HIGHLIGHTED STUDENT RESEARCH

Habitat amount mediates the effect of fragmentation on a pollinator's reproductive performance, but not on its foraging behaviour

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Abstract

Agricultural intensification, with its associated habitat loss and fragmentation, is among the most important drivers of the ongoing pollination crisis. In this quasi-experimental study, conducted in intensively managed vineyards in southwestern Switzerland, we tested the separate and interdependent effects of habitat amount and fragmentation on the foraging activity and reproductive performance of bumblebee *Bombus t. terrestris* colonies. Based on a factorial design, we selected a series of spatially replicated study sites across a dual gradient of habitat amount (area of ground-vegetated vineyards) and fragmentation (density of ground-vegetated vineyard fields) in a landscape predominantly consisting of vineyards with bare grounds. The foraging activity of individual bumblebees was measured using the radio frequency identification (RFID) technology, and we assessed final colony size to measure reproductive performance. We found an interactive effect of habitat amount and fragmentation on colony size. More specifically, the degree of fragmentation had a negative effect on bumblebee colony size when the amount of habitat was low, while it had a weak positive effect on colony size in landscapes with high amounts of habitat. At the level of individual vineyard fields, ground vegetation cover exerted a positive effect on bumblebee colony size. Fragmentation, but not habitat amount, significantly influenced foraging activity, with more foraging trips in sites with lower degrees of fragmentation. Our results emphasise the importance of studying the separate and interdependent effects of habitat amount and fragmentation to understand their influence on pollinators, providing guidance for optimising the spatial configuration of agricultural landscapes from a biodiversity viewpoint.

Keywords *Bombus* · Connectivity · Conservation · RFID · Vineyards

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With this experimental study, we provide evidence that both processes, habitat amount and fragmentation, need to be tested separately and interdependently to understand their effects on biodiversity.

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Introduction

Many species of wild pollinators, including bumblebees and honeybees, have severely declined in the past several decades (Potts et al. 2010). Lower pollinator abundance has multiple negative consequences, ranging from reduced genetic diversity of wild plant species (Rusterholz and Baur 2010), to a reduction of their reproductive success (Donaldson et al. 2002), and is also indirectly tied to decreases in crop yield due to reduced pollination services (Garibaldi et al. 2013; Potts et al. 2016). Pollinator decline is driven by a range of factors, with agricultural intensification and associated habitat loss and fragmentation being the most important (Haddad et al. 2015). Both processes lead to homogenized landscapes poor in both floral resources (Potts et al. 2010) and pollinators (Rundlof et al. 2008; Kennedy et al. 2013). Habitat fragmentation often leads to a lower connectivity between habitat patches and a decreased quality of patches, which may become too small to sustain local

populations (Fahrig 2003). This can impact the abundance and richness of wild pollinators negatively (Steffan-Dewenter and Tscharntke 1999). Consistent with this expectation, pollinator visitation was shown to be higher in landscapes with high amounts and low isolation of habitat (Schuepp et al. 2014). This suggests that various aspects of fragmentation (reduced area and increased isolation) can have severe effects on ecosystem functions such as pollination (Haddad et al. 2015). However, the relative effects of habitat loss and habitat fragmentation are often difficult to disentangle (McGarigal and Cushman 2002; Fahrig 2003).

Several studies have investigated the interactive effects of habitat amount and fragmentation on different biodiversity responses, which revealed that high habitat amount can often mitigate the negative effects of fragmentation (Flather and Bevers 2002; Rybicki and Hanski 2013; Coudrain et al. 2014). For example, parasitoid abundance was highly reduced in isolated patches, but only when habitat amount was low (Coudrain et al. 2014). The habitat amount hypothesis states that species richness should mainly be driven by habitat amount, such that habitat configuration should have little or no effect (Fahrig 2013). Testing this hypothesis has revealed contradictory results: Habitat amount has been found to be the most important single predictor for saproxylic beetle species richness (Seibold et al. 2017), while fragmentation played a crucial role in determining plant and invertebrate species richness (Haddad et al. 2017). These examples indicate that the relative importance of habitat amount and fragmentation may strongly depend on the study system and species, but also on the scale of analysis (Bosco et al. 2018).

An organism's mobility may largely determine its sensitivity to habitat fragmentation, with mobile species generally being less affected if the effect of fragmentation is on connectivity (MacDonald et al. 2018). However, they may be more affected if the effect of fragmentation is in the form of increased mortality risk while moving between habitat fragments of degraded habitats along edges or matrix (Cushman et al. 2010, 2016). For mobile pollinators, the negative effects of fragmentation might be reduced when there is sufficient habitat, i.e., when the landscape provides enough floral and nesting resources. Nevertheless, even for more mobile species, additional costs may arise in fragmented landscapes due to increased flight distances between patches to find rewarding flower resources. According to optimal foraging theory, pollinators will forage close to their nesting site in landscapes with evenly distributed resource patches, as this entails a reduction of energetic expenditure and time investment, which maximises foraging efficiency (Heinrich 1979). In contrast, feeding behaviour may have to be adaptively altered whenever foraging patches differ strongly in quality, namely flower density or nectar volume (Cresswell

et al. 2000). This has been demonstrated by field studies. For example, in landscapes with high cover and low fragmentation of semi-natural vegetation, several bumblebee species showed shorter foraging distances than under poorer feeding circumstances (Redhead et al. 2016). Similar results were found in studies with commercial *B. terrestris* colonies, where the duration of foraging trips was shorter in landscapes with abundant compared to landscapes with sparse resources (Westphal et al. 2006). This may imply fitness-related costs, as colonies gained more weight and had a higher number of workers in landscapes with abundant resources than in resource-poor landscapes (Goulson et al. 2002; Westphal et al. 2006). To the best of our knowledge, only one study so far investigated the effect of habitat amount and fragmentation on bumblebee colony performance: Herrmann and et al. (2017) found no direct effect of connectivity, but a positive correlation between local floral resources and colony performance, especially in isolated patches. These results suggested a high importance of floral resources for the successful development of a bumblebee colony, while the role of fragmentation remained equivocal.

We conducted a field study in a intensively managed vineyard landscape, which provides a comparative mensurative (sensu McGarigal and Cushman 2002) experimental design for fragmentation research: the majority (ca 80%) of the vineyards in our study area are treated with herbicides and, thus, have no ground vegetation cover, while the growth of a permanent ground vegetation cover is tolerated only in a minority (Arlettaz et al. 2012), with the latter but not the former providing resources for pollinators. These two contrasting management types create a binary system (bare vs ground-vegetated vineyards) locally differing in their habitat amount and degree of fragmentation and thus enabling researchers to disentangle the effects of both factors at a landscape scale (e.g., Bosco et al. 2018). Bumblebee *B. terrestris* colonies were placed into fields varying in habitat amount (surface covered by ground-vegetated vineyards) and fragmentation (density of ground-vegetated vineyards) to measure the effects of diverging spatial configurations on foraging activity and colony size. With this approach, we tested two main hypotheses: (1) colonies are smaller (i.e., limited growth) in landscapes offering little foraging habitat and will be smaller yet when this limited habitat is fragmented. In contrast, we predict that in landscapes with high amounts of foraging habitat the negative effects of fragmentation are weaker and colony size, therefore, greater, and (2) *B. terrestris* workers spend more time foraging in highly fragmented landscapes with low habitat amount, since resources are scarce, while they spend less time foraging, irrespective of the degree of fragmentation, in landscapes with high habitat amount.

Materials and methods

Study site and study species

The study was conducted during May and June 2017 in the vineyards of Central Valais, southwestern Switzerland. Vineyards dominate the landscape along the south-facing slopes north of the Rhône River, covering approximately 50 km². They are mainly located up to 900 m above sea level and are interspersed with small patches of dry oak stands and patches of steppe (i.e., climactic grasslands, typically occurring in the driest areas of the inner Alps) (Arlettaz et al. 2012). The climate in Central Valais vineyards is continental, with an average annual precipitation of ca 586 mm and an average annual temperature of 11.2 °C in Sion. Our study sites were located between Fully (46°8′N, 7°6′E) and Ausserberg (46°18′N, 7°51′E). All except two sites were located north of the Rhône River, both on the plain and on hillsides.

Our study species was the large earth bumblebee *Bombus terrestris terrestris*, which is naturally occurring in continental Europe, including Switzerland (Rasmont et al. 2008). This species lives in the lowlands up to 1200 m above sea level in meadows, hedges, gardens, and at forest borders. As a generalist pollinator, it exploits a broad variety of different feeding plants to collect pollen and nectar (von Hagen and Aichhorn 2014). In *B. terrestris*, the colony size typically ranges from 200 to 600 individuals (von Hagen and Aichhorn 2014). The mean foraging distances recorded in *B. terrestris* range from 267 to 551 m (Wolf and Moritz 2008; Redhead et al. 2016), with maximum foraging distances of 758–2500 m (Knight et al. 2005; Hagen et al. 2011).

Factorial design

To disentangle habitat amount and fragmentation, we used a factorial design generating four classes with varying habitat amount and fragmentation (e.g., Bosco et al. 2018). Ground vegetation cover was estimated with the Normalized Difference Vegetation Index (NDVI) from satellite imagery, recorded in March before sprouting of the vine leaves (Sentinel-2, 10 m resolution, recorded on 11-Mar-2017). We set a threshold of NDVI = 0.28 to differentiate between bare and vegetated vineyard fields, which was based on correlations with the field estimates of ground coverage (according to Bosco et al. 2018). Fields with NDVI > 0.28 represent permanent ground cover, while those with NDVI < 0.28 showed remains of winter greening and would be treated with herbicide later in the growing season. Hence, using this threshold, we distinguish

among the two major management modes, one that allows vegetation growing on the ground (vegetated vineyards), whereas the other uses herbicides to wipe out any growing plants (bare vineyards). All bare vineyards, i.e., those covered by less than 40% ground vegetation, were considered as matrix and were added to our experimental design as a fifth class. Vineyards covered by more than 40% ground vegetation were considered as habitat, i.e., representing a permanent ground cover. Based on this binary raster of bare vs ground-vegetated vineyards, we calculated habitat amount as the percentage of area covered by ground-vegetated vineyards (PLAND, percentage of landscape made up by vineyards with > 40% ground vegetation cover), and fragmentation as the number of ground-vegetated vineyard patches per 100 ha (PD, patch density) using FRAGSTATS (McGarigal et al. 2012). Patch density was chosen as our indicator of fragmentation following a series of research that assessed the redundancy and behaviour of landscape metrics (e.g., Cushman et al. 2008) and evaluated the relationships between landscape metrics and species responses to habitat heterogeneity and connectivity (e.g., Grand et al. 2004; Chambers et al. 2016). Furthermore, it fulfils the criteria that fragmentation measures should be interpretable and intuitive, should not require much data input, and be as simple as possible from a mathematical point of view (Jaeger 2000). Both metrics, habitat amount (PLAND) and fragmentation (PD), were calculated within a 250 m radius moving window (corresponding to 20 ha), representing the mean foraging distance of *B. terrestris* (Wolf and Moritz 2008). We then selected the upper and lower 40% of habitat amount (PLAND) and fragmentation (PD) values to represent high or low levels of habitat amount and fragmentation respectively, creating four contrasting classes (Table S1). With this approach, we avoided intermediate situations with 40–60% of habitat amount and fragmentation. We selected eight vineyard fields per class including the matrix as a 5th class to be able to detect field-scale effects mainly driven by the difference between ground-vegetated vs bare management types. The resulting 40 experimental fields were distributed in a stratified random manner within the landscape to account for geographical variability and to avoid clumping of fields within classes (Fig. S2).

Environmental covariates

To estimate the ground vegetation coverage and flower resources at the vineyard field scale, we mapped, during the period of experimentation, a random subsample of six ground-vegetated vineyard fields (> 40% ground vegetation cover) within the same buffer zone of 250 m radius around all experimental fields. For each of these six fields, we estimated the percentage of ground vegetation cover as a mean

for the whole field, assessed the blooming flower species richness along two transects (width: 1 m; length: 20 m), counted the number, and estimated the cover of blooming flowers in one square meter per field. The two transects were chosen as the third vine row from both field margins to avoid edge effects. For the square-meter survey, we walked 10 m into the fifth vine row from the field margin. For each mapped variable, we used the mean of these six fields per site in subsequent statistical analyses. Note that the two variables "habitat amount" and "ground vegetation estimates" give different information: while habitat amount describes the percentage of the surface covered by ground-vegetated vineyards (> 40% coverage) within the 250 m buffer, based on a binary perception of the bare *vs* ground-vegetated management system, the estimates of ground vegetation reveal how densely vegetated a vineyard field is ranging from 40 to 100% coverage per field.

To assess the role of natural habitats for bumblebees, we calculated the area of natural habitat in the 250 m buffer zones around our experimental fields and the distance to the next natural habitat patch, while we considered meadows, steppes and groves as natural habitats within our study area. Additionally, we estimated the slope of the experimental fields as a covariate. All these estimations were performed in QGIS (version 2.18.2, QGIS Development Team 2017). For the statistical analyses, we also used the quadratic terms of vegetation cover, area of natural habitats, distance to the next natural habitat patch, habitat amount, and fragmentation, since quadratic relationships of such variables have been found in several studies (e.g., Arlettaz et al. 2012).

Quasi-experimental setup of bumblebee colonies

We purchased 40 2-week-old colonies of *B. terrestris terrestris* from Andermatt Biocontrol (Biobest Belgium). Upon arrival, each colony was weighed as a proxy of their initial colony size (Miostar, 1 g precision). The colonies were randomly allocated to our experimental fields, where they remained from 08-May-2017 to 23-June-2017. In the field, they were placed on four pots 15 cm above ground, to protect them from ants. With a wooden roof, we protected the colonies from rain and sun (Fig. S1). Once installed, the sucrose solution tank (Biogluc©) provided by the manufacturer was closed to assure that bumblebees foraged outside of the hive.

Colony size

One colony declined to extinction, leaving a total of 39 colonies that were dissected in the lab to estimate population size at the end of the experiment. Several nest traits were measured following the dissection protocol of Goulson and et al. (2002). For each colony, we counted the number of queens, workers, larvae, eggs, nectar and pollen pots, healthy, dead

or hatched pupal cells, and parasitic *Aphomia sociella* larvae. Weight gain of colonies, number of workers, queens, and total number of pupal cells (as a sum of healthy, dead and hatched pupal cells, and pollen and nectar pots) were the colony size-related response variables (according to Westphal et al. 2006) used for statistical modeling.

Foraging activity

To measure foraging duration, we used fully automatic radio frequency identification (RFID) technology. Two RFID readers (iID®MAJA reader module 4.2, Microsensys GmbH, Erfurt, Germany) were installed at the entrance of the hive and automatically registered the identity of a passing tagged bee and the time and direction of movement of each bee. The two RFID readers were attached inside a cardboard box, which could easily be exchanged with the empty cardboard box at the entrance of the colony. At the beginning of the experiment, all colonies were equipped with an empty cardboard box at the entrance, so that the bumblebees would get habituated to it before installing the readers. Twenty individuals per colony were tagged 1 or 2 days before the RFID system was installed at the colony. The RFID tags (mic3®-TAG 64-bit RO, iID2000, 13.56 MHz system, $1.0 \times 1.6 \times 0.5$ mm; Microsensys GmbH, Erfurt, Germany) were glued on the thorax of the bumblebees with fast drying TempoSil2 teeth cement (Coltène/Whaledent Ohio, USA). We had five bee identification systems (iID2000, ISO15693optimized, Microsensys GmbH, Erfurt, Germany) to measure one colony of each of the five classes simultaneously. Foraging activity of bumblebees was measured once per colony for 2 full days before switching the systems during the night to five other colonies. The first session of RFID measurements started on 24-May-2017, the last on 10-June-2017. Among the 40 colonies, only 33 could be used for RFID measurements, due to too low activity at the remaining seven colonies. During all seven sessions, we measured the temperature and humidity next to the colonies (Maxim Integrated Temperature and RH i-Button logger, DS1923-F5 Hygrochron). At the end of the experiment, all colonies were collected, weighed again, and placed in a freezer to euthanize the bumblebees.

Foraging duration of a bumblebee was calculated as the difference between exit and entry times. For an exit event, a tagged bumblebee needed first to be detected by the inner RFID reader 1, followed by detection of the outer RFID reader 2 and vice versa for an enter event. We calculated foraging duration with the function *inout* of the R package "feedr" (LaZerte 2018). Foraging trips shorter than 10 min were discarded, since these short trips could be orientation and defecation flights (Westphal et al. 2006) or in our case simply hovering around the RFID readers. We also excluded trips longer than 202 min to minimise artefacts

such as missed entering detections. 96% of all trips were shorter than 202 min and we, therefore, considered this as an appropriate upper limit (according to Westphal et al. 2006). In addition, we excluded trips which began during the night (defined as 20:00–2:30 UTC; six trips, representing 0.07% of the total number of trips), since these trips are presumed not to be foraging trips (Stanley et al. 2016). We used the mean foraging trip duration and total number of foraging trips per bumblebee (across 48 h of monitoring) as response variables for the statistical modeling.

Statistical analysis

All statistical analyses were performed with the software R (version 3.3.1, R Development Core Team 2016). First, collinearity among continuous explanatory variables (Table 1) was tested using Spearman's correlation coefficient. If two variables were correlated (coefficient $|r| > 0.7$), we selected the variable which had a lower AIC in the univariate model, while the other one was dismissed from further analyses (Dormann et al. 2013). All explanatory variables were log-transformed for strongly right-skewed predictors to meet the model assumptions of normal distribution. All variables were standardized to improve the convergence of the model fitting algorithms and to provide meaningful comparisons based on standardized regression coefficients.

Colony size

Weight gain of the colonies was analysed in a linear mixed effect model (R package lme4, Bates et al. 2015) with study area as random effect to account for spatial clumping of experimental fields. Number of workers, number of queens, and total number of pupal cells were analysed with generalized linear mixed effect models, again with study area as random factor and a Poisson distribution. In these models, we additionally included an observation-level random effect to account for over-dispersion of the count data (Dormann 2016). We tested for over-dispersion itself with the function *dispersion_glmer* (R package blmeco, Korner-Nievergelt 2015). First, we tested all our response variables against all our explanatory variables in univariate models. We also univariately tested the interaction of habitat amount and fragmentation and quadratic effects of vegetation cover, area of natural habitat, distance to next natural habitat, fragmentation, and habitat amount with all response variables. If the quadratic effects included zero in their 95% confidence interval, we discarded them from the models. Next, we built a full model containing all explanatory variables with $p < 0.1$ based on univariate models. For the interaction of habitat amount and fragmentation, we set this threshold to $p < 0.2$, since it was the variable of highest interest. In a last step, we did model selection with the function *dredge* (R package MuMIn, Barton 2016). This approach is based on the best Akaike's Information Criterion (AIC) values. If there was more than one competitive model with $\Delta AIC < 2$, we used model averaging to produce the final model coefficients (function model.avg of R package MuMIn, Barton 2016). To show effect plots of significant terms, we calculated model averaged predictions using a Bayesian framework, where we drew samples from the joint posterior distribution with the function sim (R package arm, Gelman and Su 2015).

Table 1 Explanatory variables which were used for the statistical analysis. Ranges are given for all variables

Explanatory variables	Models	Source	Details
Fragmentation (PD)	Colony size and foraging	Fragstats and QGIS	Continuous (1.5–108.4 patches per 100 ha)
Habitat amount (PLAND)	Colony size and foraging	Fragstats and QGIS	Continuous (0.87–49.2% surface covered by ground-vegetated vineyards within 250 m radius)
Vegetation cover (%)	Colony size and foraging	Vegetation mapping (6 vineyards within 250 m radius)	Continuous (48–95%)
Flower species richness	Colony size and foraging	Vegetation mapping (6 vineyards within 250 m radius)	Continuous (1–9)
Flower cover (%)	Colony size and foraging	Vegetation mapping (6 vineyards within 250 m radius)	Continuous (9–20%)
Area of natural habitat within 250 m radius	Colony size and foraging	QGIS	Continuous (0.17–16.34 ha)
Distance to next natural habitat	Colony size and foraging	QGIS	Continuous (0–81.5 m)
Slope	Foraging	QGIS	Continuous (0–31.5°)
Temperature	Foraging	Temperature logger	Continuous (7.1–37 °C)
Humidity	Foraging	Humidity logger	Continuous (8.3–100% RH)

PLAND percentage of landscape, *PD* patch density, *RH* relative humidity

Foraging duration

Mean foraging trip duration (log-transformed) was analysed using the function lmer of the R package lme4 (Bates et al. 2015), where bumblebee and colony ID were included as random factors. The total number of foraging trips was analysed using the function glmer of the R package lme4 (Bates et al. 2015), applying a Poisson distribution and including an observation-level random effect in addition to the random factor colony ID (Dormann 2016). The random effect of study area was not included in the models of foraging trip duration and number of foraging trips, since variance explained in those models was < 0.0001. We then proceeded following the same protocol as described for colony size: we first screened for collinearity, fitted univariate models with the same explanatory variables as for colony size, built the full model, and performed model selection and model averaging in a next step.

Results

Colony size

The colonies had on average 71.26 ± 66.34 workers, 545.15 ± 303.75 pupal cells, 8.69 ± 12.22 queens and a mean weight gain of $221.1\,\text{g} \pm 254.04\,\text{g}$ (mean $\pm$ SD). The start weight of the colonies had no significant effect on its subsequent weight gain, and number of workers, queens, and pupal cells. Number of parasitic *Aphomia sociella* larvae also had no significant effect on number of workers, queens and pupal cells produced but a marginal effect on weight gain (univariate *lmer*: 67.24 ± 39.96, $p = 0.092$), but the variable never appeared in the competitive models.

The number of workers was best explained by a significant interaction between habitat amount and fragmentation, the quadratic effect of vegetation cover, flower cover, and area of natural habitat (Tables 2, 3). To visualize the shape of the interaction, we plotted the response variable (number of workers) as a surface (mean value) in the two-dimensional space of habitat amount (PLAND) and fragmentation (patch density) (Fig. S3). Fragmentation negatively affected the number of workers in landscapes with a little habitat (less than 30% of ground-vegetated vineyards within 20 ha, corresponding to the area of the 250 m radius buffer around the experimental fields). However, fragmentation appeared to have a positive effect in landscapes with high habitat area (above 40% in 20 ha; Fig. 1), but wide credible intervals limit this inference. By splitting the data set into two groups—one only including observations from fields with high habitat amount and one only including observations from fields with low habitat amount—we could confirm these contrasting effects of fragmentation on number of workers in a colony (univariate glmer: high habitat amount:

Table 2 Model selection tables of the best models with ΔAIC < 2 describing weight gain of colonies, total number of pupal cells, number of workers, foraging trip duration, and number of foraging trips per bumblebee

Model no.	Variables	df	ΔAIC	Akaike weight
Weight gain				
1	Area of natural habitat + flower cover + flower species richness	6	0.00	0.98
Total number of pupal cells				
1	PLAND + vegetation cover + (vegetation cover)^2	6	0.00	0.25
2	PD + PLAND + vegetation cover + (vegetation cover)^2 + PD:PLAND	8	0.00	0.25
3	PLAND	4	0.51	0.19
4	PD + PLAND + vegetation cover + (vegetation cover)^2	7	1.31	0.13
5	PD + PLAND + PD:PLAND	6	1.77	0.10
Number of workers				
1	PD + PLAND + vegetation cover + (vegetation cover)^2 + PD:PLAND	8	0.00	0.38
2	Area of natural habitat + PD + PLAND + vegetation cover + (vegetation cover)^2 + PD:PLAND	9	1.55	0.18
Foraging trip duration				
1	Humidity + (humidity)^2	6	0.00	0.52
2	Humidity + (humidity)^2 + slope	7	0.13	0.48
Number of foraging trips				
1	Distance to next NH + PD + (PD)^2	6	0.00	0.40
2	Distance to next NH + PD + (PD)^2 + PLAND	7	1.22	0.22
3	Distance to next NH + mean humidity + PD + (PD)^2	7	1.69	0.17

For each model, all included variables, degrees of freedom, the difference in AIC to the best model (ΔAIC), and Akaike weight are given

Table 3 Conditional averaged values based on best models ($\Delta AIC < 2$) for number of workers and total number of pupal cells and single best model for weight gain of colonies

Variables	Estimate $\pm$ SE	z value	p value
Number workers			
Habitat amount: fragmentation	**0.43 ± 0.19**	**2.12**	**0.04**
Fragmentation	-0.34 ± 0.19	1.73	0.08
Habitat amount	-1.4 ± 0.17	0.79	0.40
Vegetation cover	-0.04 ± 0.18	0.24	0.86
(Vegetation cover)^2	**-0.87 ± 0.21**	**3.94**	**< 0.001**
Flower cover	0.16 ± 0.16	0.96	0.34
Area of natural habitat	-0.11 ± 0.17	0.70	0.52
Total number of pupal cells			
Habitat amount: fragmentation	0.24 ± 0.13	1.74	0.08
Habitat amount	-0.25 ± 0.13	1.91	0.06
Fragmentation	-0.04 ± 0.16	0.26	0.79
Vegetation cover	-0.04 ± 0.17	0.17	0.82
(Vegetation cover)^2	**-0.29 ± 0.13**	**2.17**	**0.03**
Weight gain		t value	
Flower cover	73.04 ± 40.23	1.82	0.07
Area of natural habitat	**-83.96 ± 36.7**	**-2.29**	**0.02**
Flower species richness	55.1 ± 39.5	1.40	0.16

The estimate $\pm$ standard error, and t and p values are given. Numbers in bold indicate significant effects

estimate $\pm$ SE $= 0.29 \pm 0.38$, $z = 0.76$, $p = 0.45$, low habitat amount: -0.48 ± 0.26, $z = -1.88$, $p = 0.06$). In addition,

vegetation cover had a significant effect with an optimum at about 70% of vegetation cover at the vineyard field scale (Fig. 2), while flower cover and area of natural habitat had no significant effects (Table 3). Similar results were found for the number of pupal cells, which were marginally negatively affected by fragmentation in low habitat landscapes and neutrally in habitat-rich areas (Tables 2, 3, Fig. S4). Again, field-scale vegetation cover had a significant effect on number of pupal cells with an optimum at about 70% coverage (Tables 2, 3).

The best model explaining weight gain included the variables flower cover, area of natural habitat within 250 m buffer and flower species richness (Tables 2, 3). Flower cover had a marginal positive effect on weight gain. In contrast, area of natural habitat was significantly negatively related to weight gain, while flower species richness had no significant effect. The number of queens was unaffected by any measured variable (no variables with $p < 0.1$ in univariate models).

Foraging activity

The mean foraging trip duration of a bumblebee was 46.04 ± 32.9 min (mean $\pm$ SD) and 96% of all trips lasted shorter than 202 min. On average, a bumblebee spent 763.4 ± 469.9 min foraging across the 2-day monitoring period, amounting to 12.7 h (26.5% of the measured time). In the 2-day monitoring period, a bumblebee made on average 16.6 ± 13.3 trips, with an individual maximum of 69 trips.
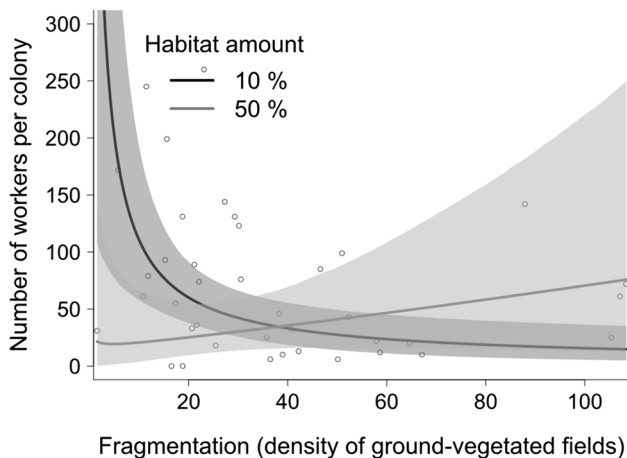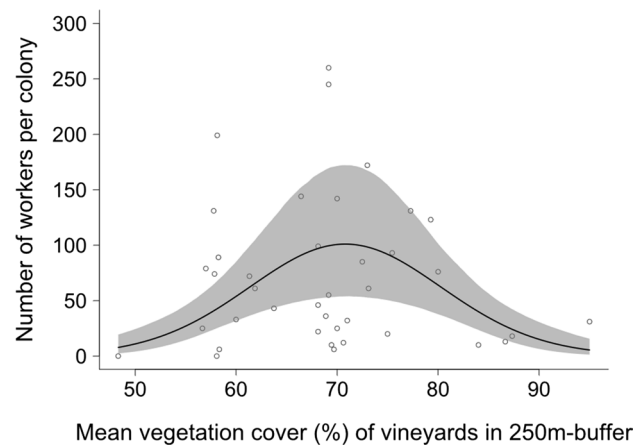

Fig. 1 Interactive effect of habitat amount and fragmentation on number of workers (0.43 ± 0.19, $z = 2.12$, and $p = 0.04$) based on averaged model predictions with 95% Bayesian credible intervals (shaded areas). All variables present in the competitive models, except the two under consideration, were fixed at their mean values for these projections. Circles show raw data. If there is low habitat amount (10%) in the 250 m buffer around the colonies, fragmentation has a negative effect. In contrast, if habitat amount is high (50%), fragmentation has a neutral effect on number of workers

Fig. 2 Quadratic effect of mean vegetation cover of vineyards in 250 m buffer on number of workers per colony (-0.87 ± 0.21, $z = 3.94$, $p < 0.001$) based on averaged model predictions with 95% Bayesian credible intervals (shaded areas). The optimum is at about 70% of vegetation cover on a vineyard field scale. All variables present in the competitive models, except the two under consideration, were fixed at their mean values for these projections. Circles show raw data

Table 4 Conditional averaged values based on best models ($\Delta AIC < 2$) for foraging trip duration and number of foraging trips. The estimate ± standard error, and t and p values are given

Variables	Estimate ± SE	t value	p value
Foraging trip duration			
Humidity	**− 0.17 ± 0.01**	**27.38**	**< 0.001**
(Humidity)^2	**− 0.04 ± 0.01**	**6.94**	**< 0.001**
Slope	**0.1 ± 0.04**	**2.66**	**0.01**
Number of foraging trips per bumblebee		z value	
Distance to next natural habitat	**0.13 ± 0.05**	**2.74**	**0.01**
Fragmentation	− 0.03 ± 0.05	0.62	0.54
(Fragmentation)^2	**− 0.18 ± 0.05**	**3.82**	**< 0.001**
Habitat amount	0.04 ± 0.05	0.89	0.38
Mean humidity	0.03 ± 0.05	0.56	0.57

Numbers in bold indicate significant effects
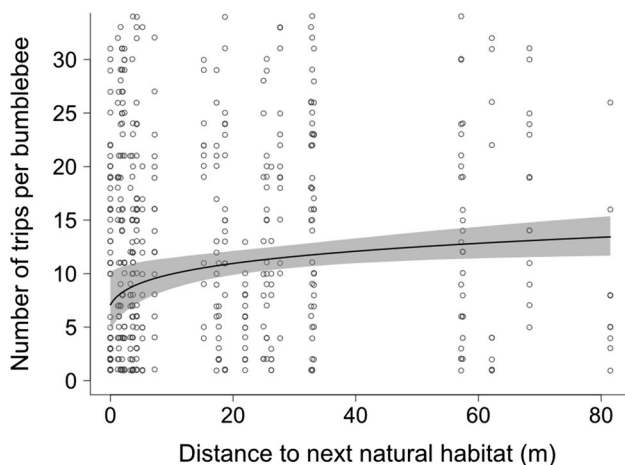
Fig. 3 Positive relationship between distance to next natural habitat (m) and number of foraging trips per bumblebee across 2 days of monitoring (0.13 ± 0.05, $z = 2.74$, $p = 0.01$), based on averaged model predictions with 95% Bayesian credible intervals (shaded areas). All variables present in the competitive models, except the two under consideration, were fixed at their mean values for these projections. Circles show raw data

Fig. 4 Quadratic effect of fragmentation (number of ground-vegetated vineyards) on number of foraging trips per bumblebee in 2 days ($- 0.18 \pm 0.05$, $z = 3.82$, $p < 0.001$), based on averaged model predictions with 95% Bayesian credible intervals (shaded areas). All variables present in the competitive models, except the two under consideration, were fixed at their mean values for these projections. Circles show raw data. Since our experiment took place under field conditions, there are less fields of high than of low or intermediate fragmentation levels. In landscapes with low fragmentation (about 20 ground-vegetated vineyards per 100 ha), bumblebees do more trips

While foraging trip duration was best explained by meteorological (quadratic term of humidity, Tables 2, 4) and topographical (positive effect of slope, Table 4) factors, the number of foraging trips per bumblebee was best explained by the distance to the next natural habitat, habitat amount, the quadratic term of fragmentation, and mean relative humidity (Tables 2, 4). Distance to the next natural habitat was significantly positively related to number of foraging trips (Fig. 3), while the quadratic term of fragmentation showed a significant effect with an optimum at about 20 ground-vegetated vineyards per 100 ha (Fig. 4). The other variables showed no significant effects.
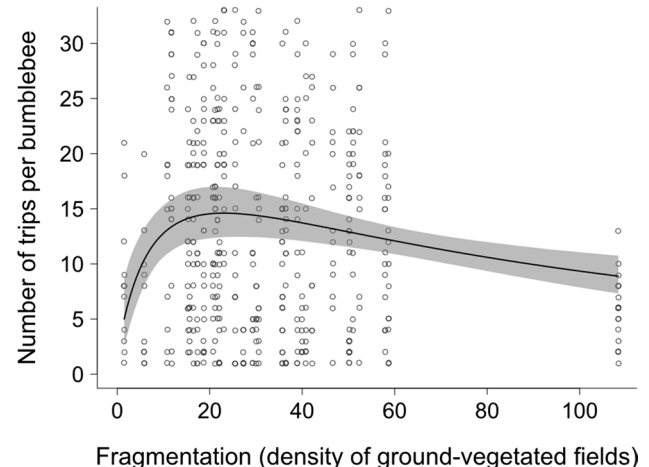
Discussion

This study emphasises the importance of studying the separate and interdependent effects of habitat amount and fragmentation to understand their respective influence on a pollinator species. In this regard, our study is one of the first to adopt an a priori comparative mensurative design (e.g., McGarigal and Cushman 2002) and statistical analyses that formally evaluate the separate and interactive effects of habitat amount and fragmentation on pollinator foraging behaviour and reproductive performance. Our results reveal that the effect of fragmentation on colony

size of bumblebees is strongly dependent on the amount of available habitat, and that fragmentation has negative effects in landscapes with low habitat amount and neutral effects in landscapes with high habitat amount. However, fragmentation influences foraging behaviour with a higher foraging activity (more foraging trips) at low levels of habitat fragmentation, irrespective of habitat amount.

Colony size

Colony size is significantly affected by habitat composition on a landscape scale. We found that when measuring metrics other than species richness, our results do not support the "habitat amount hypothesis" described by Fahrig (2013), who found that habitat amount is sufficient to predict local species richness. In effect, the effects of fragmentation on colony size are highly dependent on the amount of habitat, with strongest negative effects in landscapes with low habitat amount, which is consistent with studies in the other systems (Helzer and Jelinski 1999; Trzcinski et al. 1999). Connectivity among habitat patches, particularly when habitat area is limited, seems, therefore, essential for successful colony development in bumblebees, a fact also demonstrated in the other organisms such as wasps and leafhoppers (Schuepp et al. 2011; Rosch et al. 2013). In contrast, fragmentation does not affect colony development in areas with high habitat amount (above 40% in 20 ha). Fragmentation in habitat-rich landscapes is most likely related to heterogeneous, i.e., mosaic-like agricultural landscapes, with a high variability in management between fields and, therefore, a high spatio-temporal variability in the offer of floral resources. This leads to increased habitat diversity at the local-landscape scale, which has been shown to be beneficial for bumblebees through a stable provisioning of resources throughout the season (Benton et al. 2003; Rundlof et al. 2008; Persson and Smith 2013). Additionally, an increased habitat heterogeneity has been found to be one of the main reasons for a positive effect of fragmentation, seen for some taxa in some systems (Cushman and McGarigal 2003; Fahrig 2017), which is most likely also true for vineyard-dominated landscapes.

In addition to landscape-scale effects, colony size is also affected by fine-scaled habitat variables. Vegetation cover on a vineyard field scale seems to be a very important predictor for bumblebee colony size. We find the optimum to be around 70% vegetation cover in a vineyard field. In terms of vineyard management, this either means that every inter-row is vegetated, i.e., the vegetation is removed under the vine rows, or that the vegetation is generally patchy and sparse over the entire field. The reason why colony size drops in fields with more than 70% vegetation cover is most likely due to the benefit of a patchy, heterogeneous vegetation which often results in a higher plant diversity as compared to a dense 100% vegetation cover, which may be dominated by grass species (e.g., habitat diversity hypothesis and intermediate levels of habitat amount and fragmentation, Cushman and McGarigal 2003). Varying seed sets or soil specific factors influence plant growth and lead to a heterogeneous habitat on a smaller scale with some patches of bare ground and higher structural variability, which has been shown to benefit biodiversity (Benton et al. 2003). This might correlate with a higher amount of floral resources and, therefore, benefit pollinators such as bumblebees. Several studies confirm that the abundance of floral resources is crucial for a successful development of bumblebee colonies in terms of number of workers and/or weight gain (Westphal et al. 2006; Herrmann et al. 2017).

Apart from the ground vegetation in vineyards themselves, natural habitats in the proximity might provide resources for bumblebees. However, weight gain of colonies was negatively affected by area of natural habitat. This may reflect the fact that remnant natural habitats in this system tend to be either steeper, rockier and less productive than areas that have been converted to vineyards (Bosco et al. 2018) or groves. They probably offer limited foraging opportunities for bumblebees: a low density of flowering plants and ephemeral pollen and nectar sources.

Queen production, a good proxy for a colony's reproductive success, was unaffected by any measured habitat variable in our study. The temporal variability of flower resources is most likely the reason for a complex relationship between food resources and number and timing of produced queens. For workers, a high number of flowers early in the season are most important, while queen production depends more on a continuous availability of floral resources throughout the season (Westphal et al. 2009; Williams et al. 2012). The fact that our colonies developed very differently, and some might have been producing queens earlier than others, might thus be due to conditions that prevailed early in the season. Furthermore, young queens in certain colonies might already have left their colony before we collected them (Goulson et al. 2002).

Foraging activity

We observe that foraging activity of an individual bumblebee (total number of foraging trips) was significantly highest at low degrees of habitat fragmentation, irrespective of habitat amount. This indicates that connectivity among resource patches is the most influential factor and hence that bumblebees operate more foraging trips when the resources are aggregated. Since our experiment took place under field conditions, note that there are less fields of high than of low or intermediate fragmentation levels. Optimal foraging theory predicts that pollinators will forage close to their nesting site in landscapes with evenly distributed resource patches as this results in a reduction of energetic expenditure and time

investment, which maximises foraging efficiency (Heinrich 1979). If foraging patches differ strongly in quality, the feeding behaviour may have to be adaptively altered (Cresswell et al. 2000). Also, if bumblebees only return to their colony once fully loaded with nectar and pollen, their feeding behaviour may change in terms of doing shorter foraging trips, or as in our case a higher number of foraging trips, in resource-rich landscapes and longer foraging trips in landscapes with a low abundance of resources (Westphal et al. 2006). This finding might also explain why fragmentation was so crucial for the successful development of the colonies, especially in areas with little habitat amount. In a landscape with extensively managed, but less connected habitat, the higher amount of resources due to habitat heterogeneity might have outweighed the negative effects of fragmentation on foraging activity. The underlying mechanism might be that the nectar influx in colonies from successful foragers increases the foraging activity of the whole colony, meaning that in landscapes with many well-connected resources, overall foraging activity of a colony would become higher, possibly leading to larger colonies eventually (Dornhaus and Chittka 2001).

Besides fragmentation, distance to natural habitat as well affects foraging activity: Bumblebees undertake more trips with increasing distance to natural habitats. This might explain our result of a decreased weight gain of colonies with increasing area of natural habitat and, again, underpin the assumption that natural habitats (steppe, groves) did not provide good floral resources at the time of our experiment.

In contrast to the other results, foraging trip duration was only affected by meteorological and topographical factors. The longest foraging trips were done at a low relative ambient humidity, corroborating the findings by Sanderson et al. (2015). Additionally, foraging trip duration increased with slope. In steep slopes, the vineyards are often less ground-vegetated. This is because in steep terrain, access to mowing machinery is limited, which implies that ground vegetation cover is there mostly combatted with herbicides. Therefore, bumblebees might need to spend longer time foraging to find enough resources in steeper areas.

Conclusions

Our results reveal a significant negative impact of habitat fragmentation on a highly mobile bumblebee species in landscapes with low amounts of habitat. These detrimental effects might be even more drastic in other species of pollinators with smaller foraging ranges and more specialized resource requirements than our study species. The importance of habitat amount and ground vegetation cover for bumblebee colony size additionally shows that resource availability is crucial. Importantly, our results appear to

show non-linear effect of trade-offs, such that fragmentation of foraging habitats has negative effects when there is an overall low amount of habitat in the landscape, but seems to have neutral effects when habitat has a wider expansion. Our results also indicate a non-linear relationship with habitat amount, with optimal colony performance at intermediate ranges of habitat amount, likely due to increasing landscape-level resource richness in landscapes with intermediate to relatively high, but not the highest, extents of habitat patches. When habitat amount is low, fragmentation likely increases energetic costs and the costs inherent to foraging in landscapes characterised by spatially scattered resources. In contrast, when habitat is abundant, fragmentation is synonymous of an enhanced habitat heterogeneity, likely to increase resource diversity and richness and hence improving foraging efficiency. This suggests that habitat fragmentation is not uniformly good or bad, but depends on the context of how much habitat is available, with fragmentation negatively affecting colony performance when habitat is low in extent, but potentially positively affecting it when habitat is abundant. Our study emphasises the importance of quantifying the independent and interactive effects of habitat amount and fragmentation. Our results suggest that enhancing habitat amount, i.e., the fraction of ground-vegetated vineyards in areas where this management practice is still marginally implemented, is likely to benefit pollinators and probably other elements of biodiversity.

Compliance with ethical standards

References

Arlettaz R, Maurer ML, Mosimann-Kampe P, Nusslé S, Abadi F, Braunisch V, Schaub M (2012) New vineyard cultivation

practices create patchy ground vegetation, favouring Wood-larks. J Ornithol 153:229–238. https://doi.org/10.1007/s10336-011-0737-7

Barton K (2016) MuMIn: Multi-Model Inference. R package version 1.10.6. https://cran.R-project.Org/package=mumin, 1.10.6 edn.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182–188. https://doi.org/10.1016/s0169-5347(03)00011-9

Bosco L, Wan HY, Cushman SA, Arlettaz R, Jacot A (2018) Separating the effects of habitat amount and fragmentation on invertebrate abundance using a multi-scale framework. Landsc Ecol 34:105–117. https://doi.org/10.1007/s10980-018-0748-3

Chambers CL, Cushman SA, Medina-Fitoria A, Martínez-Fonseca J, Chávez-Velásquez M (2016) Influences of scale on bat habitat relationships in a forested landscape in Nicaragua. Landsc Ecol 31:299–1318. https://doi.org/10.1007/s10980-016-0343-4

Coudrain V, Schüepp C, Herzog F, Albrecht M, Entling MH (2014) Habitat amount modulates the effect of patch isolation on host-parasitoid interactions. Frontiers Environ Sci 2:1–8

Cresswell JE, Osborne JL, Goulson D (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. Ecol Entomol 25:249–255. https://doi.org/10.1046/j.1365-2311.2000.00264.x

Cushman SA, McGarigal K (2003) Landscape-level patterns of avian diversity in the Oregon Coast Range. Ecol Monogr 73:259–281. https://doi.org/10.1890/0012-9615

Cushman SA, McGarigal K, Neel MC (2008) Parsimony in landscape metrics: strength, iniversality, and consistency. Ecol Indic 8:691–703. https://doi.org/10.1016/j.ecolind.2007.12.002

Cushman SA, Compton BW, McGarigal K (2010) Habitat Fragmentation effects depend on complex interactions between population size and dispersal ability: modeling influences of roads agriculture and residential development across a range of life-history characteristics. Springer, Tokyo

Cushman SA, Elliot NB, Macdonald DW, Loveridge AJ (2016) A multi-scale assessment of population connectivity in African lions (*Panthera leo*) in response to landscape change. Landsc Ecol 31:1337–1353. https://doi.org/10.1007/s10980-015-0292-3

Donaldson J, Nanni I, Zachariades C, Kemper J, Thompson JD (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa. Conserv Biol 16:1267–1276. https://doi.org/10.1046/j.1523-1739.2002.99515.x

Dormann CF (2016) Overdispersion, and how to deal with it in R and JAGS. https://biometry.github.io/APES/LectureNotes/2016-JAGS/Overdispersion/OverdispersionJAGS.pdf. Accessed 12 Dec 2017

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Marquez JRG, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, 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. https://doi.org/10.1111/j.1600-0587.2012.07348

Dornhaus A, Chittka L (2001) Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. Behav Ecol Sociobiol 50:570–576. https://doi.org/10.1007/s002650100395

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Fahrig L (2017) Ecological responses to habitat fragmentation per se. Annu Rev Ecol Evol Syst 48:1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. Am Nat 159:40–56

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, Cunningham SA, Kremen C, Carvalheiro LG, Harder LD, Afik O, Bartomeus I, Benjamin F, Boreux V, Cariveau D, Chacoff NP, Dudenhoffer JH, Freitas BM, Ghazoul J, Greenleaf S, Hipolito J, Holzschuh A, Howlett B, Isaacs R, Javorek SK, Kennedy CM, Krewenka KM, Krishnan S, Mandelik Y, Mayfield MM, Motzke I, Munyuli T, Nault BA, Otieno M, Petersen J, Pisanty G, Potts SG, Rader R, Ricketts TH, Rundlof M, Seymour CL, Schuepp C, Szentgyorgyi H, Taki H, Tscharntke T, Vergara CH, Viana BF, Wanger TC, Westphal C, Williams N, Klein AM (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611. https://doi.org/10.1126/science.1230200

Gelman A, Su Y-S (2015) Arm: data analysis using regression and multilevel/hierarchical models. https://CRAN.R-project.org/package=arm

Goulson D, Hughes WOH, Derwent LC, Stout JC (2002) Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. Oecologia 130:267–273. https://doi.org/10.1007/s004420100803

Grand J, Buonaccorsi J, Cushman SA, Griffin CR, Neel MC (2004) A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. Conserv Biol 18:1063–1077. https://doi.org/10.1111/j.1523-1739.2004.00555.x

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv. https://doi.org/10.1126/sciadv.1500052

Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI (2017) Experimental evidence does not support the habitat amount hypothesis. Ecography 40:48–55. https://doi.org/10.1111/ecog.02535

Hagen M, Wikelski M, Kissling WD (2011) Space use of bumblebees (*Bombus* spp.) revealed by radio-tracking. PLoS ONE. https://doi.org/10.1371/journal.pone.0019997

Heinrich B (1979) Bumblebee Economics. Harvard University Press, Cambridge

Helzer CJ, Jelinski DE (1999) The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecol Appl 9:1448–1458

Herrmann JD, Haddad NM, Levey DJ (2017) Testing the relative importance of local resources and landscape connectivity on *Bombus impatiens* (Hymenoptera, Apidae) colonies. Apidologie 48:545–555. https://doi.org/10.1007/s13592-017-0499-1

Jaeger JA (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landsc Ecol 15:115–130. https://doi.org/10.1023/A:1008129329289

Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D, Carvalheiro LG, Chacoff NP, Cunningham SA, Danforth BN, Dudenhoffer JH, Elle E, Gaines HR, Garibaldi LA, Gratton C, Holzschuh A, Isaacs R, Javorek SK, Jha S, Klein AM, Krewenka K, Mandelik Y, Mayfield MM, Morandin L, Neame LA, Otieno M, Park M, Potts SG, Rundlof M, Saez A, Steffan-Dewenter I, Taki H, Viana BF, Westphal C, Wilson JK, Greenleaf SS, Kremen C (2013) A global quantitative synthesis of local and landscape effects on wild bee

pollinators in agroecosystems. Ecol Lett 16:584–599. https://doi.org/10.1111/ele.12082

Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, Sanderson A, Goulson D (2005) An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species. Mol Ecol 14:1811–1820. https://doi.org/10.1111/j.1365-294X.2005.02540

Korner-Nievergelt F (2015) Bayesian data analysis in ecology using linear models with R, BUGS, and Stan. Academic Press, Amsterdam

LaZerte S (2018) feedr: transforming Raw RFID Data. R package version v0.10.0, R packageversion 0.9.1.9000 edn. https://github.com/animalnexus/feedr. Accessed 25 Jan 2018

MacDonald ZG, Anderson ID, Acorn JH, Nielsen SE (2018) Decoupling habitat fragmentation from habitat loss: butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. Oecologia 186:11–27. https://doi.org/10.1007/s00442-017-4005-2

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345

McGarigal K, Cushman S, Ene E (2012) FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. https://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 15 Jan 2017

Persson AS, Smith HG (2013) Seasonal persistence of bumblebee populations is affected by landscape context. Agric Ecosys Environ 165:201–209. https://doi.org/10.1016/j.agee.2012.12.008

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts SG, Imperatriz-Fonseca V, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ (2016) Safeguarding pollinators and their values to human well-being. Nature 540:220–229. https://doi.org/10.1038/nature20588

QGIS Development Team (2017) QGIS Geographic Information System, Version 2.18 Las Palmas, 2.18 Las Palmas edn.

R Core Team (2016) R: A language and environment for statistical computing, Vienna, Austria.

Rasmont P, Coppee A, Michez D, De Meulemeester T (2008) An overview of the Bombus terrestris (L. 1758) subspecies (Hymenoptera : Apidae). Ann Soc Entomol Fr 44:243–250

Redhead JW, Dreier S, Bourke AFG, Heard MS, Jordan WC, Sumner S, Wang JL, Carvell C (2016) Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. Ecol Appl 26:726–739. https://doi.org/10.1890/15-0546

Rosch V, Tscharntke T, Scherber C, Batary P (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. J Appl Ecol 50:387–394. https://doi.org/10.1111/1365-2664.12056

Rundlof M, Nilsson H, Smith HG (2008) Interacting effects of farming practice and landscape context on bumblebees. Biol Conserv 141:417–426. https://doi.org/10.1016/j.biocon.2007.10.011

Rusterholz HP, Baur B (2010) Delayed response in a plant-pollinator system to experimental grassland fragmentation. Oecologia 163:141–152. https://doi.org/10.1007/s00442-010-1567-7

Rybicki J, Hanski I (2013) Speciesarea relationships and extinctions caused by habitat loss and fragmentation. Ecol Lett 16:27–38. https://doi.org/10.1111/ele.12065

Sanderson RA, Goffe LA, Leifert C (2015) Time-series models to quantify short-term effects of meteorological conditions on bumblebee forager activity in agricultural landscapes. Agric For Entomol 17:270–276. https://doi.org/10.1111/afe.12102

Schuepp C, Herrmann JD, Herzog F, Schmidt-Entling MH (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. Oecologia 165:713–721. https://doi.org/10.1007/s00442-010-1746-6

Schuepp C, Herzog F, Entling MH (2014) Disentangling multiple drivers of pollination in a landscape-scale experiment. Proc R Soc B. https://doi.org/10.1098/rspb.2013.2667

Seibold S, Bassler C, Brandl R, Fahrig L, Forster B, Heurich M, Hothorn T, Scheipl F, Thorn S, Muller J (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology 98:1613–1622. https://doi.org/10.1002/ecy.1819

Stanley DA, Russell AL, Morrison SJ, Rogers C, Raine NE (2016) Investigating the impacts of field-realistic exposure to a neonicotinoid pesticide on bumblebee foraging, homing ability and colony growth. J Appl Ecol 53:1440–1449. https://doi.org/10.1111/1365-2664.12689

Steffan-Dewenter I, Tscharntke T (1999) Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432–440. https://doi.org/10.1007/s004420050949

Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol Appl 9:586–593

von Hagen E, Aichhorn A (2014) Hummeln-bestimmen, ansiedeln, vermehren, schützen, 6th edn. Fauna-Verlag, Nottuln

Westphal C, Steffan-Dewenter I, Tscharntke T (2006) Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecol Entomol 31:389–394. https://doi.org/10.1111/j.1365-2311.2006.00801

Westphal C, Steffan-Dewenter I, Tscharntke T (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J Appl Ecol 46:187–193. https://doi.org/10.1111/j.1365-2664.2008.01580.x

Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93:1049–1058. https://doi.org/10.1890/11-1006.1

Wolf S, Moritz RFA (2008) Foraging distance in Bombus terrestris L. (Hymenoptera : Apidae). Apidologie 39:419–427. https://doi.org/10.1051/apido:2008020