

**Effects of habitat amount and fragmentation in vineyards on  
bumblebee colony fitness and foraging behaviour**

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# Effects of habitat amount and fragmentation in vineyards on bumblebee colony fitness and foraging behaviour

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## Abstract

Agricultural intensification with the associated habitat loss and fragmentation are among the most important drivers of the ongoing pollination crisis. In this study, conducted in intensively managed vineyards in southern Switzerland, we tested the separate and interdependent effects of habitat amount and fragmentation on fitness-relevant traits in 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 vegetated vineyards) and fragmentation (number of vegetated vineyard fields). Individual bumblebee foraging trips were measured with radio frequency identification (RFID) technology while colony fitness was assessed by quantifying parameters related to colony survival and fecundity. We found an interactive effect of habitat amount and fragmentation. More specifically, the degree of fragmentation had a negative effect on bumblebee colony fitness when the amount of habitat was low, while it positively affected colony fitness in landscapes with high amounts of habitat. Ground vegetation cover in vineyards showed a positive effect on colony fitness. Fragmentation, but not habitat amount, significantly influenced foraging behaviour, with a higher foraging activity (more foraging trips) at low fragmentation. Our results highlight the interdependency of habitat amount and fragmentation on pollinator performance and foraging behaviour, providing guidance for optimising the spatial configuration of vineyard landscapes from a biodiversity viewpoint.

## Keywords

*Bombus*, colony performance, connectivity, conservation, RFID, pollination services, social insects, vegetation cover

## Introduction

Many species of wild pollinators, including bumblebees and honeybees, are declining since the past century (Potts *et al.* 2010). Lower pollinator abundance has multiple negative consequences, ranging from reduced genetic diversity of wild plant species (Rusterholz & Baur 2010), to a reduction of their reproductive success (Donaldson *et al.* 2002) but also to a decrease in crop yield due to reduced pollination services (Garibaldi *et al.* 2013; Potts *et al.* 2016). The 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 floral re-

sources (Robinson & Sutherland 2002; Goulson, Lye & Darvill 2008; Potts *et al.* 2010) and pollinators (Rundlof, Nilsson & Smith 2008; Kennedy *et al.* 2013).

Many aspects are included in the process of habitat fragmentation: loss of habitat, increase in number of habitat patches, decrease in size of these remaining habitat patches as well as an increase in isolation (Fahrig 2003). The consequences are often impoverished habitat patches, which are at one point too small to sustain local populations and a lower connectivity between habitat patches. This can negatively impact the abundance and richness of wild pollinators (Steffan-Dewenter & Tschardt 1999). As an implication, pollinator visitation was shown to be higher in landscapes with high amount and low isolation of habitat (Schuepp, Herzog & Entling 2014). This corroborates the findings of a review showing that all aspects of fragmentation (reduced area, increased isolation and increased edge) had severe effects on ecosystem functions such as pollination (Haddad *et al.* 2015) and that their differential effects are hard to disentangle.

Several studies investigated interactive effects of habitat amount and fragmentation, which revealed that high habitat amount can mediate the negative effect of fragmentation (Rybicki & Hanski 2013; Coudrain *et al.* 2014; Bosco 2018, PhD thesis). For example, parasitoid abundance was strongly decreased in isolated patches, but only when habitat amount was low (Coudrain *et al.* 2014). Going a step further, the habitat amount hypothesis states that species richness should be mainly driven by habitat amount, meaning that fragmentation has little or no effect (Fahrig 2013). Testing this hypothesis revealed contrasting results: Habitat amount has been found to be the most important single predictor for small mammal and saproxylic beetle species richness respectively (Melo *et al.* 2017; Seibold *et al.* 2017), while experimental evidence was found for a crucial role of fragmentation in determining plant and invertebrate species richness (Haddad *et al.* 2017). Additionally, positive effects of patch size on plant species richness were shown, contradicting the habitat amount hypothesis (Evju & Sverdrup-Thygesen 2016). These examples indicate that the relative importance of habitat amount and fragmentation may depend on the study system as well as on the traits of the study species. This may be the reason that the exact mechanisms of habitat loss and fragmentation remain still quite unclear and there is a need for studies which disentangle habitat amount and fragmentation, considering species traits and the scale of analysis (McGarigal & Cushman 2002).

An organism's mobility may largely determine its sensitivity to habitat fragmentation, with mobile species being less affected (MacDonald *et al.* 2018). For mobile pollinators, the negative effects of fragmentation might be reduced, if there is sufficient habitat, i.e. providing floral and nesting resources in a given landscape. Nevertheless, additional costs may arise in fragmented landscapes due to increased flight distances to find rewarding flower patches. According to the optimal foraging theory, pollinators will forage close to their nesting site in landscapes with evenly distributed resource patches to reduce energetic and time costs and maximise energetic efficiency (Osborne *et al.* 2008; Davies, Krebs & West 2012), but may plastically alter their feeding behaviour whenever foraging patches dif-

fer strongly in quality (flower density or nectar volume) (Cresswell, Osborne & Goulson 2000). This has been demonstrated in the field: In landscapes with high cover and low fragmentation of semi-natural vegetation, several bumblebee species showed a shorter foraging distance (Redhead *et al.* 2016). Similar results were found in studies with commercial *B. terrestris* colonies (e.g. sold by Biobest Belgium), where the duration of foraging trips was shorter in landscapes with abundant resources compared to landscapes with sparse resources (Westphal, Steffan-Dewenter & Tschardtke 2006). This may imply costs, as colonies gained more weight and had a higher number of workers in landscapes with abundant resources (Goulson *et al.* 2002; Westphal, Steffan-Dewenter & Tschardtke 2006; Parmentier *et al.* 2014). To the best of our knowledge, only one study so far investigated the effect of habitat fragmentation on bumblebee colony performance: Herrmann and colleagues (2017) found no direct effect of connectivity, but a positive correlation between local floral resources and colony performance, which was stronger in isolated fragments. These results suggest a high importance of floral resources for the successful development of a bumblebee colony, while the role of fragmentation remains more elusive.

Here, we conducted a field study in intensively managed vineyards, which provide a near-experimental setup of a fragmented landscape: 80% of the vineyards are treated with herbicides and thus have no ground vegetation cover, while a minority allows ground vegetation to grow, providing resources for pollinators (Arlettaz *et al.* 2012). These two contrasting management types create a binary system (bare vs vegetated vineyards), allowing to disentangle the effects of habitat amount and fragmentation at a landscape scale. Colonies of the bumblebee *B. terrestris* were placed into fields varying in habitat amount (surface of vegetated vineyards) and fragmentation (number of vegetated vineyards) and we recorded foraging trip time and colony fitness-related traits. With this approach, we tested our main hypotheses: i) colonies have a lower fitness in strongly fragmented landscapes with low habitat amount, and ii) *B. terrestris* workers spend more time foraging in strongly fragmented landscapes with low habitat amount.

## **Material and methods**

### **Study site and study species**

The study was conducted during May and June 2017 in the vineyards of Valais, southern Switzerland. Vineyards dominate the landscape along the south-facing slopes north of the Rhône river with a total area of approximately 50 km<sup>2</sup> in Valais. They are mainly located up to 900 m above sea level and are interspersed with small patches of dry oak forest and steppe (Arlettaz *et al.* 2012). The climate in Valais is continental, with an average annual precipitation around 586 mm, and an average annual temperature around 11.2 °C (for Sion, Bundesamt für Statistik 2017). 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 in 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 as ubiquitous in the lowlands and up to 1200 m above sea level in meadows, hedges, gardens and at forest borders and they use many different feeding plants. The colony size of *B. terrestris* counts approximately 200 up to sometimes 600 individuals (after von Hagen & Aichhorn 2014). The mean foraging distances that have been found for *B. terrestris* range between 267 m and 551 m (Wolf & Moritz 2008; Redhead *et al.* 2016), while the maximum foraging distances range between 758 m and 2500 m (Walther-Hellwig & Frankl 2000; Knight *et al.* 2005; Hagen, Wikelski & Kissling 2011).

## **Fragmentation classes on landscape level**

To disentangle habitat amount and fragmentation, we used a 2x2 factorial design with four classes varying in habitat amount and fragmentation. All vineyards covered by less than 40% ground vegetation were considered as bare and were added as a fifth class in our experimental design. The vineyards covered by more than 40% ground vegetation were considered as habitat. The ground vegetation cover was calculated with the Normalized Difference Vegetation Index (NDVI) from satellite pictures, which were recorded in March before sprouting of the vine leaves started (Sentinel-2, 10m resolution, recorded on 11/3/2017). Based on this binary raster of bare and vegetated vineyards, we then calculated habitat amount as percentage covered by vegetated vineyards (PLAND, percentage of landscape) and fragmentation as number of vegetated vineyard patches per 100 ha (PD, patch density) using FRAGSTATS (McGarigal, Cushman & Ene 2012). These metrics were calculated within a 250 m radius moving window, because this range represents approximately the mean foraging distance of *B. terrestris* (Wolf & Moritz 2008). We then used the upper and lower 40% of habitat amount (PLAND) and fragmentation (PD) values to create four classes of high or low habitat amount and high or low fragmentation. We selected eight vineyard fields per class including the matrix as a 5<sup>th</sup> class. The resulting forty fields were distributed in a stratified random manner within the landscape to account for geographical variability and to avoid clumping of fields within classes (figure S 2).

## **Habitat mapping on vineyard field level**

To estimate the ground vegetation and flower resources at our sites during the experiment, we mapped the vegetation of a random subsample of six vegetated vineyard fields (> 40% ground vegetation cover) in a buffer zone of 250 m radius around our experimental fields. For each of these six fields we estimated the percentage of ground vegetation cover for the whole field, assessed the blooming flower species richness in two transects, counted the number and estimated the cover of blooming flowers in a square meter. The two transects were chosen as the third rows from both field margins to avoid edge effects. For surveying the square meter, we walked 10 m into the fifth row of one field margin. For each variable, we took the mean of these six fields per site for the statistical analyses. The two variables “habitat amount” and “ground vegetation estimates” give different information: While habitat

amount describes the percentage of the surface covered by vegetated vineyards (> 40% coverage) within the 250 m-buffer (based on a binary perception of the bare vs vegetated management system), the estimates of ground vegetation reveal how much vegetated a vineyard field is (ranging from 40 to 100% coverage).

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. Meadows, steppe and forest were considered as natural habitats within our study area. Additionally, we calculated the slope of the experimental fields. All calculations were done in QGIS (version 2.18.2, QGIS Development Team 2017).

### **Quasi-experimental setup**

We purchased forty 2-week-old colonies of *B. terrestris terrestris* from Andermatt Biocontrol (Biobest Belgium). Upon arrival, each colony was weighed (Miostar, 1g precision). The colonies were randomly allocated to our study fields from 8 to 13 May 2017. On the field, they were placed on four pots about 15 cm above ground. With a wooden roof, we protected the colonies from rain and sun (figure S 1). Once installed, the provided sucrose solution tank (Biogluc©) was closed to assure that bumblebees needed to go foraging outside of the hive.

### **Foraging time**

To measure foraging time we used the fully automatic radio frequency identification (RFID) technology (Stelzer *et al.* 2010). Two RFID readers (iID@MAJA reader module 4.2, Microsensys GmbH, Erfurt, Germany) installed at the entrance of the hive automatically registered the identity of the passing tagged bee, the time and direction of movement of the bee. 20 individuals per colony were tagged one or two days before the RFID system was installed at the colony. The RFID tags (mic3@-TAG 64-bit RO, iID2000, 13.56MHz system, 1.0x1.6x0.5 mm; Microsensys GmbH, Erfurt, Germany) were glued on the thorax of the bumblebees with fast drying TempoSil2 teeth cement (Coltène/Whaledent Ohio, USA) (Jeker, Volles & Herren 2016). We had five bee identification systems (iID2000, ISO15693optimized, Microsensys GmbH, Erfurt, Germany) to measure one colony of each of the five classes simultaneously. Foraging time of bumblebees was measured for two whole days before switching the systems during night to five other colonies. At the same time, we measured temperature and humidity outside of these five colonies (Maxim Integrated Temperature and RH i-Button logger, DS1923-F5 Hygrochron). 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. In the beginning of the experiment, all colonies have been equipped with an empty cardboard box at the entrance so that the bumblebees were already used to it before installing the readers. The first session of RFID measurements started on 24 May, the last on 10 June 2017. Among the 40 colonies, only 33 colonies could be used for RFID measurements, due to too low activity of the remaining seven colonies. At the end of

the experiment, the colonies were collected during the nights from 20 to 23 June 2017, weighed again and placed in a freezer to euthanize the bumblebees.

Foraging time of a bumblebee was calculated as the differences between the exit and enter 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. For an enter event, bumblebees passed first reader 2 and then reader 1. We calculated foraging time with the function *inout* of the R package “feedr” (LaZerte 2018). Foraging trips shorter than 10 min were excluded, since these short trips could be orientation and defecation flights (Spaethe & Weidenmuller 2002; Peat & Goulson 2005; Westphal, Steffan-Dewenter & Tschardtke 2006) or in our case simply hovering around the RFID readers. We as well excluded trips longer than 202 min to minimise artefacts such as missed detections. 96% of all trips were shorter than 202 min and we therefore considered this as an appropriate upper limit (according to Westphal, Steffan-Dewenter & Tschardtke 2006). In a next step, we additionally excluded trips which began during night (defined as 20:00-2:30 UTC), since these trips are presumed not to be real foraging trips (Stanley *et al.* 2016). We used foraging trip time, sum of foraging trip time per bumblebee (of two days) and number of foraging trips per bumblebee (of two days) as response variables for the statistical modelling.

## **Dissection of colonies**

As one colony already died in the field, 39 colonies could be dissected in the lab. Several nest traits were measured following the dissection protocol of Goulson and colleagues (2002). For each colony, we counted the number of queens, workers, larvae, eggs, nectar pots, 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 (healthy, dead and hatched pupal cells, pollen and nectar pots) were the fitness-related response variables (according to Westphal, Steffan-Dewenter & Tschardtke 2006; Parmentier *et al.* 2014) for the statistical models.

## **Statistical analysis**

All statistical analyses were done with the software R (version 3.3.1, R Core Team 2016). First, collinearity among explanatory variables (table 1) were tested using Spearman’s correlation coefficient. If two variables were correlated (coefficient  $lrl > 0.7$ ), we selected the variable which had a lower AIC in the univariate model while the other one was dismissed for further analyses (Dormann *et al.* 2013). If necessary, all explanatory variables were transformed and standardized.

### ***Fitness-related traits***

Weight gain of the colonies was analysed using the function *lmer* of the R package “lme4” (Bates *et al.* 2015) with region as random effect. Number of workers, number of queens and total number of pupal cells were analysed using the function *glmer* of the R package “lme4” (Bates *et al.* 2015), again

with region as random factor. In these models, we additionally included an observation-level random effect to account for over-dispersion of the count data (Gillies *et al.* 2006; Bolker *et al.* 2009; Dormann 2016). We tested for over-dispersion itself with the function *dispersion\_glmer* (R package "blmeco", Korner-Nievergelt 2015). First, we tested weight gain, number of workers, number of queens and total number of pupal cells against all our explanatory variables in univariate models. We as well included 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. If the quadratic effects included zero in their 95% confidence interval, we discarded them from the models (according to Guyot *et al.* 2017). Next, we built a full model containing all explanatory variables with  $p < 0.1$ . In the model with number of workers, we still included the interaction of habitat amount and fragmentation ( $p = 0.139$ ) into the full model, because 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 model selection approach is based on the best Akaike's Information Criterion (AIC) values. If there was more than one best model with  $\Delta AIC < 2$ , we did model averaging to get our final model estimates (function "model.avg" of R package "MuMIn", Barton 2016).

### ***Foraging time***

Repeatability of foraging trip time, sum of foraging time per bumblebee and number of foraging trips per bumblebee was calculated using the functions *rptGaussian* and *rptPoisson* (for number of foraging trips) (R package "rptR", Stoffel, Nakagawa & Schielzeth 2017).

Foraging trip time (log-transformed) and sum of foraging trip time were analysed using the function *lmer* of the R package "lme4" (Bates *et al.* 2015). Number of foraging trips was analysed using the function *glmer* of the R package "lme4" (Bates *et al.* 2015). For foraging trip time, we used animal and colony ID as random factors, while region and colony ID were used as random factors for sum of foraging trip time. To account for over-dispersion in the models with number of foraging trips, we included an observation-level random factor in addition to the random factor colony ID (Gillies *et al.* 2006; Bolker *et al.* 2009; Dormann 2016). We then proceeded in the same way as described for the fitness-related traits: we first fitted univariate models and performed model selection in a next step.

## **Results**

The best models ( $\Delta AIC < 2$ ) for all response variables from the model selection approach are shown in table 2.

### **Colony fitness**

The colonies had on average  $71.26 \pm 66.34$  workers,  $545.15 \pm 303.75$  pupal cells,  $8.69 \pm 12.22$  queens and a mean weight gain of  $221.1g \pm 254.04$  g. The start weight of the colonies had no significant effect on weight gain of a colony, number of workers, queens and pupal cells produced. Number of parasitic *Aphomia sociella* larvae had as well no significant effect on number of workers, queens and pupal

cells produced but a marginal effect on weight gain (univariate lmer:  $67.24 \pm 39.96$ ,  $p=0.092$ ), but this variable never appeared in the best 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 (table 3). Fragmentation negatively affected the number of workers in landscapes with little habitat (less than 30% in 20 ha) but showed a positive effect in landscapes with high habitat amount (above 40% in 20 ha), (figures 1 and 2). In addition, vegetation cover had a significant effect with an optimum at about 70% of vegetation cover at the vineyard field scale (figure 3), 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 in low habitat landscapes and positively in habitat-rich areas (table 3). Again, vegetation cover had a significant effect on number of pupal cells with an optimum at about 70% cover (table 3). However, NDVI had no significant effect on number of pupal cells (table 3).

The number of queens was independent of any measured variables in our field study (no variables with  $p<0.1$  in univariate models). The best model explaining weight gain included the variables flower cover, area of natural habitat within 250 m-buffer and flower species richness (table 3). Flower cover had a marginal positive effect on weight gain. In contrary, area of natural habitat was significantly negatively related to weight gain and flower species richness had no significant effect.

## **Foraging time**

The mean foraging trip time of a bumblebee was  $46.04 \pm 32.9$  min and 96% of all trips lasted shorter than 202 min. On average, a bumblebee spent  $763.4 \pm 469.9$  min foraging in two days, which is 12.7 hours (26.5 % of time). In two days, a bumblebee made  $16.6 \pm 13.3$  trips, with a maximum of 69 trips.

Repeatability of foraging trip time was significant within both grouping factors, individual ( $R=0.38 \pm 0.022$ ,  $p<0.001$ ) and colony ( $R=0.094 \pm 0.028$ ,  $p<0.001$ ). For sum of foraging trip time per day, repeatability was significant for individual ( $R=0.555 \pm 0.033$ ,  $p<0.001$ ), but not for colony ( $R=0.014 \pm 0.013$ ,  $p=0.128$ ). Repeatability of number of foraging trips per day was again significant for individual ( $R=0.676 \pm 0.029$ ,  $p<0.001$ ), but not for colony ( $R=0.004 \pm 0.008$ ,  $p=0.381$ ).

While foraging trip time was best explained by meteorological (quadratic term of humidity, figure 4, table 4) and topographic (positive effect of slope, figure 5, table 4) factors, the summed time of all foraging trips per bumblebee was best explained by the interaction between the amount of habitat in a landscape and the quadratic term of fragmentation (figure S3, table 4). The marginal significant interaction showed, that in the case of high habitat amount (50% in 20 ha), bumblebees spent more time foraging when fragmentation was low (10-50 patches per 100 ha) than when fragmentation was high (50-100 patches per 100 ha). But in the case of low habitat amount (10% in 20 ha), bumblebees spent overall less time foraging (only a little more at very low fragmentation).

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 (table 4). Distance to the next natural habitat was significantly positively related to number of foraging trips (figure 6), while the quadratic term of fragmentation showed a significant effect with an optimum at about 20 vegetated vineyards per 100 ha (figure 7). The other variables showed no significant effects.

## Discussion

Our results reveal that the effect of fragmentation on fitness-related traits of bumblebee colonies is strongly dependent on the amount of available habitat. This interactive effect of habitat amount and fragmentation is in line with several other study outcomes (With & Pavuk 2011; Rybicki & Hanski 2013; Coudrain *et al.* 2014; Bosco 2018, PhD thesis). Further, we found that a vegetation cover of 70% on a vineyard field scale seems to be optimal for bumblebee colony size. Fragmentation, but not habitat amount, significantly influences foraging behaviour, with a higher foraging activity (more foraging trips) at low fragmentation. This study emphasises the importance to study the separate and interdependent effects of habitat amount and fragmentation in order to understand their influence on an important pollinator species. With our results we can give clear recommendations to farmers on different spatial scales to protect the habitat and manage the vineyards in a pollinator-friendly way.

## Colony fitness

Colony fitness, estimated using the number of produced workers and pupal cells, was significantly affected by habitat composition on a landscape scale. Our results refute the “habitat amount hypothesis” stating that amount of habitat is the only underlying process determining an organism’s fitness (Fahrig 2013). The effects of fragmentation interacted with the amount of habitat with most pronounced negative effects in landscapes with low habitat amount. Connectivity among few remaining habitat patches seems therefore essential for the successful colony development in bumblebees, a fact also demonstrated in other organisms (Schuepp *et al.* 2011; Rosch *et al.* 2013; Olsen, Evju & Endrestol 2018). In contrast, fragmentation positively affected colony development in areas with high habitat amount (above 40% in 20 ha). Fragmentation in habitat-rich landscapes is most likely related to mosaic-like agricultural landscapes, with a high variability in management and therefore a high variability in floral resources. This leads to a heterogeneous surrounding, which has been shown to be beneficial for bumblebees through a stable provisioning of resources throughout the seasons (Benton, Vickery & Wilson 2003; Rundlof, Nilsson & Smith 2008; Persson & Smith 2013; Cole *et al.* 2017). Additionally, this increased habitat heterogeneity has been found to be one of the main reasons for a positive effect of fragmentation (reviewed by Fahrig 2017), which is most likely also true for vineyards. Diverse management styles in terms of different time and frequency of mowing and spontaneous or sown vegetation lead to a very distinct vegetation structure and composition among the different vineyards.

Besides landscape-scale characteristics, colony fitness was also affected by fine-scale habitat variables. Differential seed set or soil specific factors influence plant growth and lead to a heterogeneous habitat on a smaller scale with some patches of bare ground and patches of larger plants, which has been shown to benefit biodiversity (Benton, Vickery & Wilson 2003). Vegetation cover on a vineyard field scale seems to be a very important predictor for bumblebee colony fitness in terms of number of workers and pupal cells. We found the optimum to be around 70% vegetation cover in a vineyard field. For vineyard management, this usually means that every inter-row is vegetated, but the vegetation is removed in the area directly under the vines, or that the vegetation is generally patchy with bare ground in between. The reason that the curve is dropping after 70% vegetation cover are most likely the benefits of a patchy, heterogeneous vegetation which results in a higher plant diversity. This might correlate with a higher amount of floral resources and therefore benefitting bumblebee colonies. 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 of colonies (Westphal, Steffan-Dewenter & Tscharntke 2006; Parmentier *et al.* 2014; Herrmann, Haddad & Levey 2017). In our study, we only detected a trend of a positive direct effect of flower cover on weight gain of colonies. An explanation for this could be that we only measured a sample of six vineyards per 250 m-buffer and therefore our measure of flower cover is not representative enough due to the heterogeneity of the vegetated vineyards. Additionally, we conducted the vegetation mapping only once during the whole experiment and only mapped open flowers, due to time constraints, and hence might not have captured the temporal variability of flower resources. Therefore, vegetation cover is the better predictor for resources than flower cover.

Apart from the vegetation in vineyards, natural habitats in the proximity might as well provide resources for bumblebees. However, weight gain of colonies was negatively affected by area of natural habitat. The importance of natural habitats for bumblebees might depend on the resources they provide, which are very variable throughout the seasons. Natural habitats such as forest and steppe clearly differ in floral composition from vineyards, and thus they could become more important later in the season. Therefore, the amount of natural habitat might have correlated with a decrease of areas containing more flower resources at the time of our experiment and negatively affect bumblebee colonies, found also by another study (Kamper *et al.* 2016). It has as well be shown that *B. terrestris* prefers open habitats and rarely forages in forests (Kreyer *et al.* 2004; Diaz-Forero *et al.* 2011). Future studies are clearly needed to quantify the peaks in floral resources for the distinct types of natural habitats (e.g. steppe, meadows, hedges, forests) and to identify their importance for bumblebee colony fitness.

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 more complicated relationship between resources and queens. For workers, a high number of flowers early in the season is most important, while queen production depends on a continuous availability of floral resources throughout the seasons (Westphal, Steffan-Dewenter & Tscharntke 2009; Williams,

Regetz & Kremen 2012). The fact that our colonies developed very differently, and some were producing queens earlier than others, could have as well influenced our results. Thus, queens in certain colonies might already have left their colony before we collected them.

## **Foraging time**

The summed time of all foraging trips per bumblebee was only marginally significantly affected by habitat composition on a landscape scale. When habitat amount was high (50% in 20 ha), bumblebees spent more time foraging in a little fragmented than in a strongly fragmented surrounding. In the case of low habitat amount (10% in 20 ha), bumblebees spent overall less time foraging (only a little more at very low fragmentation). In line, foraging activity of a bumblebee (number of foraging trips) was significantly highest at low fragmentation, but irrespective of habitat amount. These results indicate that connectivity among resource patches is most important and hence bumblebees invest more time in foraging when the resources are aggregated. It might explain why connectivity was also crucial for the successful development of the colonies, especially in areas with little habitat. In a landscape with much, but less connected habitat, the higher amount of resources due to heterogeneity might have outweighed the negative effects of fragmentation on foraging activity. The underlying mechanism might be the following: Nectar influx in colonies by successful foragers increases the foraging activity of the colonies, meaning that in a surrounding with many resources, overall foraging activity of a colony is higher, probably leading to larger colonies (Dornhaus & Chittka 2001). To our knowledge there are no other studies investigating the effect of fragmentation on time and number of foraging trips of bumblebees. However, it has been shown that bumblebees do shorter foraging trips in landscapes with a high abundance of resources (Westphal, Steffan-Dewenter & Tschardtke 2006). Furthermore, foraging distance (which might be related to foraging time) has been shown to decrease as resource availability increases and fragmentation of semi-natural habitats decreases (Carvell *et al.* 2012; Redhead *et al.* 2016).

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

In contrast to the other results, foraging trip time was only affected by meteorological and topographic factors. At a low relative humidity, the longest foraging trips were done, which has been demonstrated as well by Sanderson *et al.* (2015). Additionally, foraging trip time increased with slope. In steep slopes, the vineyards are often less vegetated, because they cannot be accessed with machines and manual management of steep slopes is challenging. Therefore, bumblebees might need to spend longer time foraging to find enough resources in steeper slopes.

## Conclusions and recommendations for conservation

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 pollinators with smaller foraging ranges and more specialized resource requirements. Our results suggest increasing and aggregating the surface of vegetated vineyards if habitat amount is low (<30% within 20 ha). If habitat amount within 20 ha is above 40%, vegetated vineyards should be distributed mosaic-like (ideally 40-100 patches) to create a heterogeneous landscape of differently managed vineyards, providing a continuous availability of resources. Within vineyard fields, we recommend increasing the vegetation cover up to 70% to provide enough floral resources for pollinators, while maintaining a heterogeneous vegetation composition. Further studies are needed to closer investigate the effects of habitat amount and fragmentation and the composition and quality of vegetation cover in vineyards on other pollinator species to give more generalizable recommendations.

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*Table 1 All explanatory variables which were used for the statistical analysis.*

<b>Explanatory variables</b>	<b>Models</b>	<b>Source</b>
Vegetation cover (%)	Fitness and foraging	Vegetation mapping
Flower species richness	Fitness and foraging	Vegetation mapping
Number of flowers	Fitness and foraging	Vegetation mapping
Flower cover (%)	Fitness and foraging	Vegetation mapping
Area of natural habitat within 250m	Fitness and foraging	QGIS
Distance to next natural habitat	Fitness and foraging	QGIS
Slope	Foraging	Satellite images (QGIS)
Fragmentation	Fitness and foraging	Fragstats and QGIS
Habitat amount	Fitness and foraging	Fragstats and QGIS
Temperature	Foraging	Temperature logger
Humidity	Foraging	Humidity logger

Table 2 Model selection tables of the best models with  $\Delta AIC < 2$  describing weight gain of colonies, total number of pupal cells, number of workers, foraging trip time, sum of foraging trips per bumblebee and number of foraging trips per bumblebee. For each model, all included variables, degrees of freedom, the difference in AIC to the best model ( $\Delta AIC$ ) and Akaike weight are given.

Model No.	Variables	df	$\Delta AIC$	Akaike weight
<b>Weight gain</b>				
8	Area of natural habitat + flower cover + species richness	6	0.00	0.982
<b>Total number of pupal cells</b>				
6	NDVI + PLAND	5	0.00	0.093
29	PLAND + vegetation cover + (vegetation cover) <sup>2</sup>	6	0.27	0.082
63	PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup> + PD:PLAND	8	0.27	0.082
30	NDVI + PLAND + vegetation cover + (vegetation cover) <sup>2</sup>	7	0.36	0.078
64	NDVI + PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup> + PD:PLAND	9	0.5	0.073
5	PLAND	4	0.78	0.063
40	NDVI + PD + PLAND + PD:PLAND	7	0.8	0.063
31	PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup>	7	1.59	0.042
8	NDVI + PD + PLAND	6	1.95	0.035
32	NDVI + PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup>	8	1.97	0.035
14	NDVI + PLAND + vegetation cover + (vegetation cover) <sup>2</sup>	6	1.99	0.035
<b>Number of workers</b>				
63	PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup> + PD:PLAND	8	0.00	0.378
64	Area of natural habitat + PD + PLAND + vegetation cover + (vegetation cover) <sup>2</sup> + PD:PLAND	9	1.55	0.175
<b>Foraging trip time</b>				
4	Humidity + (humidity) <sup>2</sup>	6	0.00	0.516
8	Humidity + (humidity) <sup>2</sup> + slope	7	0.13	0.484
<b>Sum of foraging trip time</b>				
32	PD + (PD) <sup>2</sup> + PLAND + PD:PLAND + (PD) <sup>2</sup> :PLAND	9	0.00	0.975
<b>Number of foraging trips</b>				
14	Distance to next NH + PD + (PD) <sup>2</sup>	6	0.00	0.399
30	Distance to next NH + PD + (PD) <sup>2</sup> + PLAND	7	1.22	0.217
16	Distance to next NH + mean humidity + PD + (PD) <sup>2</sup>	7	1.69	0.172

Table 3 Averaged best models for number of workers and total number of pupal cells and single best model for weight gain of colonies. The estimate  $\pm$  standard error, *t* and *p* values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>z value</b>	<b>p value</b>
<b><i>Number workers</i></b>			
<b>Habitat amount:fragmentation</b>	<b>0.43 <math>\pm</math> 0.19</b>	<b>2.115</b>	<b>0.0399</b>
Fragmentation	-0.34 $\pm$ 0.19	1.733	0.081
Habitat amount	-1.4 $\pm$ 0.17	0.787	0.404
Vegetation cover	-0.04 $\pm$ 0.18	0.243	0.859
<b>(Vegetation cover)<sup>2</sup></b>	<b>-0.87 <math>\pm</math> 0.21</b>	<b>3.939</b>	<b>&lt;0.001</b>
Flower cover	0.16 $\pm$ 0.16	0.956	0.3389
Area of natural habitat	-0.11 $\pm$ 0.17	0.65	0.5159
<b><i>Total number of pupal cells</i></b>			
Habitat amount:fragmentation	0.24 $\pm$ 0.13	1.795	0.0726
Habitat amount	-0.25 $\pm$ 1.27	1.896	0.058
Fragmentation	-0.025 $\pm$ 0.16	0.153	0.8785
Vegetation cover	-0.03 $\pm$ 0.17	0.169	0.8657
<b>(Vegetation cover)<sup>2</sup></b>	<b>-0.28 <math>\pm</math> 0.13</b>	<b>2.02</b>	<b>0.0436</b>
NDVI	-0.17 $\pm$ 0.11	1.494	0.1353
<b><i>Weight gain</i></b>		<b>t value</b>	
Flower cover	73.04 $\pm$ 40.23	1.815	0.06945
<b>Area of natural habitat</b>	<b>-83.96 <math>\pm</math> 36.7</b>	<b>-2.288</b>	<b>0.02215</b>
Flower species richness	55.1 $\pm$ 39.5	1.395	0.16307

Table 4 Averaged best models for foraging trip time and number of foraging trips and single best model for sum of foraging trip time. The estimate  $\pm$  standard error, t and p values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>t value</b>	<b>p value</b>
<i>Foraging trip time</i>			
<b>Humidity</b>	<b>-0.17 <math>\pm</math> 0.006</b>	<b>27.384</b>	<b>&lt;0.001</b>
<b>(Humidity)<sup>2</sup></b>	<b>-0.04 <math>\pm</math> 0.006</b>	<b>6.935</b>	<b>&lt;0.001</b>
<b>Slope</b>	<b>0.1 <math>\pm</math> 0.04</b>	<b>2.659</b>	<b>0.00783</b>
<i>Sum of foraging trip time per bumblebee</i>			
Habitat amount	0.18 $\pm$ 32.97	0.005	0.5183
Fragmentation	64.29 $\pm$ 56.19	1.144	0.29142
(Fragmentation) <sup>2</sup>	-121.88 $\pm$ 56.97	-2.139	0.17276
Habitat amount:fragmentation	25.36 $\pm$ 49.29	0.515	0.60685
Habitat amount:(fragmentation) <sup>2</sup>	-77.06 $\pm$ 45.95	-1.677	0.09353
<i>Number of foraging trips per bumblebee</i>		<b>z value</b>	
<b>Distance to next natural habitat</b>	<b>0.13 <math>\pm</math> 0.05</b>	<b>2.741</b>	<b>0.006</b>
Fragmentation	-0.03 $\pm$ 0.05	0.616	0.537
<b>(Fragmentation)<sup>2</sup></b>	<b>-0.18 <math>\pm</math> 0.05</b>	<b>3.824</b>	<b>&lt;0.001</b>
Habitat amount	0.04 $\pm$ 0.05	0.886	0.3757
Mean humidity	0.03 $\pm$ 0.05	0.564	0.573

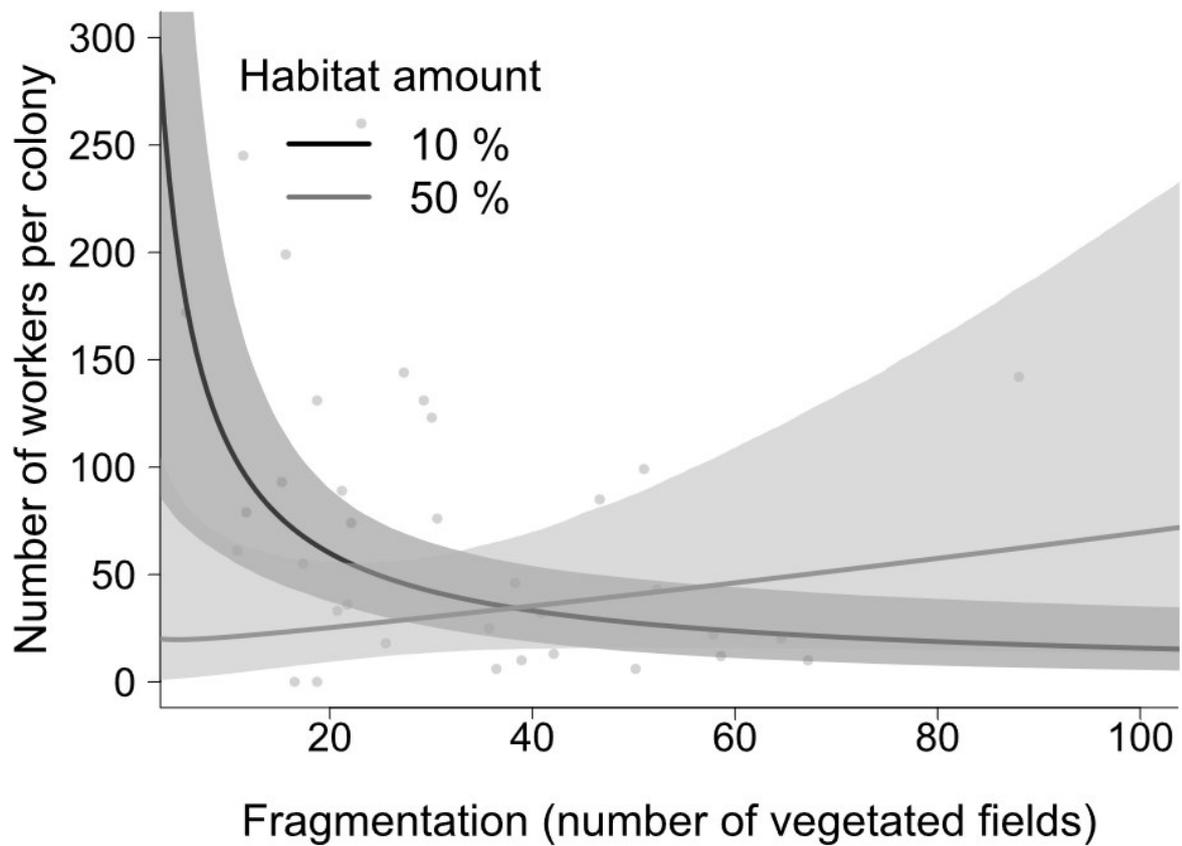


Figure 1 Interactive effect of habitat amount and fragmentation on number of workers ( $0.43 \pm 0.19$ ,  $z=2.12$ ,  $p=0.0399$ ). If there is a low habitat amount (10%) in the 250 m-buffer around the colonies, fragmentation has a negative effect. In contrast, if there is a high habitat amount (50%), fragmentation even has a positive effect on number of workers.

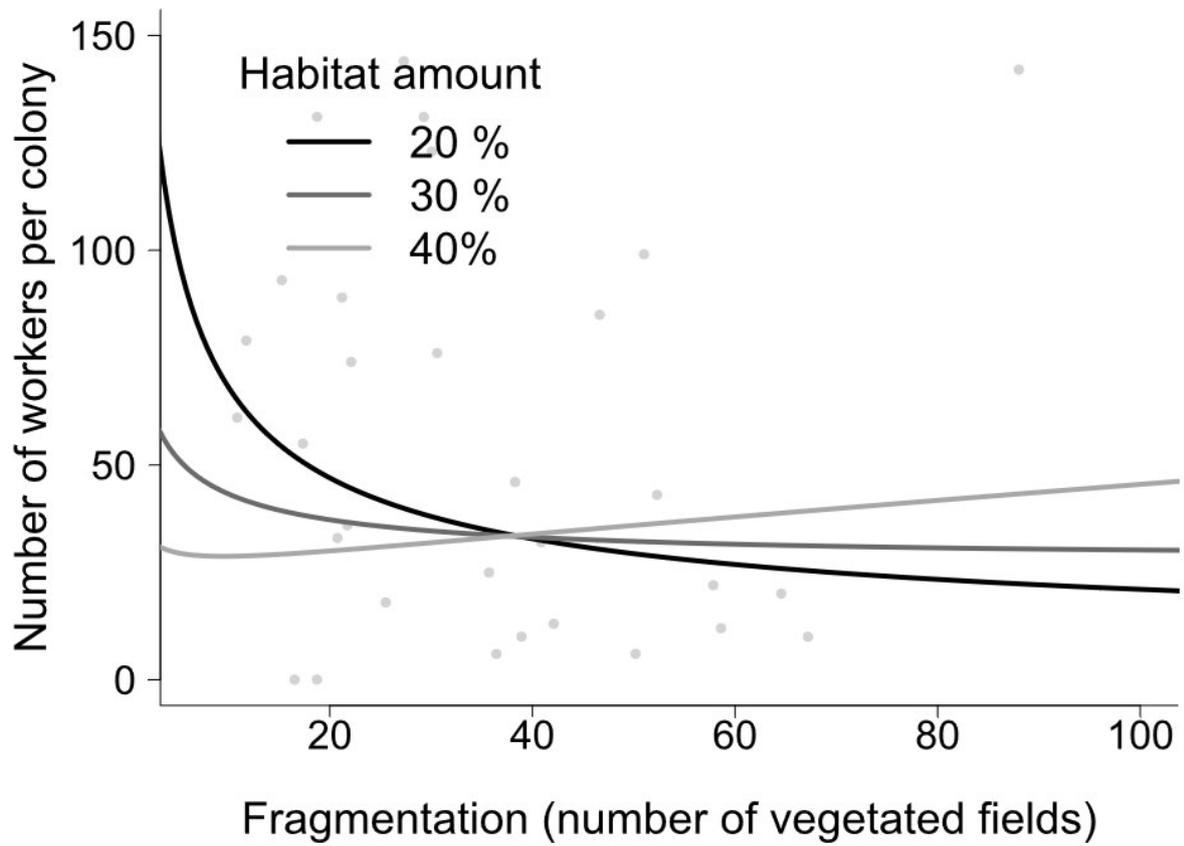


Figure 2 With a habitat amount in the 250m-buffer around the colonies above 30%, the effect of fragmentation on number of workers gets positive.

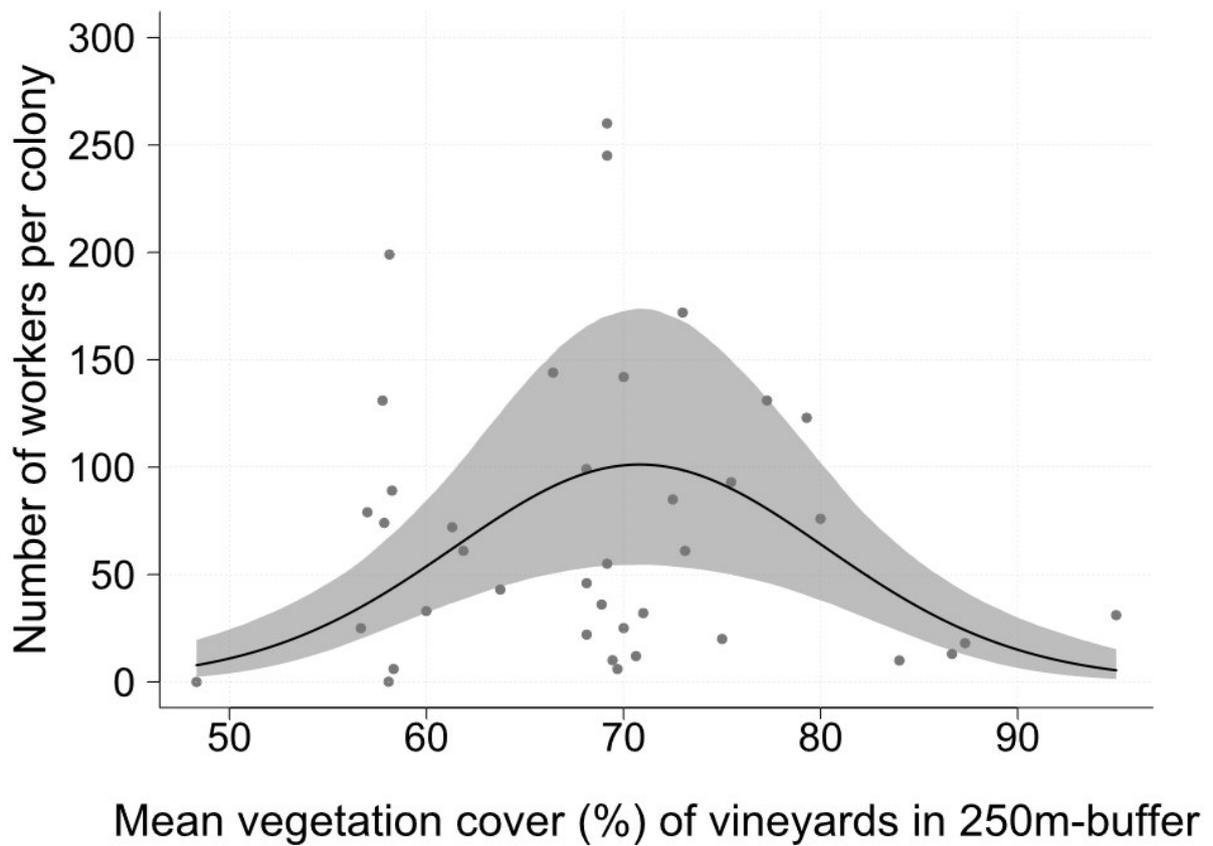


Figure 3 Quadratic effect of mean vegetation cover on number of workers per colony ( $-0.87 \pm 0.21$ ,  $z=3.94$ ,  $p<0.001$ ) with an optimum at about 70% of vegetation cover on a vineyard field scale.

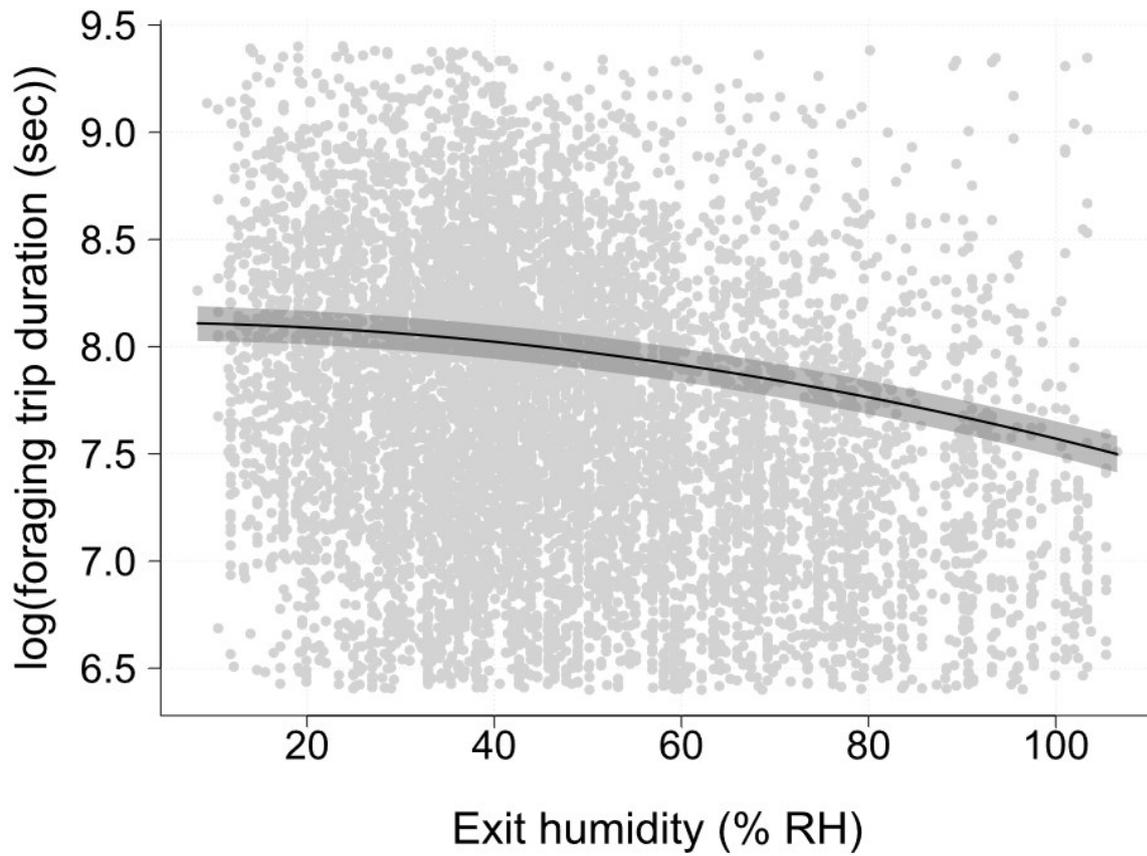


Figure 4 Quadratic effect of humidity when a bumblebee left the colony to forage on foraging trip duration ( $-0.04 \pm 0.006$ ,  $t=6.94$ ,  $p<0.001$ ). The lower the relative humidity, the longer the foraging trip of a bumblebee.

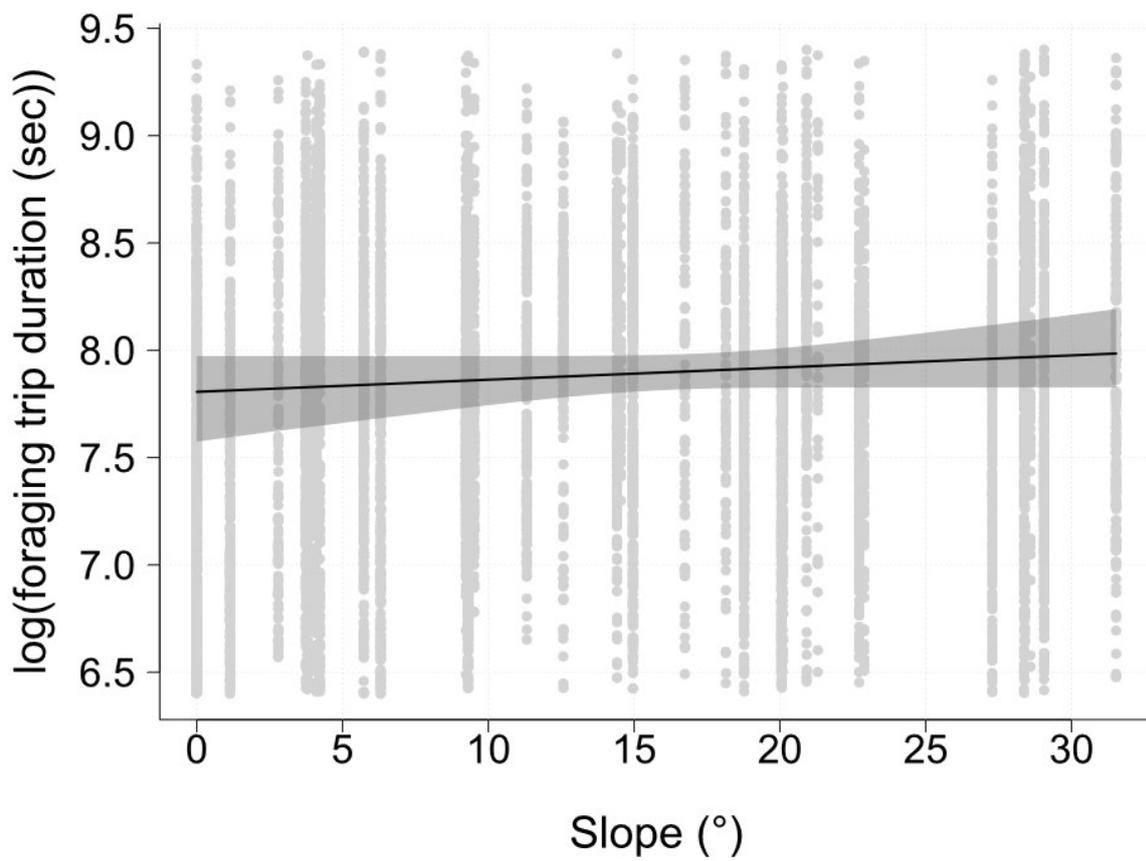


Figure 5 Positive relationship between slope and foraging trip duration ( $0.1 \pm 0.04$ ,  $t=2.66$ ,  $p=0.00783$ ).

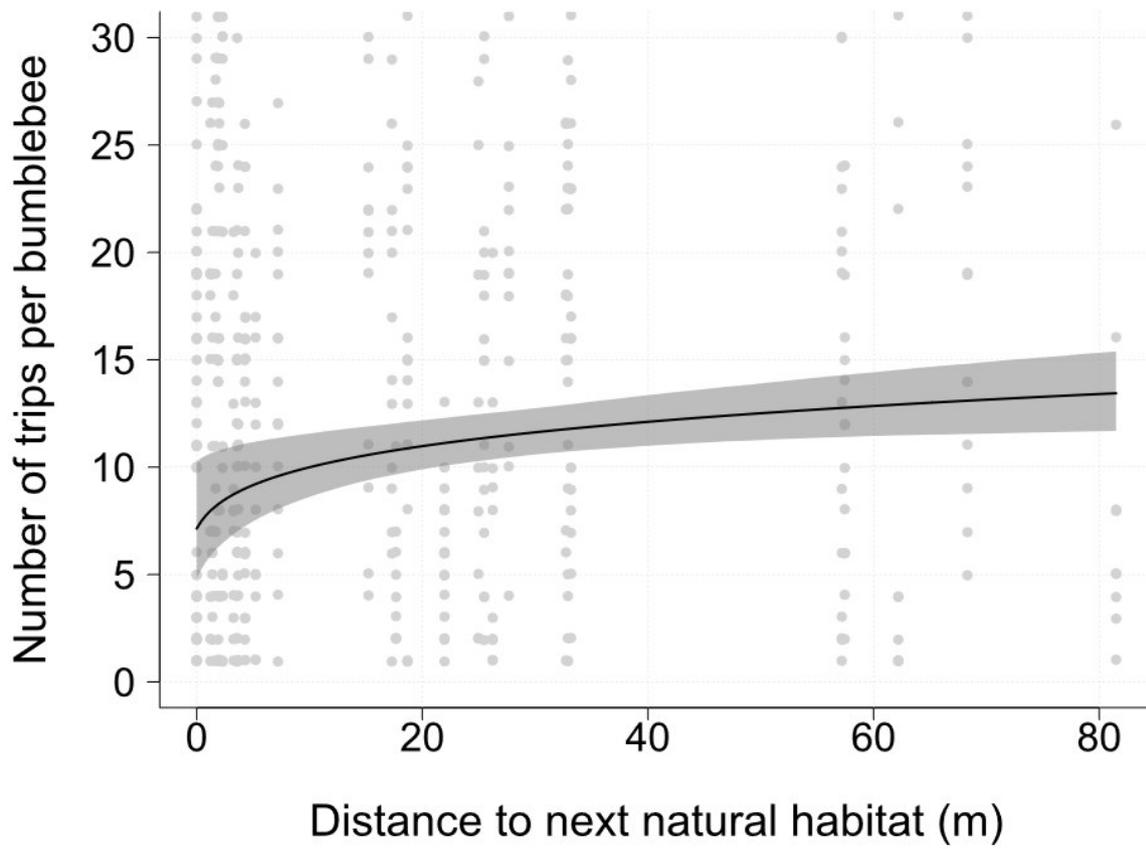


Figure 6 Positive relationship between distance to next natural habitat (m) and number of foraging trips per bumblebee in two days ( $0.13 \pm 0.05$ ,  $z=2.74$ ,  $p=0.006$ ).

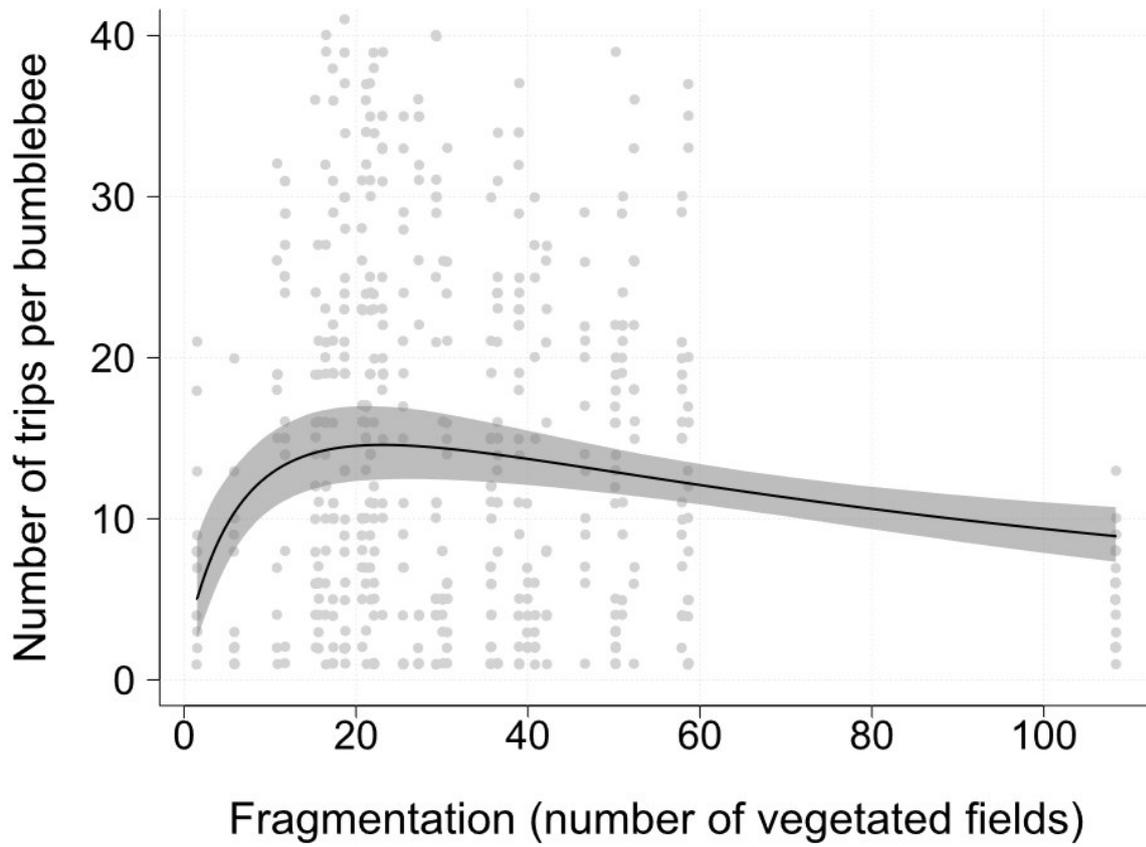


Figure 7 Quadratic effect of fragmentation (number of single vegetated vineyards) on number of foraging trips per bumblebee in two days ( $-0.18 \pm 0.05$ ,  $z=3.82$ ,  $p<0.001$ ). With a low fragmentation of about 20 vegetated vineyards, bumblebees do more trips.

## Supporting material

Table S 1 Univariate Models for weight gain. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, *t* and *p* values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>t value</b>	<b>p value</b>
<b>Weight gain</b>			
Vegetation cover	-9.01 $\pm$ 41.60	-0.217	0.829
(Vegetation cover) <sup>2</sup>	-52.76 $\pm$ 41.8	-1.263	0.207
Flower species richness	66.08 $\pm$ 39.9	1.656	0.098
Number of flowers	27.24 $\pm$ 41.6	0.655	0.513
<b>Flower cover</b>	87.59 $\pm$ 39.95	2.192	<b>0.028</b>
<b>Area of natural habitat</b>	-71.94 $\pm$ 39.33	-1.829	<b>0.067</b>
(Area of natural habitat) <sup>2</sup>	25.12 $\pm$ 40.42	0.621	0.534
Distance to natural habitat	17.87 $\pm$ 41.23	0.433	0.665
(Distance to natural habitat) <sup>2</sup>	-13.89 $\pm$ 41.89	-0.332	0.74
Fragmentation	-42.82 $\pm$ 41.12	-1.041	0.297
(Fragmentation) <sup>2</sup>	-7.93 $\pm$ 42.219	-0.188	0.851
Habitat amount	-52.39 $\pm$ 40.62	-1.29	0.197
(Habitat amount) <sup>2</sup>	5.89 $\pm$ 42.29	0.139	0.889
Fragmentation:Habitat amount	36.32 $\pm$ 45.1	0.805	0.42

Table S 2 Univariate models for number of pupal cells. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, z and p values are given.

Variables	Estimate $\pm$ SE	z value	p value
<b>Number of pupal cells</b>			
Vegetation cover	0.11 $\pm$ 0.18	0.629	0.53
<b>(Vegetation cover)<sup>2</sup></b>	-0.3 $\pm$ 0.13	-2.363	<b>0.018</b>
Flower species richness	0.15 $\pm$ 0.14	1.053	0.293
Number of flowers	0.09 $\pm$ 0.15	0.583	0.56
Flower cover	0.17 $\pm$ 0.15	1.189	0.234
Area of natural habitat	-0.19 $\pm$ 0.12	-1.567	0.117
(Area of natural habitat) <sup>2</sup>	0.13 $\pm$ 0.14	0.945	0.345
Distance to natural habitat	-0.08 $\pm$ 0.14	-0.624	0.533
(Distance to natural habitat) <sup>2</sup>	0.008 $\pm$ 0.14	0.057	0.955
Fragmentation	-0.12 $\pm$ 0.14	-0.856	0.392
(Fragmentation) <sup>2</sup>	0.03 $\pm$ 0.16	0.2	0.842
<b>Habitat amount</b>	-0.31 $\pm$ 0.12	-2.52	<b>0.012</b>
(Habitat amount) <sup>2</sup>	0.09 $\pm$ 0.15	0.642	0.521
<b>Fragmentation:Habitat amount</b>	0.23 $\pm$ 0.14	1.713	<b>0.087</b>

Table S 3 Univariate models for number of workers. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, z and p values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>z value</b>	<b>p value</b>
<b>Number of workers</b>			
Vegetation cover	0.13 $\pm$ 0.21	0.625	0.532
<b>(Vegetation cover)<sup>2</sup></b>	-3.89 $\pm$ 1.45	-2.671	<b>0.0076</b>
Flower species richness	0.08 $\pm$ 0.19	0.412	0.68
Number of flowers	0.05 $\pm$ 0.2	0.258	0.797
Flower cover	0.26 $\pm$ 0.2	1.314	0.189
<b>Area of natural habitat</b>	-0.36 $\pm$ 0.18	-1.929	<b>0.054</b>
(Area of natural habitat) <sup>2</sup>	-0.08 $\pm$ 0.19	-0.409	0.683
Distance to natural habitat	0.25 $\pm$ 0.19	1.253	0.21
(Distance to natural habitat) <sup>2</sup>	0.99 $\pm$ 1.28	0.776	0.438
Fragmentation	-0.24 $\pm$ 0.19	-1.221	0.222
(Fragmentation) <sup>2</sup>	-0.07 $\pm$ 1.23	-0.06	0.952
Habitat amount	-0.31 $\pm$ 0.2	-1.523	0.128
(Habitat amount) <sup>2</sup>	-0.44 $\pm$ 1.24	-0.36	0.719
<b>Fragmentation:Habitat amount</b>	0.31 $\pm$ 0.21	1.481	<b>0.139</b>

Table S 4 Univariate models for foraging trip time. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, *t* and *p* values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>t value</b>	<b>p value</b>
<b>Foraging trip time</b>			
Vegetation cover	0.02 $\pm$ 0.04	0.4	0.685
(Vegetation cover) <sup>2</sup>	0.03 $\pm$ 0.04	0.68	0.4993
Flower species richness	-0.05 $\pm$ 0.04	-1.45	0.146
Number of flowers	-0.03 $\pm$ 0.04	-0.67	0.5017
Flower cover	-0.01 $\pm$ 0.04	-0.3	0.765
Area of natural habitat	0.004 $\pm$ 0.04	0.12	0.9047
(Area of natural habitat) <sup>2</sup>	0.07 $\pm$ 0.03	2.12	0.0343
Distance to natural habitat	-0.05 $\pm$ 0.04	-1.36	0.174
(Distance to natural habitat) <sup>2</sup>	-0.03 $\pm$ 0.04	-0.73	0.4663
Fragmentation	0.002 $\pm$ 0.03	0.06	0.9506
(Fragmentation) <sup>2</sup>	0.05 $\pm$ 0.03	1.53	0.1251
Habitat amount	-0.03 $\pm$ 0.04	-0.69	0.488
(Habitat amount) <sup>2</sup>	0.05 $\pm$ 0.04	1.23	0.2195
Fragmentation:Habitat amount	0.02 $\pm$ 0.03	0.72	0.4712
<b>Slope</b>	0.09 $\pm$ 0.04	2.52	<b>0.01167</b>
<b>Humidity</b>	-0.17 $\pm$ 0.006	-27.38	<b>&lt;0.001</b>
<b>(Humidity)<sup>2</sup></b>	-0.04 $\pm$ 0.006	-6.93	<b>&lt;0.001</b>

Table S 5 Univariate models for sum of foraging trip time per bumblebee. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, *t* and *p* values are given.

Variables	Estimate $\pm$ SE	t value	p value
<b>Sum of foraging trip time per bumblebee</b>			
Vegetation cover	-9.63 $\pm$ 30.99	-0.311	0.756
(Vegetation cover) <sup>2</sup>	-27.05 $\pm$ 30.95	-0.874	0.3821
Flower species richness	15.74 $\pm$ 31.03	0.507	0.612
Number of flowers	45.03 $\pm$ 31.15	1.445	0.1483
Flower cover	-2.76 $\pm$ 31.71	-0.087	0.9306
Area of natural habitat	-17.29 $\pm$ 30.73	-0.563	0.5736
(Area of natural habitat) <sup>2</sup>	-13.96 $\pm$ 31.18	-0.448	0.6544
Distance to natural habitat	36.19 $\pm$ 30.98	1.168	0.2427
(Distance to natural habitat) <sup>2</sup>	2.27 $\pm$ 31.767	0.071	0.9431
Fragmentation	7.07 $\pm$ 30.31	0.233	0.8157
<b>(Fragmentation)<sup>2</sup></b>	<b>-67.05 <math>\pm</math> 28.47</b>	<b>-2.355</b>	<b>0.01851</b>
Habitat amount	24.75 $\pm$ 31.11	0.796	0.4263
(Habitat amount) <sup>2</sup>	-10.89 $\pm$ 31.45	-0.346	0.7291
<b>Fragmentation:Habitat amount</b>	<b>-56.54 <math>\pm</math> 31.21</b>	<b>-1.812</b>	<b>0.07005</b>
<b>(Fragmentation)<sup>2</sup>:Habitat amount</b>	<b>-76.83 <math>\pm</math> 45.89</b>	<b>-1.674</b>	<b>0.09408</b>
Slope	-9.06 $\pm$ 31.63	-0.286	0.7746
Mean humidity	19.86 $\pm$ 31.43	0.632	0.5274
Mean Temperature	-40.08 $\pm$ 30.8	-1.301	0.1932

Table S 6 Univariate models for number of foraging trips per bumblebee. The variables highlighted in bold entered the full model. Estimated coefficients  $\pm$  standard error, z and p values are given.

<b>Variables</b>	<b>Estimate <math>\pm</math> SE</b>	<b>z value</b>	<b>p value</b>
<b>Number of foraging trips per bumblebee</b>			
Vegetation cover	-0.04 $\pm$ 0.06	-0.64	0.52
(Vegetation cover) <sup>2</sup>	-0.07 $\pm$ 0.06	-1.11	0.267
Flower species richness	0.07 $\pm$ 0.06	1.11	0.266
Number of flowers	0.11 $\pm$ 0.07	1.56	0.118
Flower cover	0.02 $\pm$ 0.06	0.24	0.81
Area of natural habitat	-0.04 $\pm$ 0.06	-0.66	0.507
(Area of natural habitat) <sup>2</sup>	-0.09 $\pm$ 0.06	-1.39	0.165
<b>Distance to natural habitat</b>	0.14 $\pm$ 0.06	2.26	<b>0.0236</b>
(Distance to natural habitat) <sup>2</sup>	0.01 $\pm$ 0.06	0.21	0.8312
Fragmentation	0.009 $\pm$ 0.06	0.14	0.892
<b>(Fragmentation)<sup>2</sup></b>	-0.19 $\pm$ 0.05	-3.45	<b>&lt;0.001</b>
Habitat amount	0.07 $\pm$ 0.06	1.07	0.284
(Habitat amount) <sup>2</sup>	-0.07 $\pm$ 0.06	-1.14	0.256
<b>Fragmentation:Habitat amount</b>	-0.12 $\pm$ 0.06	-1.93	<b>0.0531</b>
(Fragmentation) <sup>2</sup> :Habitat amount	-0.09 $\pm$ 0.08	-1.12	0.263
Slope	-0.09 $\pm$ 0.06	-1.34	0.18
<b>Mean humidity</b>	0.1 $\pm$ 0.06	1.7	<b>0.09</b>
Mean Temperature	-0.06 $\pm$ 0.06	-1.05	0.295

*Figure S 1 Bumblebee hive with wooden roof and cardboard box attached to the entrance.*



Figure S 2 Forty study sites, distributed along the Rhône valley from Martigny to Visp (map.geo.admin.ch).

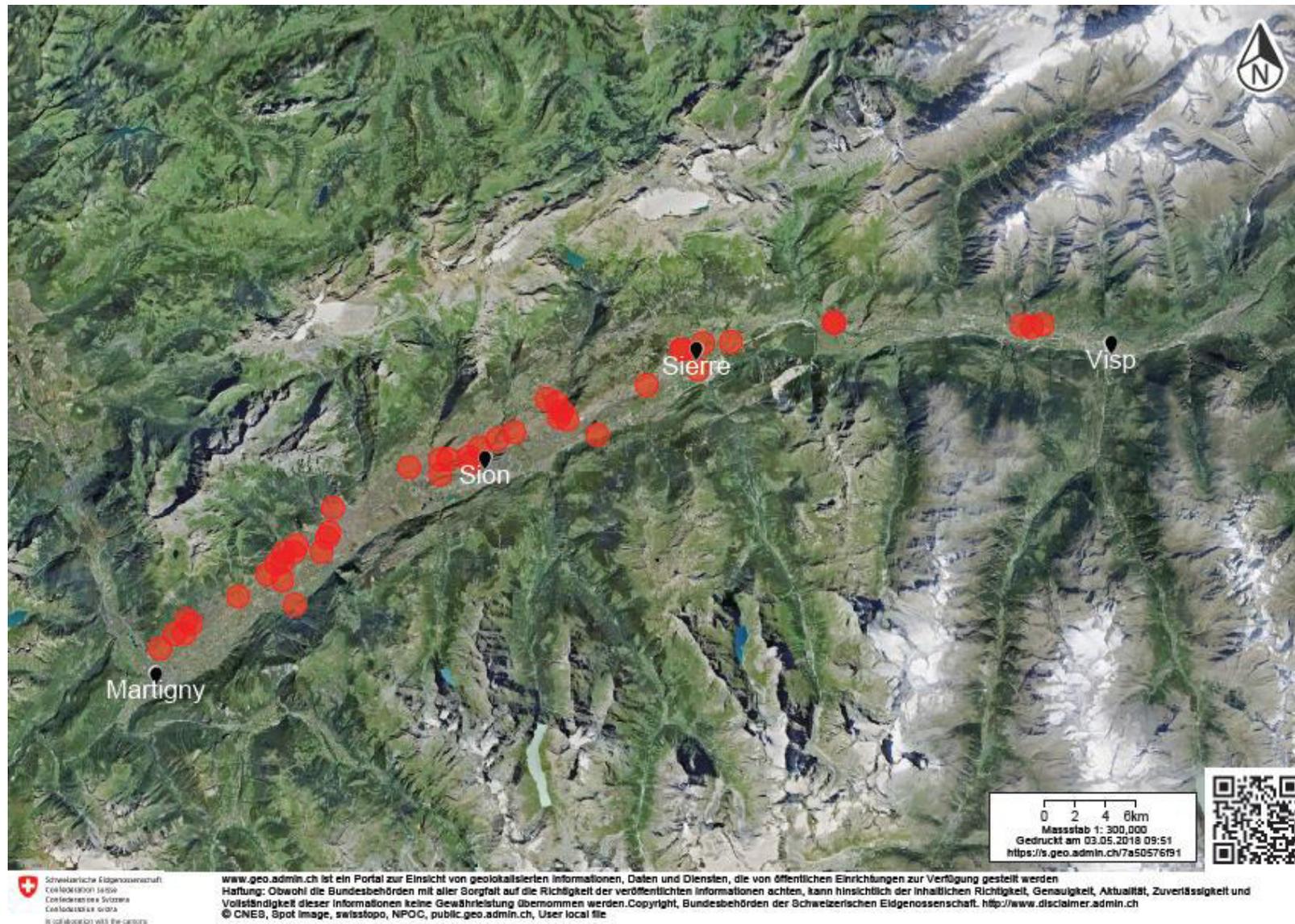
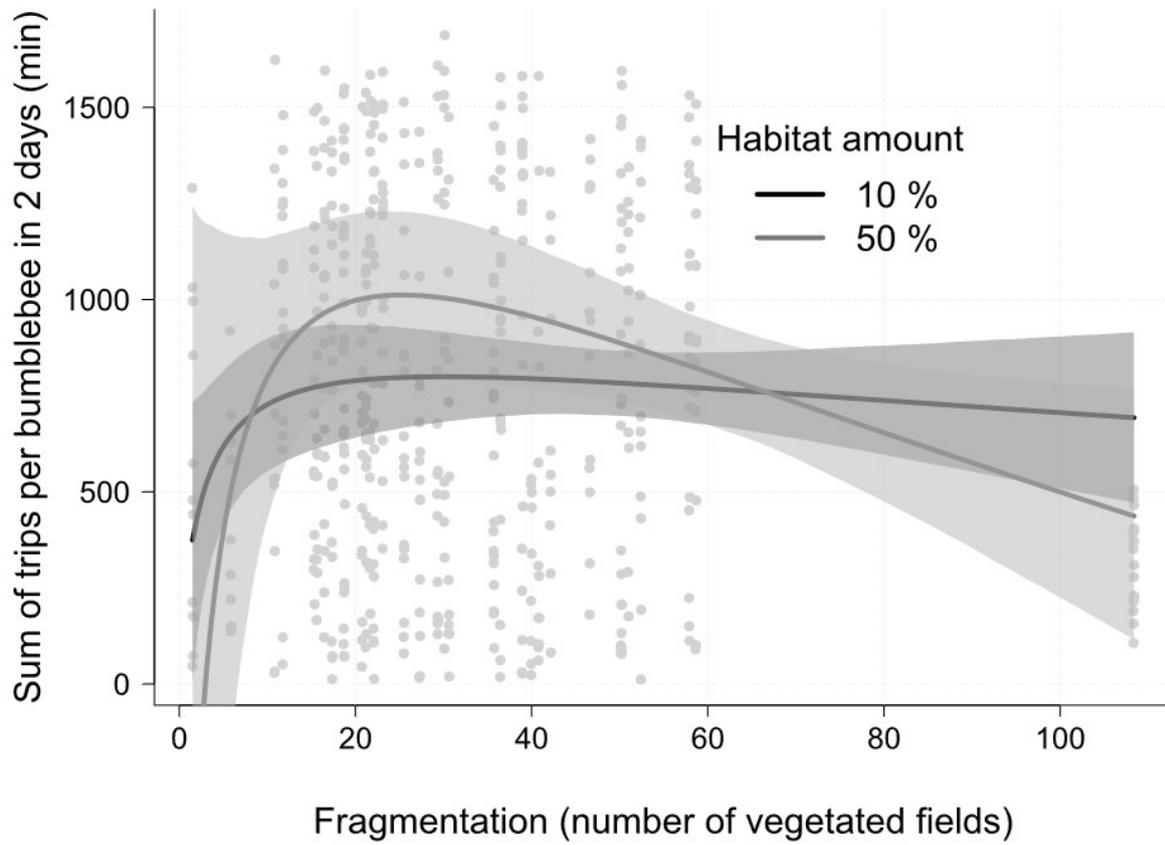


Figure S 3 Interactive effect of the quadratic term of fragmentation and habitat amount on sum of foraging trips per bumblebees in two days (min) ( $-77.06 \pm 45.95$ ,  $t=-1.68$ ,  $p=0.094$ ). With a high habitat amount of 50% in a 250 m-buffer zone, highest sum of foraging trips is at a higher fragmentation than with low habitat amount of 10%.



## Declaration of consent

on the basis of Article 28 para. 2 of the RSL05 phil.-nat.

Name/First Name: Maurer Corina

Matriculation Number: 13-120-050

Study program: MSc in Ecology and Evolution with specialization in Animal Ecology and <sup>+</sup>

Bachelor  Master  Dissertation

Title of the thesis: Effects of habitat amount and fragmentation in vineyards on  
bumblebee colony fitness and foraging behaviour

Supervisor: Dr. A. Jacot, Prof. R. Arlettaz

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 para. 1 lit. r of the University Act of 5 September, 1996 is authorised to revoke the title awarded on the basis of this thesis. I allow herewith inspection in this thesis.

Lyss, 18.08.2018

Place/Date

C. Maurer

Signature