadratic effect with an optimum between 25 - 35 g (table 5, fig 6).

Centaurea jacea

Of 160 plants at the start, we could use 114 with 1'472 fruits and 63'344 seeds (extrapolation of mean number of seeds with total number of fruits per plant). For the subset of six fruits per plant (503 fruits in total), we counted 21'696 seeds. Mean ± SD number of seeds per fruit was 43.13 ± 25.52, mean seed weight 65.41 ± 51.94 mg and mean number of fruit per plant 14.04 ± 7.72. Of 503 fruits, we found 177 (35.2%) with signs of predation of larvae or adult flies in the fruits. For *C. jacea,* treatment was only significantly better for seed weight (*glmer*: estimate ± SE = 2.508 ± 0.514; z = 4.878; p < 0.001) but not for number of seeds and fruits (fig S3).

For number of seeds, plant biomass had a significant positive and seed predation a significant negative effect (table 6, fig 7). Habitat amount and pollinator visits showed significant positive quadratic effects with a minimum between 20-30% and 300 - 500 visits on seed weight. Seed weight was highly correlated with number of seeds (spearman correlation coefficient $|r_s|$ = 0.86) which is why results for these two variables are similar (table 6, fig 8).

The best model for seed predation included fragmentation and NDVI with both their linear and quadratic terms, the quadratic term of plant biomass, and linear relationships of aspect and number of honeybee hives (table 3). Seed predation was not correlated to habitat amount but showed a quadratic negative relationship with fragmentation with an optimum between 30-50 vegetated vineyard fields per 100 ha. Also NDVI showed a quadratic negative relationship with an optimum between 0.3-0.38. For plant biomass the correlation was positive quadratic with a minimum between 20-30 g. Number of honeybee hives was significantly positively correlated and aspect negatively (table 6, fig 9).

Pollinator Visitation Rate

In total we counted 19'671 flower visitations of pollinators, of which 18'388 were solitary bees, 314 honeybees (*Apis mellifera*), 337 syrphids, 42 bumblebees, 131 wasps, 191 butterflies, 53 other flies, 68 bugs, 33 beetles and 101 ants (table S1). As the vast majority of pollinators (93.5%) were solitary bees, we analysed all groups together. For *S. alba* one observation with an extreme value of 1'317 pollinator visits was excluded from the analysis to avoid over-estimation of responses. *S. alba* was visited by a total of 6'656 pollinators (without the outlier), with a mean ± SD of 44.37 ± 78.75 (range: 0-416), *L. corniculatus* by 1'577 with a mean ± SD of 9.56 ± 18.78 (range: 0-160) and *C. jacea* by 10'173 with a mean ± SD of 79.48 ± 123.01 (range: 0-736). The number of open flowers of the study species appeared to be very important to explain pollinator visits, which is why we included this

variable, additionally to habitat amount and fragmentation, as a fixed factor in all models. The number of open flowers of the study species appeared to be very important to explain pollinator visits, which is why we included this variable, additionally to habitat amount and fragmentation, as a fixed factor in all models.

For *S. alba*, the best model included habitat amount, open flowers and daytime (table 7). The quadratic term of habitat amount showed a negative correlation with an optimum between 15-25%. Open flowers were correlated positively and daytime negatively (table 8).

The best model for *L. corniculatus* contained fragmentation, habitat amount, open flowers, distance to next honeybee hive and temperature (table 7). Fragmentation had a significant negative effect and habitat amount a significant positive relationship. Open flowers and temperature were positively correlated and distance to next honeybee hive negatively (table 8).

For *C. jacea*, the best model included fragmentation with its quadratic term, open flowers, temperature, slope and wind (table 7). Fragmentation had a significantly negative quadratic effect with an optimum between 30-60 vegetated vineyard fields. Open flowers and temperature were correlated positively with pollinator visits. Slope and wind showed negative relationships (table 8).

Discussion

This study shows that the reproductive success of insect-pollinated generalist plants is more strongly driven by habitat amount than by fragmentation, since only one of our three study species, *S. alba*, responded to habitat fragmentation *per se* in this intensively used vineyard-agroecosystem. Responses of pollinator visits to habitat amount and fragmentation were plant-species specific. Neither for reproductive success nor for pollinator visitation rate could we detect any interactive effects between habitat amount and fragmentation. Our results emphasize the importance of disentangling the effects of habitat amount and fragmentation and highlight species-specific responses to both processes, particularly for the different pollinator groups with variable requirements for feeding and nesting resources.

Variable Effects of Habitat Amount and Fragmentation on Plant Reproduction and Pollinator Abundance

Seed set of all three plant species was lowest at intermediate amounts of 20 to 30% habitat, but fragmentation *per se* showed an optimum at intermediate levels of 40 to 60 vegetated vineyard

fields for *S. alba*, stressing the higher importance of habitat composition rather than configuration. However, pollinator abundance did not respond accordingly to both variables but effects appeared to be plant species-specific. Highest visitor numbers for habitat amount occurred at an optimum of 15 to 25% of vegetated vineyard area for *S. alba* and pollinator abundance increased linearly for *L. corniculatus*. Pollinator abundance responded to fragmentation for two plant species, with *L. corniculatus* showing a negative correlation and *C. jacea* a negative quadratic curve reaching an optimum at intermediate levels of 30 to 60 vegetated vineyard fields. These findings suggest that a compositional shift of pollinator assemblages occurred at varying levels of habitat amount and fragmentation (Steffan-Dewenter, Munzenberg & Tscharntke 2001). Changes in pollinator composition, abundance or behaviour are known to affect pollen deposition and pollen quality (Ashworth *et al.* 2004) with inevitable consequences on pollination efficiency.

Solitary wild bees were by far the most abundant group of pollinators with predominant presence of 96% for *S. alba*, 70% for *L. corniculatus* and 95% for *C. jacea*. Bees are the most important insect group primarily pollinating flowering plants (Ollerton, Winfree & Tarrant 2011). The pollination success of mainly wild bee visited plants increases if they are pollinated by several different bee assemblages (Blaauw & Isaacs 2014). Solitary bees are rather smaller-bodied and known to range on small spatial scales (Greenleaf *et al.* 2007). Larger-bodied pollinators like bumblebees or honeybees with greater flight ranges (Greenleaf *et al.* 2007) are less vulnerable to fragmented landscapes with low habitat amounts and might have profited from the absence of smaller-bodied wild bees in these areas (Steffan-Dewenter, Munzenberg & Tscharntke 2001; Heard *et al.* 2007; Hopfenmüller, Steffan-Dewenter & Holzschuh 2014), particularly since all study species can be efficiently pollinated by honeybees and bumblebees (Turkington & Franko 1980; Conner & Neumeier 1995; Steffan-Dewenter & Tscharntke 1999; Hennig & Ghazoul 2011), whereby our observations imply that honeybees were more abundant than bumblebees. This hypothesis is supported by the significant effect of distance to honeybee hives to both seed set and pollinator visitation rate of *L. corniculatus*, with lowest reproductive success at intermediate levels of 400 to 700m and a linear decrease of pollinator abundance the further away from the next honeybee hive. These findings highlight the shifts in pollinator assemblages according to different spatial scales and the subsequent consequences on pollination efficiency. Honeybees foraging ranges vary between 45 to 6'000 m but on average flowers are visited 800 m away from their hive (Hagler *et al.* 2011). Competition between more aggressive, social honeybees and solitary wild bees has been reported with direct negative effects on solitary bee visitations (Conner & Neumeier 1995; Hudewenz & Klein 2013). Detrimental effects of limited pollinator visitations to reproductive success may therefore occur for plant species exclusively dependent on solitary wild bees (Steffan-Dewenter & Tscharntke 1999).

A relevant influence might have been induced by the maximal amount of 50% vegetated fields, indicating a general limitation of habitat amount in this vineyard agroecosystem. It is possible that with higher habitat amounts plant reproduction would have increased according to differences in pollinator abundance, species richness and behaviour. More diverse pollinator assemblages are more stable which improves pollination success and therefore explains higher seed sets with increasing habitat amounts (Blaauw & Isaacs 2014). A patchy arrangement of vegetated fields reflecting intermediate fragmentation may provide a mosaic-like landscape with a variety of habitat types offering feeding and nesting sites at different spatial and temporal scales (Fahrig *et al.* 2011), on which pollinator assemblages depend to complete their life cycles (Winfree *et al.* 2009).

The Impacts of Habitat Quality

Surprisingly, the amount of ground vegetation in vineyards only affected the seed set of *S. alba* positively but was irrelevant for the other species. Positive effects of ground vegetation in vineyards have been proven for several taxa such as birds, arthropods (Bosco 2018, PhD thesis) and plants (Nascimbene *et al.* 2013). The three different plant species differ in their attractiveness for different pollinator groups with *S. alba* and *C. jacea* being visited by a wide array of insects from different orders, while *L. corniculatus* is more specialized on larger sized bee species (Turkington & Franko 1980; Klotz, Kühn & Durka 2002). According to our observations, *S. alba* was visited preferably by small-bodied wild bees, that might have profited from a higher flower abundance of the surrounding due to their limited foraging range. Nevertheless, it remains unclear why *C. jacea*, which was also mainly visited by small-bodied wild bees, did not respond in a similar way as *S. alba* to ground vegetation. Possibly, effects of ground vegetation might be more pronounced if focus would be laid on quality improvement by using flower-rich seed mixtures offering floral resources for pollinators and might act as corridors between otherwise isolated habitats. It has been shown that organic farming in vineyards which forbids herbicide usage supports plant diversity of especially perennial species (Nascimbene *et al.* 2016). Different management types can be highly valuable, as open areas represented by bare vineyards can provide nesting resources for below-ground nesting wild bee species (Cane 1991). Spatiotemporal variation of floral resources causes shifts of pollinators with varying importance of different habitat types between seasons (Sahli & Conner 2007), stressing the need of a heterogeneous landscape offering a continuous supply of feeding resources (Mandelik *et al.* 2012; Mallinger, Gibbs & Gratton 2016). This hypothesis is supported by our findings that semi-natural habitats fail to improve reproductive success and sustain pollinator abundance. Seed set of *S. alba* increased the further away semi-natural habitats were located which opposes findings for *Sinapis arvense* where fruit numbers declined with increasing distance to nearest calcareous

grasslands (Steffan-Dewenter & Tscharntke 1997; Carré *et al.* 2009). A relevant influence might have been obtained by pooling steppe, grasslands and forests together as the latter could have adversely affected nesting and floral availability particularly for solitary wild bee species (Winfree, Griswold & Kremen 2007; Mallinger, Gibbs & Gratton 2016). Flowering plants in forests and other semi-natural habitats are particularly important early in the season, while other habitat types such as croplands predominate later (Mallinger, Gibbs & Gratton 2016). Complementary habitat use of pollinator assemblages according to floral availability (Mandelik *et al.* 2012) may impact pollination efficiency with subsequent variability of plant reproductive success.

Similar Predator and Pollinator Reactions

Seed predation was tested for *C. jacea*, for which microlepidopterans and tephritid fly larvae are common predators (Steffan-Dewenter, Munzenberg & Tscharntke 2001). We found that more than one third of *C. jacea* capitulae were invaded by larvae, significantly lowering seed set. Predators responded to fragmentation showing an optimum of 30 to 50 vegetated vineyard fields which is a similar result as for pollinators of *C. jacea*. The positive curve with an optimum at intermediate levels of ground vegetation highlights the predator dependency on vegetation cover. Steffan-Dewenter et al. (2001) demonstrated that predators of *C. jacea* profit from higher landscape heterogeneity which is supported by our results as intermediate degrees of fragmentation and ground vegetation provide a greater habitat diversity. The positive response of seed predators to the amount of honeybee hives in the surroundings might be an artefact due to preferences of beekeepers to place hives in resource-rich or diverse areas but might also indicate a close connection between predators and pollinators for habitat requirements.

Conclusions and Recommendations for Conservation

Our results highlight the variability of responses of both plant species and pollinator groups to habitat amount and fragmentation most probably resulting from shifts in pollinator assemblages with consequences on pollination efficiency and thereby on plant reproductive success. The importance of habitat amount underlines the need to provide more suitable conditions which benefits both plant reproductive success and pollinator abundance. Therefore, we recommend encouraging ground vegetation within vineyards with special enforcement on vegetation quality by promoting plant species richness and flower abundance. The positive effects of intermediate levels of fragmentation indicate that different management types providing more heterogeneity can be

advantageous. Alternation of vegetated resource-rich and intensively managed vineyards has the potential to support and sustain a diverse pollinator assemblage.

Acknowledgements

Literature

Abel, C.A., Wilson, R.L. & Luhman, R.L. (2003) Pollinating efficacy of Osmia cornifrons and Osmia lignaria subsp lignaria (Hymenoptera : Megachilidae) on three Brassicaceae species grown under field cages. *Journal of Entomological Science,* **38,** 545-552.

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters,* **9,** 968-980.

Aguirre-Gutierrez, J., Biesmeijer, J.C., van Loon, E.E., Reemer, M., WallisDeVries, M.F. & Carvalheiro, L.G. (2015) Susceptibility of pollinators to ongoing landscape changes depends on landscape history. *Diversity and Distributions,* **21,** 1129-1140.

Aizen, M.A., Ashworth, L. & Galetto, L. (2002) Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science,* **13,** 885-892.

Aizen, M.A. & Harder, L.D. (2007) Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. *Ecology,* **88,** 271-281.

Albrecht, M., Duelli, P., Muller, C., Kleijn, D. & Schmid, B. (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology,* **44,** 813-822.

Andrén, H. (1994) Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. *Oikos,* **71,** 355-366.

Anonymous (2017) Klimadaten: Sonnenscheindauer, Niederschlag, Temperatur und Neuschnee. Bundesamt für Statistik, Neuchâtel.

Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nussle, S., Abadi, F., Braunisch, V. & Schaub, M. (2012) New vineyard cultivation practices create patchy ground vegetation, favouring Woodlarks. *Journal of Ornithology,* **153,** 229-238.

Ashworth, L., Aguilar, R., Galetto, L. & Aizen, M.A. (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *Journal of Ecology,* **92,** 717-719.

Barrett, S.C.H. & Harder, L.D. (2017) The Ecology of Mating and Its Evolutionary Consequences in Seed Plants. *Annual Review of Ecology, Evolution, and Systematics, Vol 48,* **48,** 135-157.

Bartlewicz, J., Vandepitte, K., Jacquemyn, H. & Honnay, O. (2015) Population genetic diversity of the clonal self-incompatible herbaceous plant Linaria vulgaris along an urbanization gradient. *Biological Journal of the Linnean Society,* **116,** 603-613.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software,* **67,** 1-48.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science,* **313,** 351-354.

Blaauw, B.R. & Isaacs, R. (2014) Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wild flowers. *Basic and Applied Ecology,* **15,** 701-711.

Bond, W.J. (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **344,** 83-90.

Bosco, L. (2018) Effects of vineyard management and fragmentation on Woodlarks (Lullula arborea) and their invertebrate prey. Doctoral Thesis, University of Berne.

Cane, J.H. (1991) Soils of Ground-Nesting Bees (Hymenoptera: Apoidea): Texture, Moisture, Cell Depth and Climate. *Journal of the Kansas Entomological Society,* **64,** 406-413.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M. & Vaissiere, B.E. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture Ecosystems & Environment,* **133,** 40-47.

Conner, J.K. & Neumeier, R. (1995) Effects Of Black Mustard Population-Size On The Taxonomic Composition Of Pollinators. *Oecologia,* **104,** 218-224.

Dauber, J., Biesmeijer, J.C., Gabriel, D., Kunin, W.E., Lamborn, E., Meyer, B., Nielsen, A., Potts, S.G., Roberts, S.P.M., Sober, V., Settele, J., Steffan-Dewenter, I., Stout, J.C., Teder, T., Tscheulin, T., Vivarelli, D. & Petanidou, T. (2010) Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *Journal of Ecology,* **98,** 188-196.

Delmas, C.E.L., Fort, T.L.C., Escaravage, N. & Pornon, A. (2016) Pollen transfer in fragmented plant populations: insight from the pollen loads of pollinators and stigmas in a mass-flowering species. *Ecology and Evolution,* **6,** 5663-5673.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., Marquez, J.R.G., Gruber, B., Lafourcade, B., Leitao, P.J., Munkemuller, T., McClean, C., Osborne, P.E., Reineking, B., Schroder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography,* **36,** 27-46.

Evju, M., Blumentrath, S., Skarpaas, O., Stabbetorp, O.E. & Sverdrup-Thygeson, A. (2015) Plant species occurrence in a fragmented grassland landscape: the importance of species traits. *Biodiversity and Conservation,* **24,** 547-561.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics,* **34,** 487-515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters,* **14,** 101-112.

Fijen, T.P.M. & Kleijn, D. (2017) How to efficiently obtain accurate estimates of flower visitation rates by pollinators. *Basic and Applied Ecology***,** 8.

Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography,* **16,** 265-280.

Franklin, J.F. & Lindenmayer, D.B. (2009) Importance of matrix habitats in maintaining biological diversity. *Proceedings of the National Academy of Sciences of the United States of America,* **106,** 349-350.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology,* **71,** 757-764.

Gomez-Fernandez, A., Alcocer, I. & Matesanz, S. (2016) Does higher connectivity lead to higher genetic diversity? Effects of habitat fragmentation on genetic variation and population structure in a gypsophile. *Conservation Genetics,* **17,** 631-641.

Gonzalez-Varo, J.P., Arroyo, J. & Aparicio, A. (2009) Effects of fragmentation on pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle (Myrtus communis). *Biological Conservation,* **142,** 1058-1065.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia,* **153,** 589-596.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X. & Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances,* **1**.

Haddad, N.M., Gonzalez, A., Brudvig, L.A., Burt, M.A., Levey, D.J. & Damschen, E.I. (2017) Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography,* **40,** 48-55.

Hadley, A.S. & Betts, M.G. (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews,* **87,** 526-544.

Hagler, J.R., Mueller, S., Teuber, L.R., Machtley, S.A. & Van Deynze, A. (2011) Foraging range of honey bees, Apis mellifera, in alfalfa seed production fields. *Journal of Insect Science,* **11**.

Hardy, O.J. & Vekemans, X. (2001) Patterns of allozyme variation in diploid and tetraploid Centaurea jacea at different spatial scales. *Evolution,* **55,** 943-954.

Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *Peerj,* **2**.

Harrod, R.J. & Taylor, R.J. (1995) Reproduction And Pollination Biology Of Centaurea And Acroptilon Species, With Emphasis On Centaurea Diffusa. *Northwest Science,* **69,** 97-105.

Hartig, F. (2018) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. pp. R package Version 0.2.0. Regensburg.

Heard, M., Carvell, C., Carreck, N., Rothery, P., Osborne, J. & Bourke, A.J.B.L. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. **3,** 638-641.

Hegland, S.J. & Totland, O. (2008) Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Oikos,* **117,** 883-891.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation,* **13,** 207-251.

Hennig, E.I. & Ghazoul, J. (2011) Plant-pollinator interactions within the urban environment. *Perspectives in Plant Ecology Evolution and Systematics,* **13,** 137-150.

Hobbs, R.J. & Yates, C.J. (2003) Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. *Australian Journal of Botany,* **51,** 471-488.

Hopfenmüller, S., Steffan-Dewenter, I. & Holzschuh, A. (2014) Trait-Specific Responses of Wild Bee Communities to Landscape Composition, Configuration and Local Factors. *Plos One,* **9**.

Hudewenz, A. & Klein, A.M. (2013) Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *Journal of Insect Conservation,* **17,** 1275-1283.

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998) Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics,* **29,** 83-112.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhoffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S. & Kremen, C.

(2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters,* **16,** 584-599.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences,* **274,** 303-313.

Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Bundesamt für Naturschutz, Bonn.

Kolb, A. (2008) Habitat fragmentation reduces plant fitness by disturbing pollination and modifying response to herbivory. *Biological Conservation,* **141,** 2540-2549.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt, P. (2015) *Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan,* 1st edition edn. Elsevier, Amsterdam.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J. & Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters,* **10,** 299-314.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications,* **10,** 689-710.

Mallinger, R.E., Gibbs, J. & Gratton, C. (2016) Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology,* **31,** 1523-1535.

Mandelik, Y., Winfree, R., Neeson, T. & Kremen, C. (2012) Complementary habitat use by wild bees in agro-natural landscapes. *Ecological Applications,* **22,** 1535-1546.

Matesanz, S., Gómez-Fernández, A., Alcocer, I. & Escudero, A. (2015) Fragment size does not matter when you are well connected: effects of fragmentation on fitness of coexisting gypsophiles. *Plant Biology,* **17,** 1047-1056.

McGarigal, K., Cushman, S. & Ene, E. (2012) FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst.

McGarigal, K. & Cushman, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications,* **12,** 335-345.

McKersie, B.D., Tomes, D.T. & Yamamoto, S. (1981) Effect of seed size on germination, seedling vigor, electrolyte leakage, and establishment of birds-foot trefoil (*Lotus corniculatus* L.). *Canadian Journal of Plant Science,* **61,** 337-343.

Menz, M.H.M., Phillips, R.D., Winfree, R., Kremen, C., Aizen, M.A., Johnson, S.D. & Dixon, K.W. (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science,* **16,** 4-12.

Nascimbene, J., Marini, L., Ivan, D. & Zottini, M. (2013) Management Intensity and Topography Determined Plant Diversity in Vineyards. *Plos One,* **8**.

Nascimbene, J., Zottini, M., Ivan, D., Casagrande, V. & Marini, L. (2016) Do vineyards in contrasting landscapes contribute to conserve plant species of dry calcareous grasslands? *Science of the Total Environment,* **545,** 244-249.

Naumkin, V. & Velkova, N. (2013) Species diversity of insects-pollinators on crops of white mustard. *Вестник ОрелГАУ,* 28.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos,* **120,** 321-326.

Orrock, J.L. & Damschen, E.I. (2005) Corridors cause differential seed predation. *Ecological Applications,* **15,** 793-798.

Papanikolaou, A.D., Kuhn, I., Frenzel, M., Kuhlmann, M., Poschlod, P., Potts, S.G., Roberts, S.P.M. & Schweiger, O. (2017) Wild bee and floral diversity co-vary in response to the direct and indirect impacts of land use. *Ecosphere,* **8**.

Peat, J. & Goulson, D. (2005) Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, Bombus terrestris. *Behavioral Ecology and Sociobiology,* **58,** 152-156.

Pellissier, V., Muratet, A., Verfaillie, F. & Machon, N. (2012) Pollination success of *Lotus corniculatus* (L.) in an urban context. *Acta Oecologica-International Journal of Ecology,* **39,** 94-100.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution,* **25,** 345-353.

Potts, S.G., Ngo, H.T., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A. (2016) The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 20770-20775.

QGIS Development Team (2017) QGIS Geographic Information System, Version 2.18.2 Las Palmas. pp. Open Source Geospatial Foundation Project. Open Source Geospatial Foundation Project.

Rasmussen, I.R. & Brodsgaard, B. (1992) Gene flow inferred from seed dispersal and pollinator behaviour compared to DNA analysis of restriction site variation in a patchy population of *Lotus corniculatus* L. *Oecologia,* **89,** 277-283.

Rathcke, B.J. & Jules, E.S. (1993) Habitat fragmentation and plant pollinator interactions. *Current Science,* **65,** 273-277.

Ricketts, T.H. (2001) The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist,* **158,** 87-99.

Rybicki, J. & Hanski, I. (2013) Species-area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters,* **16,** 27-38.

Sahli, H.F. & Conner, J.K. (2007) Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, Raphanus raphanismum (Brassicaceae). *American Journal of Botany,* **94,** 203-209.

Sakamoto, Y., Ishiguro, M. & Kitagawa, G. (1986) *Akaike information criterion statistics*. Dordrecht, The Netherlands: D. Reidel.

Steffan-Dewenter, I., Munzenberg, U. & Tscharntke, T. (2001) Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society B-Biological Sciences,* **268,** 1685-1690.

Steffan-Dewenter, I. & Tscharntke, T. (1997) Bee diversity and seed set in fragmented habitats. *Seventh International Symposium on Pollination - Pollination: from Theory to Practise***,** 231-234.

Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia,* **121,** 432-440.

Townsend, P.A. & Levey, D.J. (2005) An experimental test of whether habitat corridors affect pollen transfer. *Ecology,* **86,** 466-475.

Turkington, R. & Franko, G.D. (1980) The biology of Canadian weeds .41. Lotus corniculatus L. *Canadian Journal of Plant Science,* **60,** 965-979.

Van Rossum, F. (2010) Reproductive success and pollen dispersal in urban populations of an insect-pollinated hay-meadow herb. *Perspectives in Plant Ecology Evolution and Systematics,* **12,** 21-29.

Wilcove, D.S., McLellan, C.H. & Dobson, A.P.J.C.b. (1986) Habitat fragmentation in the temperate zone. **6,** 237-256.

Winfree, R., Aguilar, R., Vazquez, D.P., LeBuhn, G. & Aizen, M.A. (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology,* **90,** 2068-2076.

Winfree, R., Griswold, T. & Kremen, C. (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology,* **21,** 213-223.

Wolf, S. & Moritz, R.F.A. (2008) Foraging distance in Bombus terrestris L. (Hymenoptera : Apidae). *Apidologie,* **39,** 419-427.

Table 1: Characteristics of studied plant species

Species	Plant family	Origin	Lifecycle	Reproduction	Breeding system *	Typical pollinators	Flower class	Reward
Sinapis alba	Brassicaceae	Neophyte	Annual	Seeds	SI; allogamous	Beetles, flies, syrphids, wasps, bees with medium sized proboscis length	Flowers with open nectar	Nectar
Lotus corniculatus	Fabaceae	Native	Perennial	Mostly seeds; seldom vegetative	SI; allogamous	Bees	Bee flowers	Nectar
Centaurea jacea	Asteraceae	Native	Perennial	Seeds	SI; allogamous	Bees, bumble bees, wasps, bee flies, syrphids	Flower associations with totally hidden nectar	Nectar

* SI - self-incompatible. (Harrod & Taylor 1995; Klotz, Kühn & Durka 2002), allogamous - obligate outcrossing; gametes originate from different sporophytes

Table 2: Explanatory variables derived from GIS or field assessments used for statistical analyses of plant reproductive success and pollinator visitations

Category	Covariate	Description	Model	Source	Details
Compositional	PD	Fragmentation, vegetated vineyard fields per 100 ha	Reproductive success & pollinator visitations	Fragstats & QGIS	Continuous 1.5-107.1, mean = 37.0
	PLAND	Habitat amount, area of vegetated vineyard fields within 250m radius [%]	Reproductive success & pollinator visitations	Fragstats & QGIS	Continuous 0.9-49.2, mean = 23.7
	NDVI	Mean NDVI	Reproductive success & pollinator visitations	Satellite pictures	Continuous 0.2-0.5, mean = 0.3
	area NH	Area of natural habitat within 250m radius [m^2]	Reproductive success & pollinator visitations	QGIS	Continuous 3'125-163'426, mean = 37'854.4
	dist. NH	Distance to next natural habitat within 250m radius [m]	Reproductive success & pollinator visitations	QGIS	Continuous 0.0-81.5, mean = 27.3
	no. HB	Number of honeybee hives within 250m radius	Reproductive success & pollinator visitations	QGIS	Continuous 0-4, mean = 1.2
	dist. HB	Distance to next honeybee hive within 250m radius [m]	Reproductive success & pollinator visitations	QGIS	Continuous 78.5-1077.2, mean = 458.0
Observational	pollinator visits	Pollinator visits	Reproductive success	Recorded in the field	Continuous *S. alba*: 0-416, mean = 44.4 *L. corn.*: 0-160, mean = 9.6 *C. jacea*: 0-736, mean = 79.5
	predation	Seed predation, either seeds with holes or fruits with predator larvae/adults	Reproductive success	Recorded in the field	Binomial

Category	Covariate	Description	Model	Source	Details
	open flow	Open flowers of study plants	Pollinators visitations	Recorded in the field	Continuous *S. alba*: 1-62, mean = 9.9 *L. corn.*: 1-95, mean = 15.7 *C. jacea*: 1-13, mean = 3.7
	biomass	Plant biomass [g]	Reproductive success	Recorded in the field	Continuous *S. alba*: 1.5-19.9, mean = 7.2 *L. corn.*: 14.3-44.4, mean = 26.6 *C. jacea*: 8.9-43.7, mean = 22.1
Topographic	slope	Slope [°]	Reproductive success & pollinator visitations	DEM 25 m & QGIS	Continuous 0-31.5, mean = 14.5
	aspect	Aspect [°]: 0 and 360° - north, 180° - south	Reproductive success & pollinator visitations	DEM 25 m & QGIS	Continuous 107.92-318.84, mean = 169.3
Climatic	wind	Wind speed at scale of 0 to 3: 0 - still air; 1 - a gentle breeze with leaves moving; 2 - stronger breeze with small branches moving; 3 - anything stronger than that	Pollinators visitations	Recorded in the field	Factorial (3 levels)
	temp	Temperature during pollinator observations [°C]	Pollinators visitations	Recorded in the field	Continuous 22.1-43.0, mean = 29.7
	sun	Sunny or cloudy (more than 40% clouds)	Pollinators visitations	Recorded in the field	Factorial (sunny, cloudy)
	daytime	Time of observation; am: 8:30-13h, pm: 13-17:30h	Pollinators visitations	Recorded in the field	Factorial (am, pm)

Table 3: Competitive models (Δ AICc < 2), including degrees of freedom (Df), logLink, AICc, ΔAICc and model weights shown for number of seeds, seed weight, number of fruits and predation models.

Plant species	Rank	Model	Df	logLink	AICc	ΔAICc	Model weight
S. alba		***Number of seeds*** *(lmer, Gaussian)*					
	1	PD + (PD)^2 + PLAND + (PLAND)^2 + NDVI	8	-1098.988	2214.2	0	1
		Seed weight *(glmer, Poisson)*					
	1	PLAND + (PLAND)^2 + NDVI + bm.log + (bm.log)^2	9	-1977.839	3974.0	0.00	0.371
	2	PLAND + (PLAND)^2 + PD + NDVI + bm.log + (bm.log)^2	10	-1977.025	3974.4	0.44	0.298
	3	PLAND + NDVI + bm.log + (bm.log)^2	8	-1979.863	3976.0	1.99	0.137
		Number of fruits.log *(lmer, Gaussian)*					
	1	PD + (PD)^2 + PLAND + (PLAND)^2 + bm.log + dist.NH + poll.log					
L. corni-culatus		***Number of seeds*** *(glmer, Poisson)*					
	1	PD + PLAND + (PLAND)^2 + bm.log + (bm.log)^2 + dist.HB + (dist.HB)^2	10	-1892.002	3804.4	0.00	0.128
	2	bm.log + (bm.log)^2	6	-1896.316	3804.8	0.40	0.105
	3	PLAND + (PLAND)^2 + bm.log + (bm.log)^2	8	-1894.836	3805.9	1.54	0.059
	4	PLAND + bm.log + (bm.log)^2	7	-1896.014	3806.2	1.84	0.051
		Seed weight *(glmer, Poisson)*					
	1	PLAND + (PLAND)^2 + bm.log + (bm.log)^2	8	-1903.476	3823.2	0.00	0.389
	2	bm.log + (bm.log)^2	6	-1906.361	3824.9	1.67	0.169
		Number of fruits *(glmer, Poisson)*					
	1	PLAND + bm.log + (bm.log)^2 + poll.log +	8	-4281.776	8579.8	0.00	0.489

Plant species	Rank	Model	Df	logLink	AICc	ΔAICc	Model weight
		pred					
C. jacea		**Number of seeds** *(glmer, Poisson)*					
	1	bm + predation	6	-2360.430	4733.0	0.00	0.510
	2	PLAND + bm + predation	7	-2360.277	4734.8	1.75	0.213
	3	PD.log + bm + pred	7	-2360.397	4735.0	1.99	0.189
		Seed weight *(glmer, Poisson)*					
	1	$(PLAND)^2$ + bm + poll.log + $(poll.log)^2$ + predation	9	-2584.588	5187.5	0.00	0.314
		Seed weight *(glmer, Poisson)*					
	2	PD.log + $(PLAND)^2$ + bm + poll.log + $(poll.log)^2$ + pred	10	-2584.392	5189.2	1.69	0.135
	3	bm + poll.log + $(poll.log)^2$ + pred	8	-2586.509	5189.3	1.77	0.130
		Predation *(glmer, binomial)*					
	1	PD.log + $(PD.log)^2$ + asp.log + $(bm)^2$ + NDVI + $(NDVI)^2$ + No.HB.log	9	-263.800	546.0	0.00	0.167
	2	PD.log + $(PD.log)^2$ + asp.log + NDVI + No.HB.log	8	-265.191	546.7	0.71	0.117
	3	PD.log + $(PD.log)^2$ + PLAND + asp.log +$(bm)^2$ + NDVI + $(NDVI)^2$ + No.HB.log	10	-263.220	546.9	0.92	0.105
	4	PD.log + $(PD.log)^2$ + PLAND + asp.log +$(NDVI)^2$ + No.HB.log	8	-265.351	547.0	1.03	0.100
	5	PD.log + $(PD.log)^2$ + asp.log +$(NDVI)^2$ + No.HB.log	7	-266.606	547.4	1.47	0.080
	6	PD.log + $(PD.log)^2$ + asp.log + bm + $(bm)^2$ + NDVI + $(NDVI)^2$ + No.HB.log	10	-263.582	547.6	1.65	0.073
	7	PD.log + $(PD.log)^2$ + PLAND + asp.log + NDVI + $(NDVI)^2$ + No.HB.log	9	-264.774	547.9	1.95	0.063

*Table 4: Model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5% confidence intervals (CI) for number of seeds, seed weight and number of fruits for reproductive success of **S. alba**. Variables with significant effects are set in bold.*

Term	Estimate	SE	z or t value	2.5% CI	97.5% CI
Number of seeds					
(Intercept)	3.633	0.142	25.641	3.377	3.894
Fragmentation	5.008	3.789	1.322	-1.933	11.892
(Fragmentation)^2	-6.447	3.518	-1.833	-12.870	0.014
Habitat amount	-7.095	3.645	-1.946	-13.773	-0.390
(Habitat amount)^2	5.923	3.780	1.567	-1.006	12.782
NDVI	**0.395**	**0.151**	**2.613**	**0.120**	**0.672**
Seed weight					
(Intercept)	1.729	0.108	15.996	1.517	1.941
Fragmentation	0.140	0.111	1.260	-0.078	0.357
Habitat amount	**-6.199**	**2.568**	**2.409**	**-11.242**	**-1.156**
(Habitat amount)^2	**5.613**	**2.622**	**2.136**	**0.464**	**10.763**
Plant biomass.log	2.381	1.294	1.835	-0.162	4.923
(Plant biomass.log)^2	**-3.334**	**1.092**	**3.045**	**-5.479**	**-1.188**
NDVI	**0.345**	**0.107**	**3.205**	**0.134**	**0.555**
Number of fruits.log					
(Intercept)	4.257	0.105	4.722	4.063	4.453
Fragmentation	3.891	2.449	1.589	-0.655	8.403
(Fragmentation)^2	**-5.1260**	**2.267**	**-2.261**	**-9.334**	**-0.929**
Habitat amount	**-5.158**	**2.213**	**-2.331**	**-9.253**	**-1.015**
(Habitat amount)^2	**9.114**	**2.587**	**3.524**	**4.370**	**13.971**
Plant biomass.log	**0.387**	**0.037**	**10.440**	**0.309**	**0.457**
Distance next natural habitat	**0.341**	**0.100**	**3.399**	**0.156**	**0.527**
Pollinator visits.log	**0.348**	**0.034**	**10.236**	**0.284**	**0.418**

*Table 5: Model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5% confidence intervals (CI) for number of seeds, seed weight and number of fruits for reproductive success of **L. corniculatus**. Variables with significant effects are set in bold.*

Term	Estimate	SE	z or t value	2.5% CI	97.5% CI
Number of seeds					
(Intercept)	2.067	0.0422	48.916	1.983	2.145
Habitat amount	-1.380	1.166	1.182	-3.668	0.908
(Habitat amount)^2	2.011	1.057	1.899	-0.065	4.087
Plant biomass	0.477	0.736	0.647	-0.968	1.922
(Plant biomass)^2	**-1.829**	**0.732**	**2.492**	**-3.267**	**-0.390**
Distance next honeybee hive	-0.078	0.948	0.082	-1.939	1.784
(Distance next honeybee hive)^2	**2.622**	**1.038**	**2.521**	**0.583**	**4.660**
Seed weight					
(Intercept)	1.910	0.065	29.236	1.782	2.038
Habitat amount	-1.241	1.596	0.776	-4.375	1.893
(Habitat amount)^2	**3.792**	**1.605**	**2.357**	**0.639**	**6.945**
Plant biomass.log	0.045	0.876	0.052	-1.675	1.765
(Plant biomass.log)^2	**-2.662**	**0.880**	**3.017**	**-4.390**	**-0.933**
Number of fruits					
(Intercept)	3.538	0.158	22.396	3.191	3.866
Fragmentation	0.015	0.122	0.123	-0.231	0.261
Habitat amount	**-0.253**	**0.125**	**-2.027**	**-0.504**	**-0.002**
Plant biomass.log	**1.059**	**0.182**	**5.821**	**0.703**	**1.416**
(Plant biomass.log)^2	**-2.044**	**0.190**	**-10.749**	**-2.417**	**-1.672**
Predation	**-0.016**	**0.006**	**-2.557**	**-0.129**	**-0.017**
Pollinator visits.log	**0.487**	**0.010**	**49.768**	**0.468**	**0.506**

*Table 6: Model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5% confidence intervals (CI) for number of seeds, seed weight and number of fruits for reproductive success of **C. jacea**. Variables with significant effects are set in bold.*

Term	Estimate	SE	z or t value	2.5% CI	97.5% CI
Number of seeds					
(Intercept)	3.393	0.133	25.537	3.133	3.654
Fragmentation.log	0.027	0.105	0.256	-0.179	0.233
Habitat amount	-0.065	0.117	0.553	-0.295	0.165
Plant biomass	**0.164**	**0.039**	**4.221**	**0.088**	**0.240**
Predation	**-0.168**	**0.037**	**4.550**	**-0.241**	**-0.096**
Seed weight					
(Intercept)	3.565	0.191	18.639	3.185	3.933
Fragmentation.log	0.095	0.150	0.633	-0.199	0.390
(Habitat amount)^2	**7.325**	**3.611**	**2.024**	**0.232**	**14.419**
Plant biomass	**0.177**	**0.051**	**3.490**	**0.077**	**0.276**
Predation	**-0.254**	**0.047**	**5.331**	**-0.347**	**-0.160**
Pollinator visits	**-2.807**	**1.244**	**2.251**	**-5.250**	**-0.363**
(Pollinator visits)^2	**3.405**	**1.322**	**2.570**	**0.809**	**6.001**
Predation					
(Intercept)	-0.819	0.179	4.569	-1.171	-0.468
Fragmentation.log	**-21.318**	**5.669**	**3.752**	**-32.456**	**-10.181**
(Fragmentation.log)^2	**-13.154**	**4.214**	**3.114**	**-21.434**	**-4.874**
Habitat amount	0.296	0.250	1.184	-0.194	0.787
NDVI	6.669	4.726	1.408	-2.615	15.953
(NDVI)^2	**-17.440**	**4.308**	**4.038**	**-25.904**	**-8.986**
Plant biomass	1.869	2.808	0.664	-3.648	7.386
(Plant biomass)^2	5.415	3.076	1.756	-0.630	11.459
Aspect.log	**-1.007**	**0.222**	**4.535**	**-1.442**	**-0.572**
No. HB.log	**0.647**	**0.231**	**2.798**	**0.194**	**1.101**

*Table 7: Competitive models (Δ AICc < 2), including degrees of freedom (Df), logLink, AICc, ΔAICc and model weights shown for **pollinator visitations** of S. alba, L. corniculatus and C. jacea.*

Plant species	Rank	Model	Df	logLink	AICc	ΔAICc	Model weight
S. alba		*Glmer.nb*					
	1	open.flow + daytime	6	-637.509	1287.6	0.00	0.462
	2	PLAND + (PLAND)^2 + open.flow + daytime	8	-635.596	1288.2	0.61	0.341
L. corni- culatus		*Glmer, Poisson*					
	1	PD + PLAND + open.flow + dist.HB.log + temp	9	-440.405	900.0	0.00	0.610
C. jacea		*Glmer, Poisson*					
	1	PD + (PD)^2 + open.flow + temp.log + slope + wind	10	-629.241	1280.4	0.00	0.265
	2	open.flow + temp.log + slope + wind	8	-631.779	1280.8	0.41	0.216

*Table 8: Model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5% confidence intervals (CI) for **pollinator visits** for S. alba, L. corniculatus and C. jacea. Variables with significant effects are set in bold.*

Term	Estimate	SE	z or t value	2.5% CI	97.5% CI
S. alba					
(Intercept)	2.952	0.211	13.896	2.536	3.368
PLAND	0.058	0.136	0.422	-0.211	0.326
(PLAND)^2	**-0.297**	**0.143**	**2.064**	**-0.579**	**-0.015**
open.flow	**1.287**	**0.196**	**6.510**	**0.900**	**1.675**
daytime	**-0.400**	**0.137**	**2.893**	**-0.671**	**-0.129**
L. corniculatus					
(Intercept)	0.766	0.186	4.120	0.345	1.116
PD	**-0.463**	**0.214**	**-2.163**	**-0.903**	**-0.040**
PLAND	**0.488**	**0.177**	**2.757**	**0.143**	**0.859**
open.flow	**0.847**	**0.108**	**7.862**	**0.637**	**1.066**
temp	**0.659**	**0.158**	**4.171**	**0.348**	**1.004**
dist.hb.log	**-0.558**	**0.189**	**-2.945**	**-0.946**	**-0.186**
C. jacea					
(Intercept)	3.418	0.134	25.307	3.153	3.682
PD	-1.576	1.509	1.034	-4.564	1.412
(PD)^2	**-3.238**	**1.467**	**2.184**	**-6.144**	**-0.333**
open.flow	**0.763**	**0.090**	**8.429**	**0.585**	**0.940**
temp.log	**0.549**	**0.131**	**4.174**	**0.292**	**0.807**
slope	**-0.381**	**0.142**	**2.665**	**-0.661**	**-0.101**
wind	**-0.264**	**0.111**	**2.356**	**-0.483**	**-0.044**

*Figure 1: Model-averaged prediction from Gaussian regression models for number of seeds of **S. alba** with 95%–Bayesian credible intervals (grey areas) for NDVI is shown. Grey dots show raw data.*
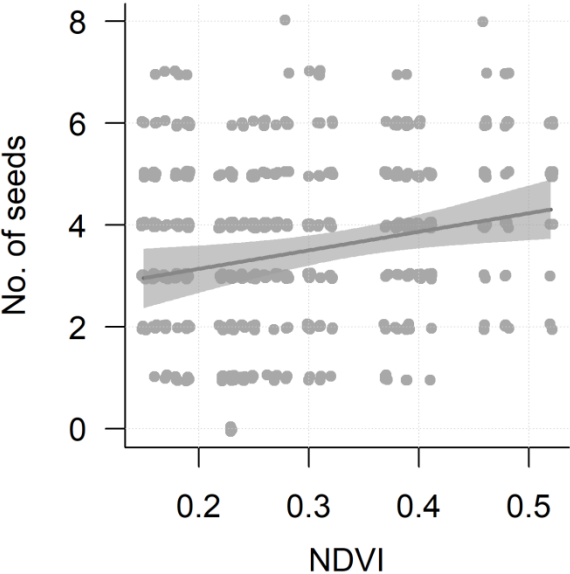
*Figure 2: Model-averaged predictions from Poisson regression models for seed weight of **S. alba** with 95%–Bayesian credible intervals (grey areas) for a) habitat amount (PLAND), b) NDVI and c) plant biomass are shown. Grey dots show raw data.*
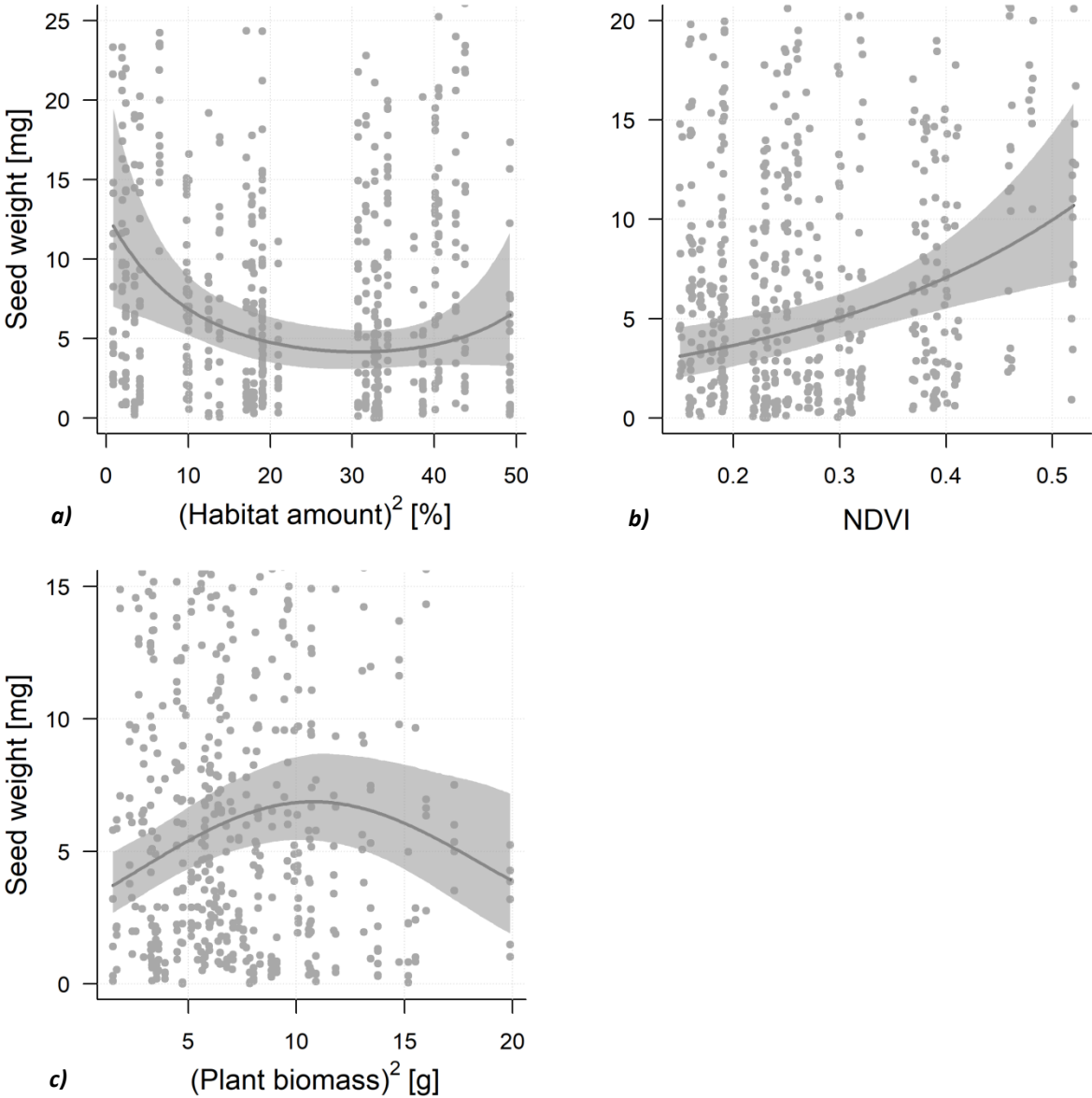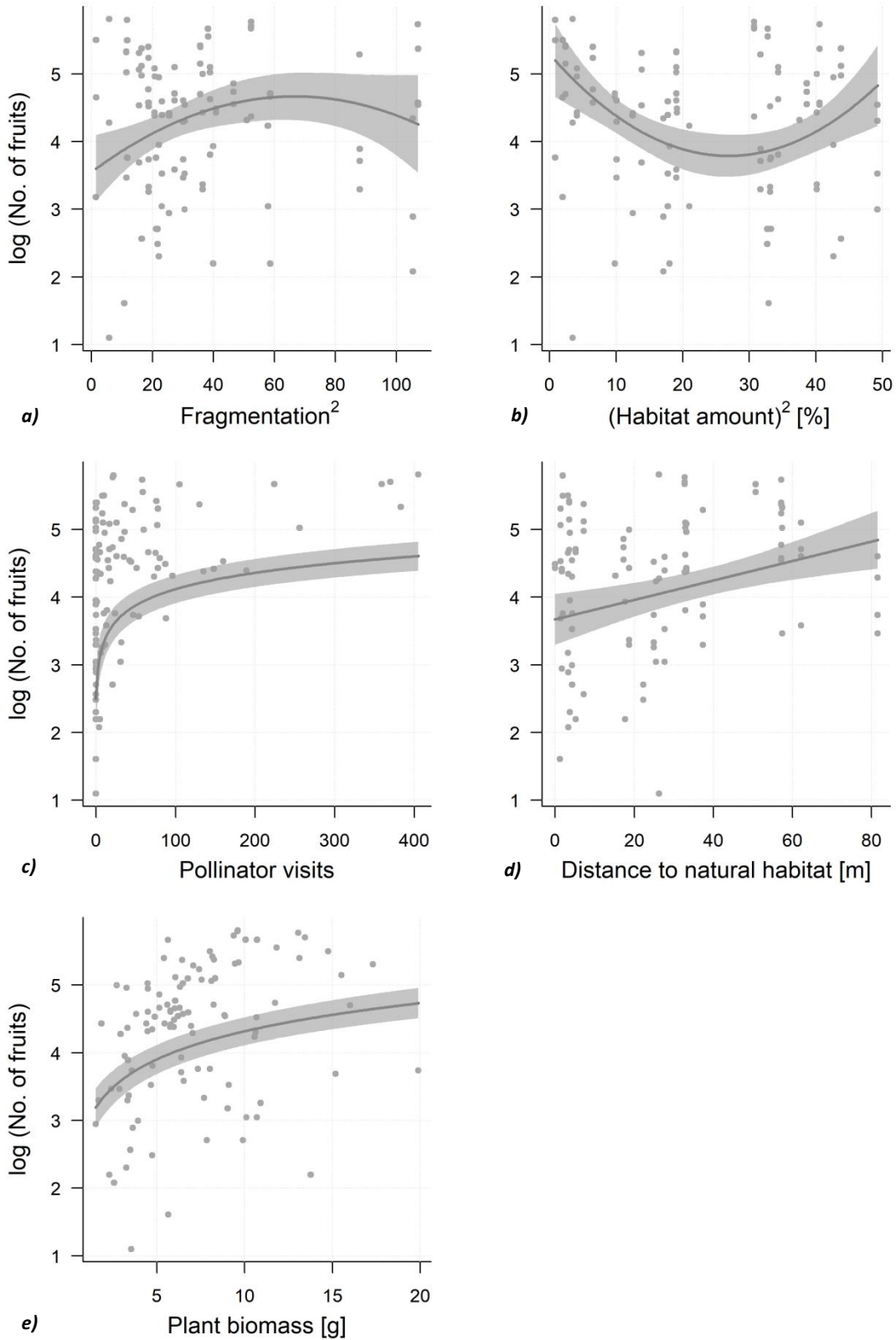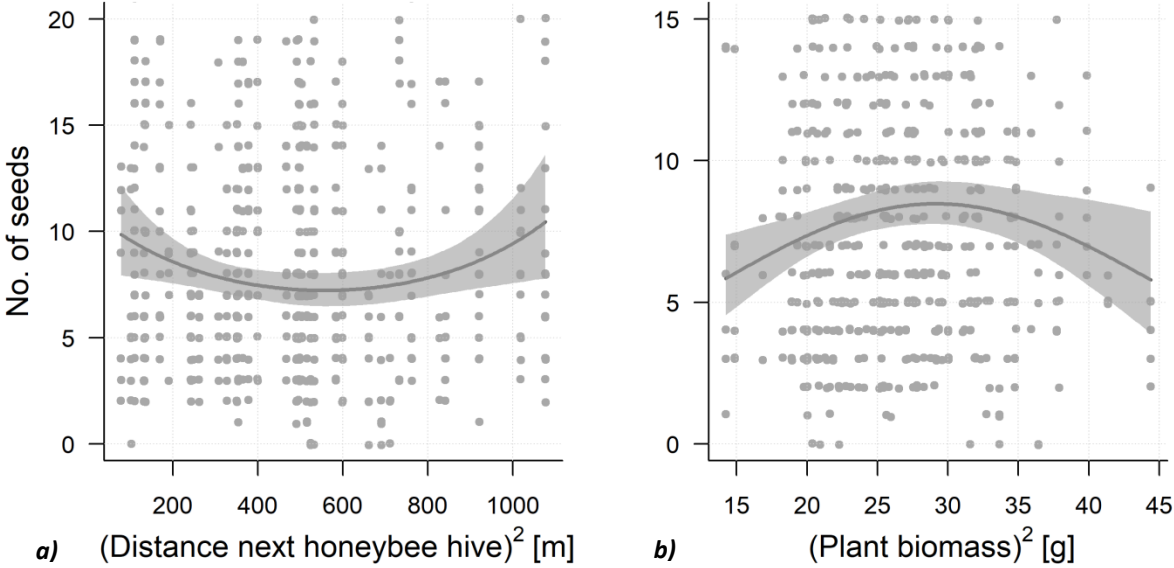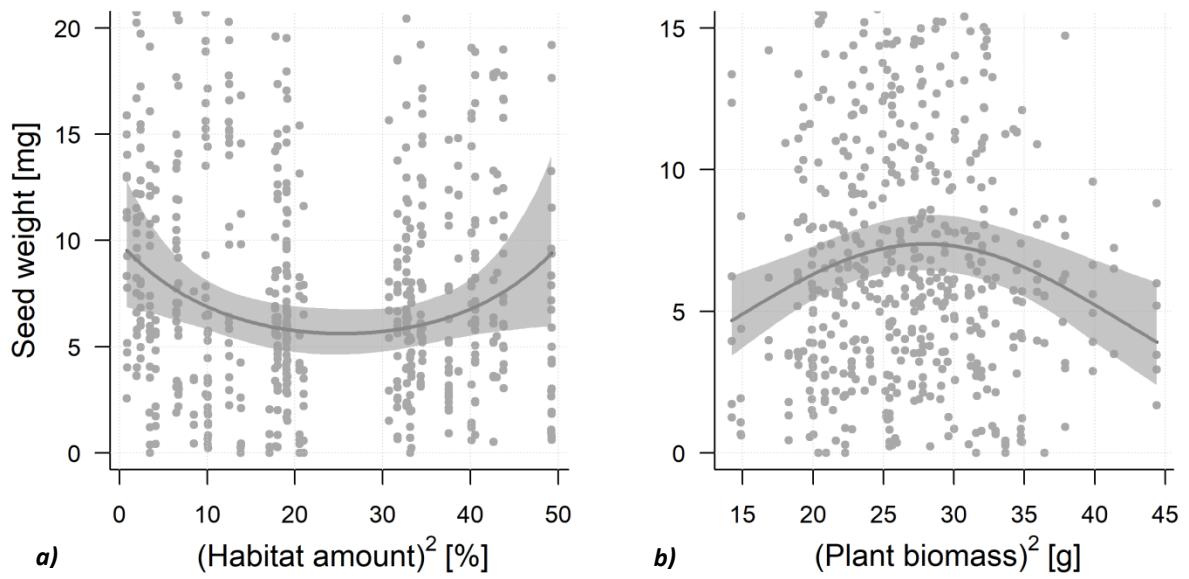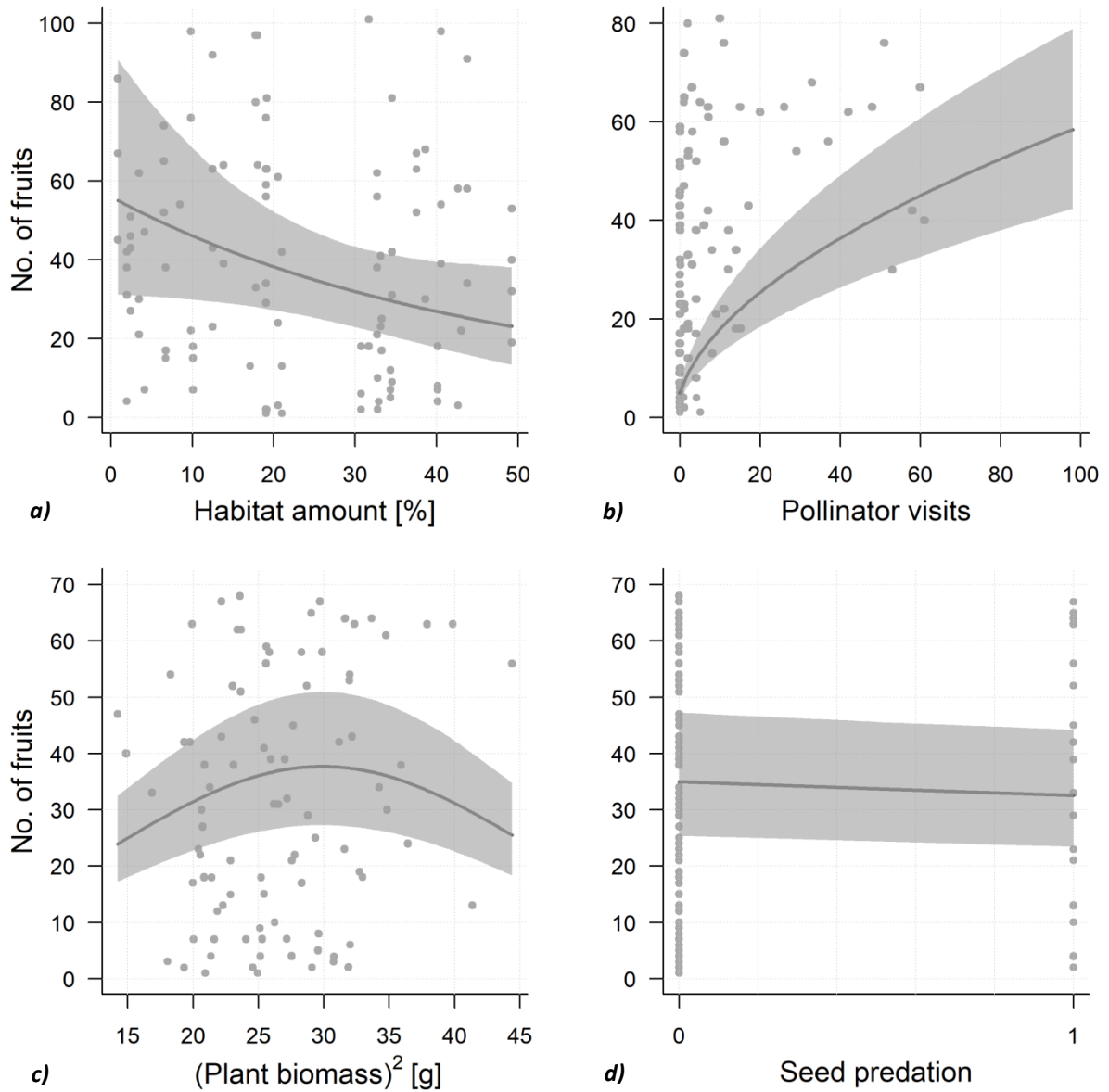
*Figure 3: Model-averaged predictions from Gaussian regression models for number of fruits of **S. alba** with 95%–Bayesian credible intervals (grey areas) for a) fragmentation (PD), b) habitat amount (PLAND), c) pollinator visits, d) distance to next natural habitat and e) plant biomass are shown. Grey dots show raw data.*

*Figure 4: Model-averaged predictions from Poisson regression models for number of seeds of **L. corniculatus** with 95%–Bayesian credible intervals (grey areas) for a) distance to next honeybee hive and b) plant biomass are shown. Grey dots show raw data.*
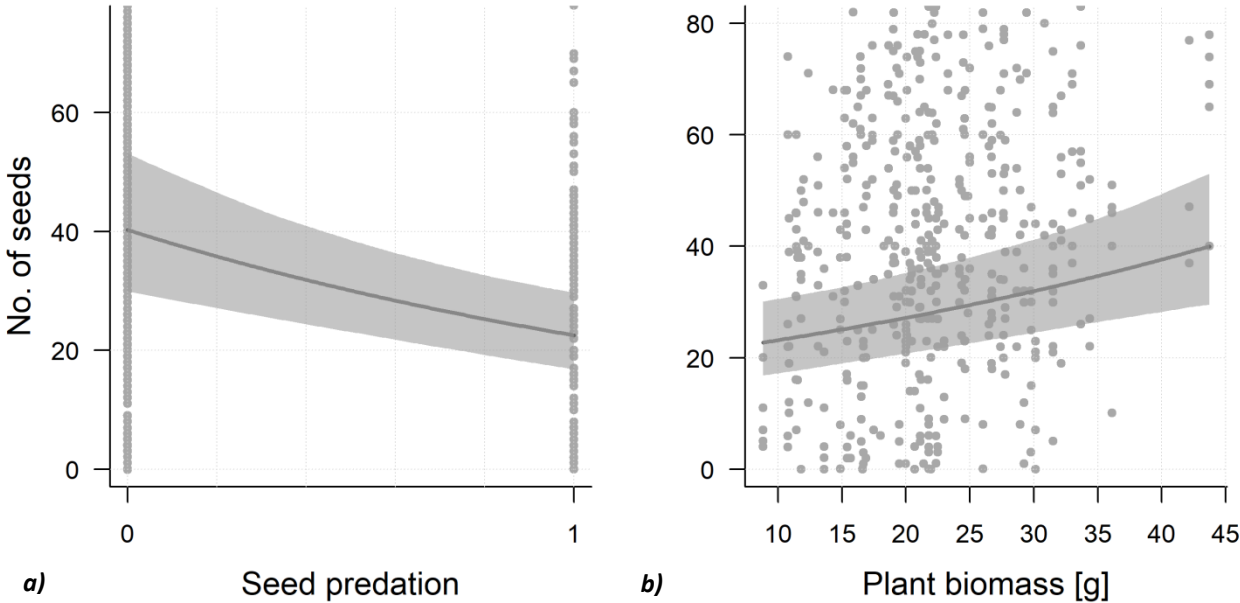
*Figure 5: Model-averaged predictions from Poisson regression models for seed weight of **L. corniculatus** with 95%–Bayesian credible intervals (grey areas) for a) habitat amount (PD) and b) plant biomass are shown. Grey dots show raw data.*

*Figure 6: Model-averaged predictions from Poisson regression models for number of fruits of **L. corniculatus** with 95%–Bayesian credible intervals (grey areas) for a) habitat amount (PLAND), b) pollinator visit, c) plant biomass and d) seed predation are shown. Grey dots show raw data.*
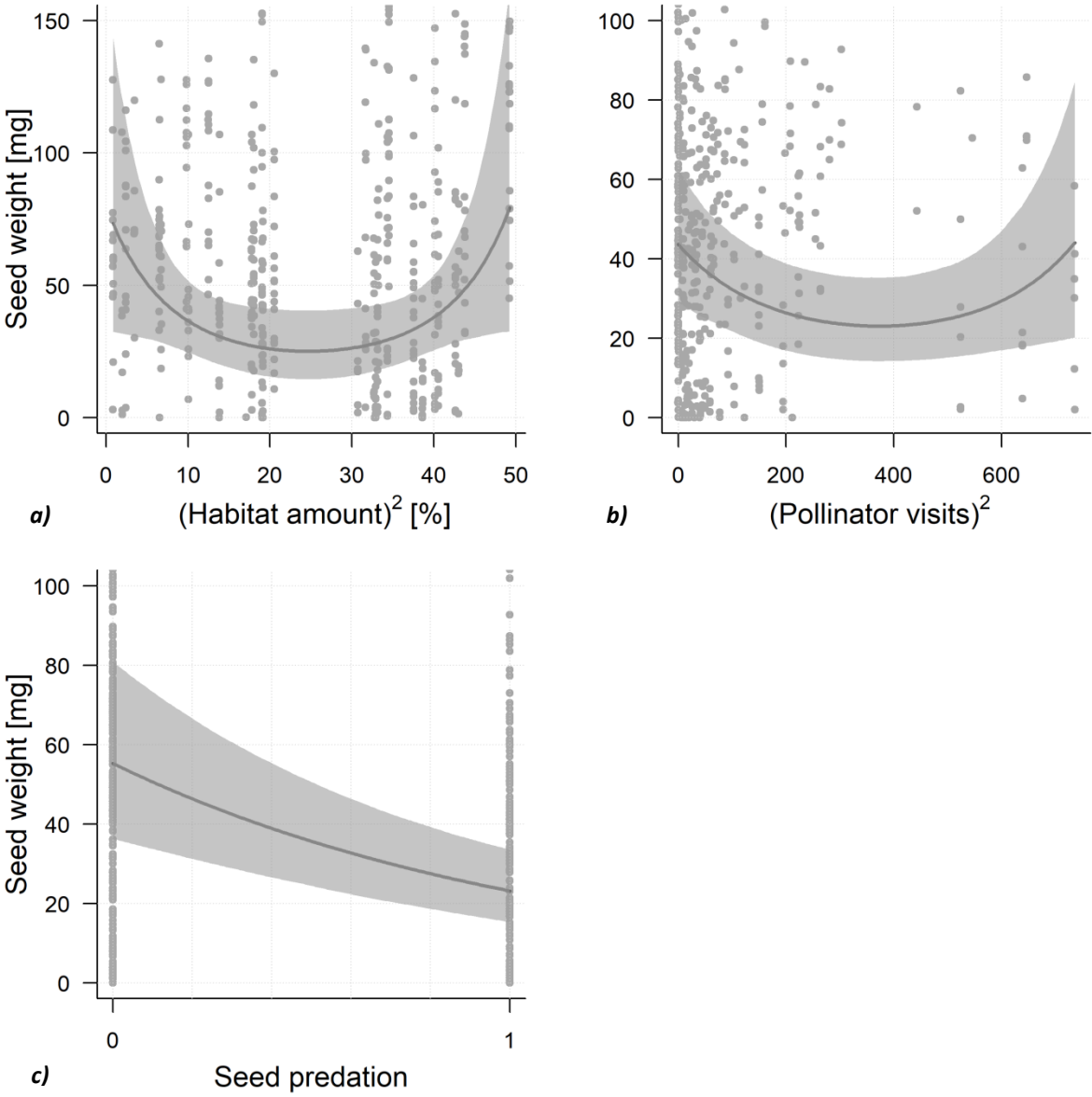
*Figure 7: Model-averaged predictions from Poisson regression models for number of seeds of **C. jacea** with 95%–Bayesian credible intervals (grey areas) for a) seed predation and b) plant biomass are shown. Grey dots show raw data.*

*Figure 8: Model-averaged predictions from Poisson regression models for seed weight of **C. jacea** with 95%–Bayesian credible intervals (grey areas) for a) habitat amount (PLAND), b) pollinator visits and c) seed predation are shown. Grey dots show raw data.*
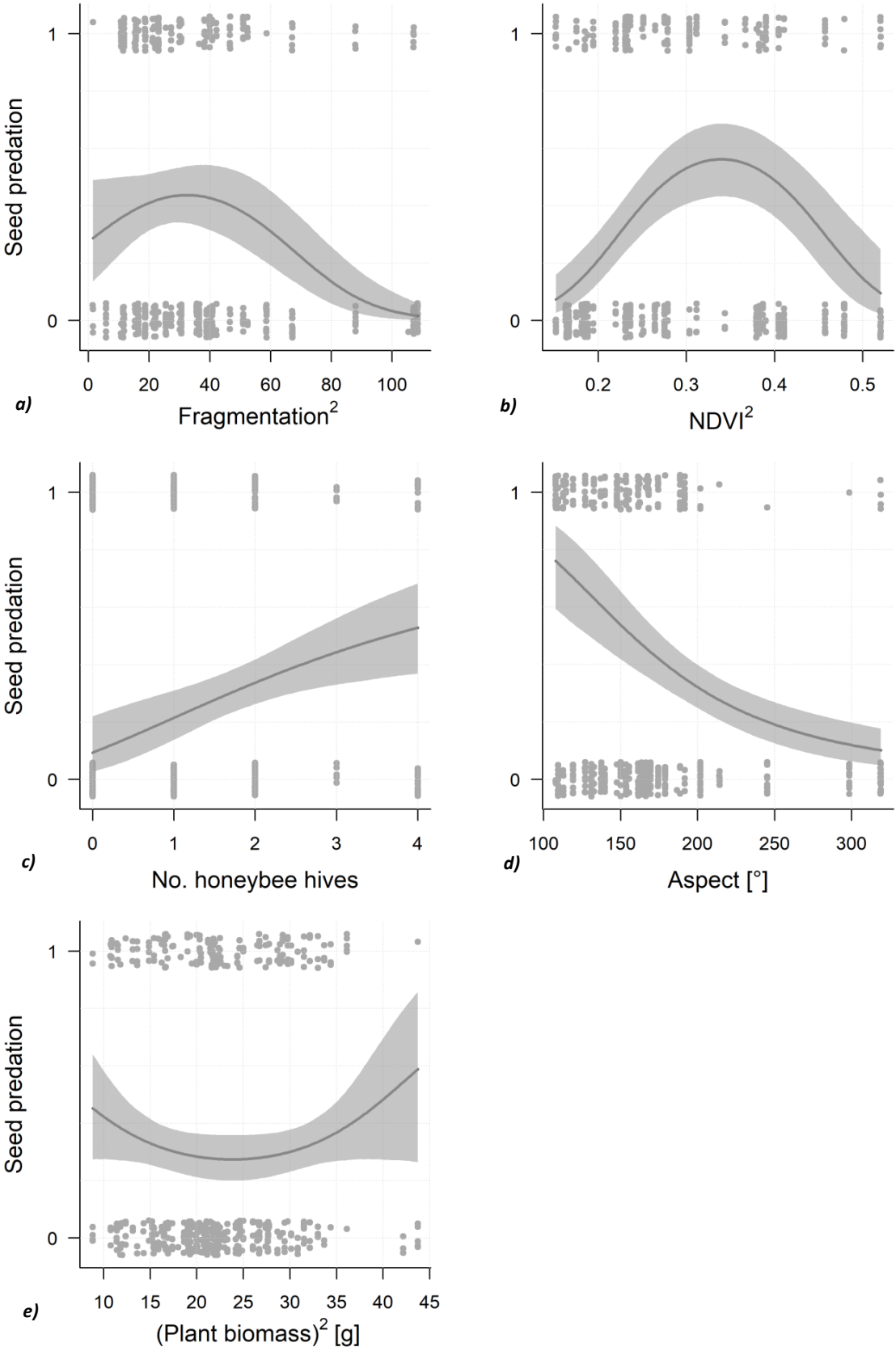
*Figure 9: Model-averaged predictions from binomial regression models for seed predation of **C. jacea** with 95%–Bayesian credible intervals (grey areas) for a) fragmentation, b) NDVI, c) number of honeybee hives, d) aspect and e) plant biomass are shown. Grey dots show raw data.*

Table S1: Pollinator visits separated for groups and plant species given with amounts and percentages of total amount of pollinators.

	S. alba		L. corniculatus		C. jacea		Total	
	count	%	count	%	count	%	count	%
Solitary bees (except *Apis* and *Bombus*)	6'367	95.66	1'111	70.45	9'646	94.82	18'388	93.48
Honeybees (*Apis mellifera*)	4	0.06	29	1.84	281	2.76	314	1.60
Hover flies(Syrphidae)	101	1.52	214	13.57	22	0.22	337	1.71
Bumblebees (*Bombus* spp.)	0	0.00	25	1.59	17	0.17	42	0.21
Hymenoptera (except Apoidea and Formicidae)	14	0.21	7	0.44	110	1.08	131	0.67
Butterflies (Lepidoptera)	8	0.12	150	9.51	33	0.32	191	0.97
Flies (Diptera except Syrphidae)	19	0.29	6	0.38	28	0.28	53	0.27
Bugs (Heteroptera)	61	0.92	0	0.00	7	0.07	68	0.35
Beetles (Coleoptera)	14	0.21	9	0.57	10	0.10	33	0.17
Ants (Formicidae)	59	0.89	25	1.59	17	0.17	101	0.51
Unidentified	10	0.15	1	0.06	2	0.02	13	0.07
Total	6'657	100	1'577	100	10'173	100	19'671	100

Figure S1: Locations of 40 selected vineyard fields located along the river Rhône between Martigny and Visp. Colours represent the five different classes with low and high habitat amount (PLAND) and fragmentation (PD) plus the matrix. © Swisstopo 2018
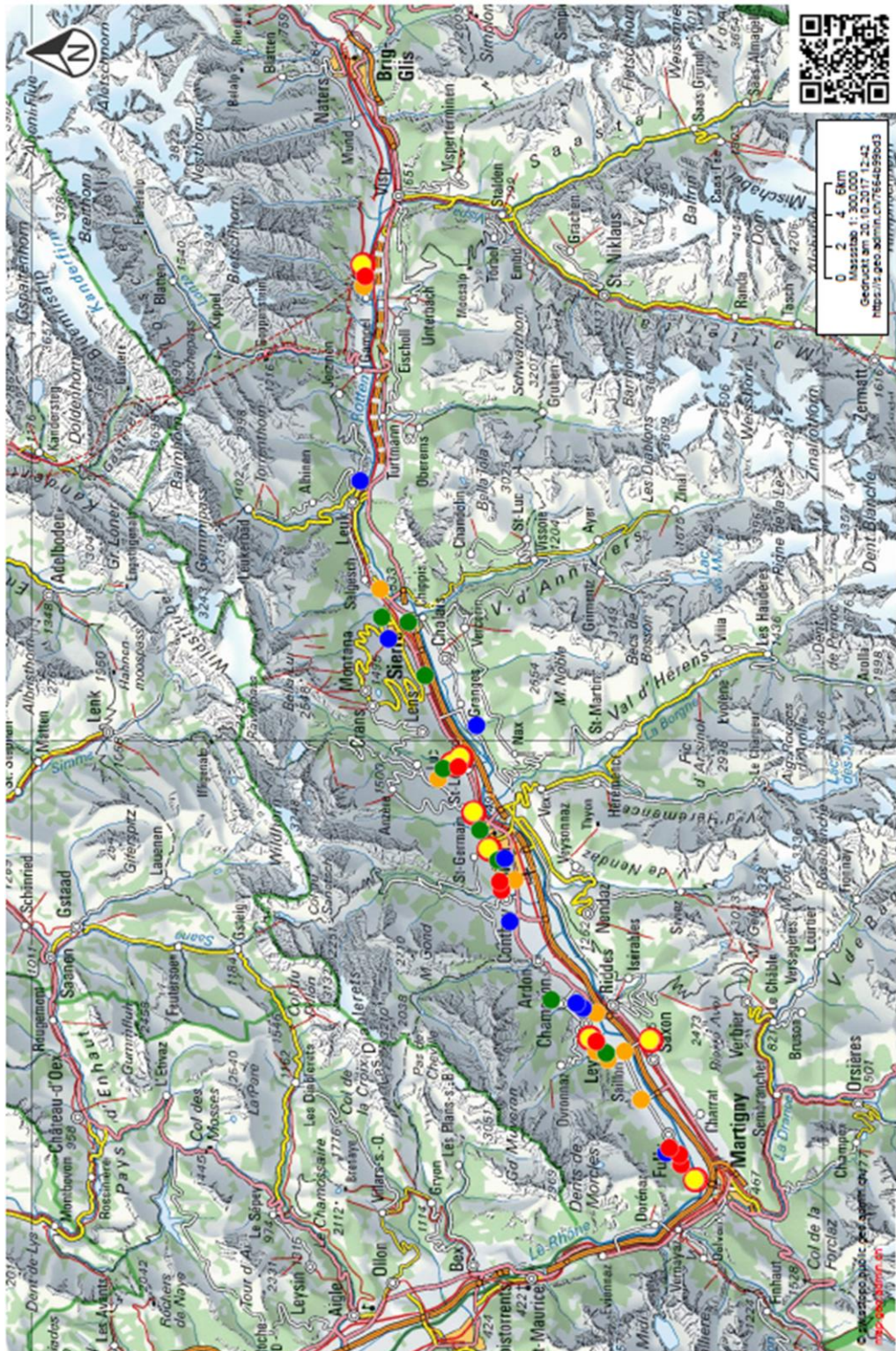
*Fig S2: Difference between treatment and control for **S. alba** (n = 121) for a) number of seeds (p = 0.019), b) seed weight and c) number of fruits. The horizontal lines show medians, boxes the standard errors, and error bars the 95% confidence limits. Shown are raw data while the model estimates are given in the results section.*
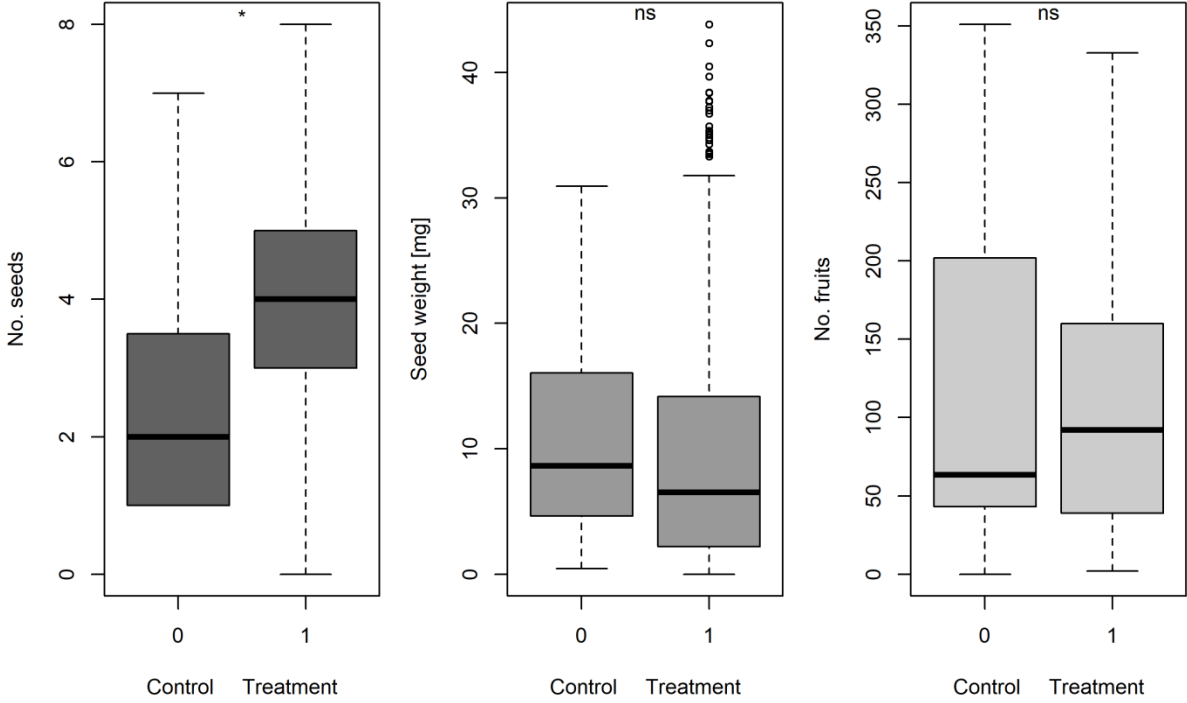
*Fig S3: Difference between treatment and control for **L. corniculatus** (n = 129) for a) number of seeds (p < 0.001), b) seed weight (p < 0.001) and c) number of fruits (p < 0.001). The horizontal lines show medians, boxes the standard errors, and error bars the 95% confidence limits. Shown are raw data while the model estimates are given in the results section.*
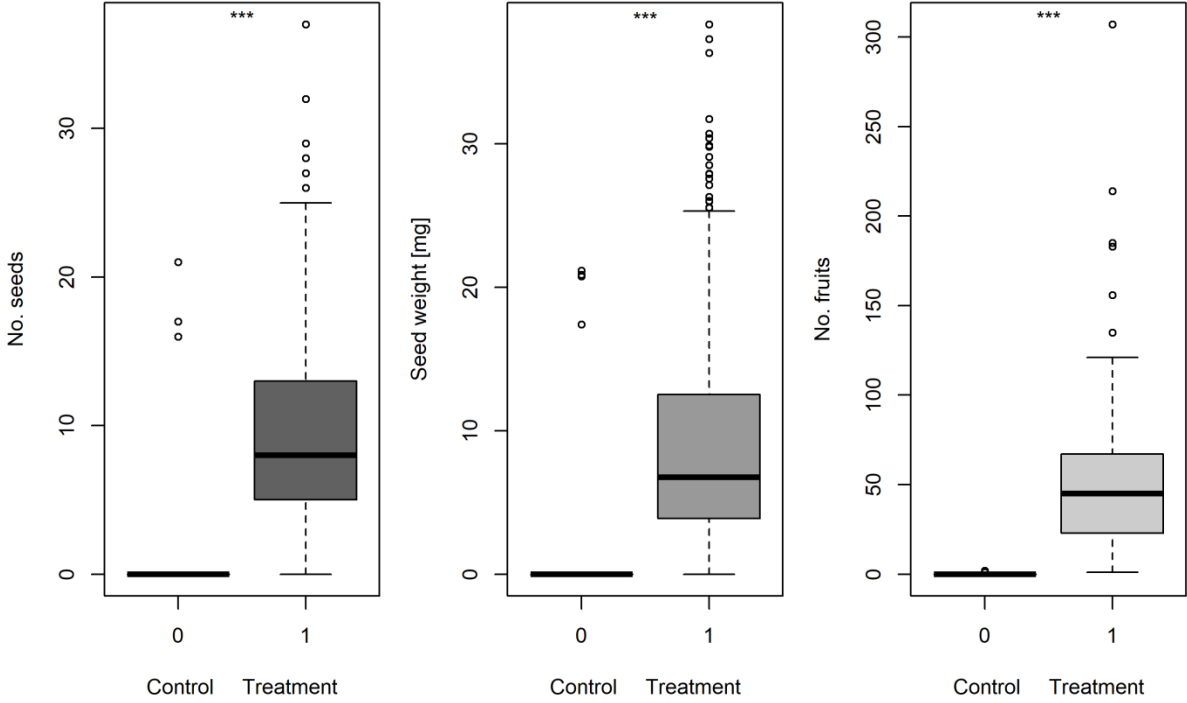
*Fig S4: Difference between treatment and control for **C. jacea** (n =114) for a) number of seeds, b) seed weight (p < 0.001) and c) number of fruits. The horizontal lines show medians, boxes the standard errors, and error bars the 95% confidence limits. Shown are raw data while the model estimates are given in the results section.*