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RESEARCH ARTICLE

Habitat area and local habitat conditions outweigh fragmentation effects on insect communities in vineyards

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Abstract

1. Fragmentation of habitat, for example by intensive agricultural practices, can be detrimental to local biodiversity. However, it often remains unclear whether such biodiversity declines are caused by loss of habitat area or increased fragmentation, and how habitat quality factors into it. In our study system, vegetated vineyards are typically small, and isolated from one another, potentially limiting the distribution and dispersal of organisms.
2. In a full-factorial experiment of a priori selected vegetated vineyard patches of differing size and fragmentation, we aimed to disentangle the effects of habitat area (area of vegetated vineyards), habitat fragmentation (number of vegetated vineyards per 100 ha) and field-scale ground vegetation density on ground beetle, leafhopper and wild bee communities using a combined framework of multiscale and multispecies modelling (Hierarchical Model of Species Communities).

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3. We demonstrate variable effects of habitat area, fragmentation and local ground vegetation density on the three insect groups: Increased habitat area at fine scales favours higher species richness of leafhoppers, while local vegetation density boosts species richness of both leafhoppers and ground beetles, whereas no community-level responses were detected for wild bees.
4. We conclude that increased ground vegetation density at both field and landscape scales (i.e. higher habitat area) favours more diverse and abundant insect communities, while fragmentation effects are highly variable and species specific. In addition, our results highlight that mainly ground beetles and leafhoppers will benefit from simple ground greening measures in vineyards, while for wild bees environmental factors other than the ones tested here may drive community structure.
5. We recommend increasing the number and area of vegetated vineyards (even at small spatial scales) requiring more nature-friendly farming practices especially regarding a reduction or renunciation from herbicide applications, while the within-field vegetation density should optimally be intermediate or high to favour a diverse insect community.

KEYWORDS

agriculture, ground beetles, ground vegetation, Hierarchical Model of Species Communities (HMSC), joint species distribution models, leafhoppers, vineyards, wild bees

1 | INTRODUCTION

There is broad consensus that habitat loss and fragmentation resulting from anthropogenic land-use change and urbanization are major causes of declines and contractions in wildlife populations (Haddad et al., 2015; Sánchez-Bayo & Wyckhuys, 2019; Tilman et al., 2017). One major driver of habitat loss and fragmentation is the ongoing transformation of complex, heterogeneous habitats into simplified and intensively managed agricultural systems to feed a growing global human population (Tilman et al., 2002). Habitat fragmentation reduces the connectivity and, in many cases, the quality of habitat patches (Chase et al., 2020), which may become too small to sustain local populations (Fahrig, 2003; MacArthur & Wilson, 1967).

Because habitat fragmentation in cultivated landscapes is almost always associated with habitat loss, the relative influences of habitat area, habitat fragmentation and habitat quality on biodiversity responses are difficult to disentangle (Thompson & McGarigal, 2002). It has nonetheless been hypothesized that species richness is driven mainly by habitat area rather than habitat configuration (the habitat amount hypothesis; Fahrig, 2013). This hypothesis has since been tested extensively, revealing variable results for a range of taxa, where, for example, both habitat area and fragmentation influenced plant species richness (Haddad et al., 2017), bird occurrence (Bosco et al., 2021), invertebrate abundance (Bosco, Wan, et al., 2019) or bumblebee colony fitness (Maurer et al., 2020), while a global review on species densities showed support for the habitat amount hypothesis (Watling

et al., 2020). Furthermore, a recent simulation study revealed complex interactive effects of habitat loss and fragmentation on species diversity (Rybicki et al., 2020).

In general, fragmentation tends to increase species diversity at the landscape scale when the total habitat area is large, in accordance with the known benefits of habitat heterogeneity (Benton et al., 2003; Stein et al., 2014; Weibull et al., 2000). When the total habitat area is small, however, fragmentation may instead reduce species diversity (Rybicki & Hanski, 2013). Recent findings further indicate that the relative importance of habitat area and fragmentation depends on the study system, the species and measured response metric, and the scale of analysis (Bosco, Wan, et al., 2019; Rybicki et al., 2020; Zeller et al., 2012). In addition, species traits are known to influence species-level responses to habitat loss and fragmentation including, for example, dispersal abilities, trophic level and habitat specialization (Ewers & Didham, 2006), but also plant survival or growth patterns (Tremlová & Münzbergová, 2007).

Recently, rapid and steep insect declines driven by, inter alia, habitat loss and fragmentation have been reported in numerous studies (Sánchez-Bayo & Wyckhuys, 2019; van Klink et al., 2020; Wagner et al., 2021). Hence, using insects as model organisms is not only crucial for understanding fundamental ecological concepts such as these of habitat area and fragmentation, but is also pivotal from an insect conservation, and ecosystem service provisioning point of view. In this study, we thus aimed to disentangle the effects of habitat area, fragmentation, and field-scale habitat condition on insect communities

representing different trophic levels and ecosystem services, namely carabid beetles, leafhoppers and wild bees. We used a factorial design (sensu Bosco, Arlettaz, et al., 2019), ensuring both the habitat area and fragmentation gradients were sufficiently covered (Thompson & McGarigal, 2002), in combination with multiscale optimization and joint species distribution modelling (Hierarchical Model of Species Communities [HMSC]; Ovaskainen et al., 2017; Tikhonov et al., 2020). Our study system is a highly contrasted vineyard agro-ecosystem in Southern Switzerland, where we considered vegetated vineyards to be suitable habitat, while bare vineyards constituted the matrix based on earlier findings on invertebrates in Southern Swiss vineyards (Bosco, Arlettaz, et al., 2019; Bosco, Wan, et al., 2019; Maurer et al., 2020). Thus, habitat area refers to the percentage of area covered by vegetated vineyards and fragmentation to the number of separate patches of vegetated vineyards in a given buffer area. We sought to answer the following questions: (i) What are the separate and interdependent effects of fragmentation and habitat area on the three insect communities and what role does within-field ground vegetation density play? (ii) Do species traits and phylogeny explain their responses to habitat area, fragmentation and ground vegetation density?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in eight different landscapes in the canton of Valais, SW Switzerland (Figure 1). The study landscapes (between Fully 46°08' N 7°07' E and Varen 46°19.20' N 7°36.47' E; 480–780 m a.s.l.) constitute the largest continuous vineyard areas in this region. About 70%–80% of the vineyards are intensively managed and support virtually no ground vegetation cover due to regular herbicide application, whereas the remaining 20%–30% are cultivated through more environmentally friendly management practices, promoting the growth of ground vegetation (Arlettaz et al., 2011; Bosco, Wan, et al., 2019). In many cases, vineyards with ground vegetation were also managed more extensively with regard to pesticide and, obviously, herbicide applications—sometimes even under an organic or biodynamic regime which have been shown to be beneficial for invertebrates compared to conventional management (Bosco et al., 2022). At the landscape level, these two management regimes represent a near binary system (vegetated vineyards as habitat versus bare ground vineyards as surrounding matrix; Figures 1, S2 and S3), presenting a system well suited to evaluating the influence of vineyard ground cover at a field scale, and habitat area and fragmentation at larger scales (Bosco, Wan, et al., 2019). Furthermore, the fields represent uniformly managed units, with ground vegetation densities and cultivation practices that are distinct from those of neighbouring fields, and mostly independent of underlying environmental gradients because they reflect the farmers' management practices, and hence resemble a quasi-experimental setup (sensu McGarigal & Cushman, 2002).

2.2 | Factorial sampling design to disentangle the effects of habitat area and fragmentation

We used a factorial, stratified sampling design to disentangle the effects of habitat area and fragmentation and to ensure that insect sampling was well distributed across these two gradients, as suggested by McGarigal and Cushman (2002). See Bosco, Wan, et al. (2019) for detailed description of the study design. In brief, we calculated the metrics patch density as a measure of fragmentation (PD; the number of vegetated vineyard patches per 100 ha) and percentage of landscape (PLAND) as a measure of vegetated vineyard habitat area with FRAGSTATS (McGarigal, 2015) using a moving window of 150 m radius (Bosco et al., 2019). The lower and upper 40% of patch density and habitat area values were used to represent relatively low and high levels of habitat area and fragmentation, respectively, creating four classes (Table S1). We included bare fields (defined as those with <40% ground vegetation density) as a fifth sampling class (Bosco et al., 2019), to be able to detect field-scale effects of vegetated versus bare management modes. Across eight landscapes, we sampled 120 vineyard fields in total, with 15 fields per landscape.

2.3 | Ground beetle sampling

Ground beetle (GB) sampling was conducted twice in 2015 in four landscapes ($4 \times 15 = 60$ fields; Table S9) during late April and late May, with a sampling duration of 1 week per sampling session. Given the relatively small size of our selected vineyard fields (average = 0.41 ± 0.09 ha), sampling was carried out with two pitfall traps per field (500-ml plastic cup with 7.5 cm diameter), each being a quarter filled with a mixture of water and ethylene glycol (1:1) and a scentless detergent to reduce water surface tension. After each trapping session, we collected the traps from the fields and stored the trapped specimens in 70% ethanol. We recorded the number of carabid specimens in each trap and identified them to species level using identification guides (Müller-Motzfeld, 2004; Table S3). Traps from the same field were pooled for analysis, resulting in one sample per field, that is 120 trap samples. Out of those, 15 (12.5%) were damaged or missing (either one or both traps per field) and thus discarded from the dataset. There was no apparent bias in kept versus discarded samples related to ground vegetation density, habitat area, patch density, sampling period or location of the fields (see Figure S4). To account for trait-specific responses to habitat area, patch density and vegetation cover, we included traits related to movement ability (measured as mean adult body size) and habitat strictness (based on Müller-Motzfeld, 2004) for ground beetles (see details in Table S2).

2.4 | Wild bee and leafhopper sampling

Leafhopper (LH) and wild bee (WB) sampling was conducted in 2016 in all eight landscapes (120 fields; Table S9) during one session in June

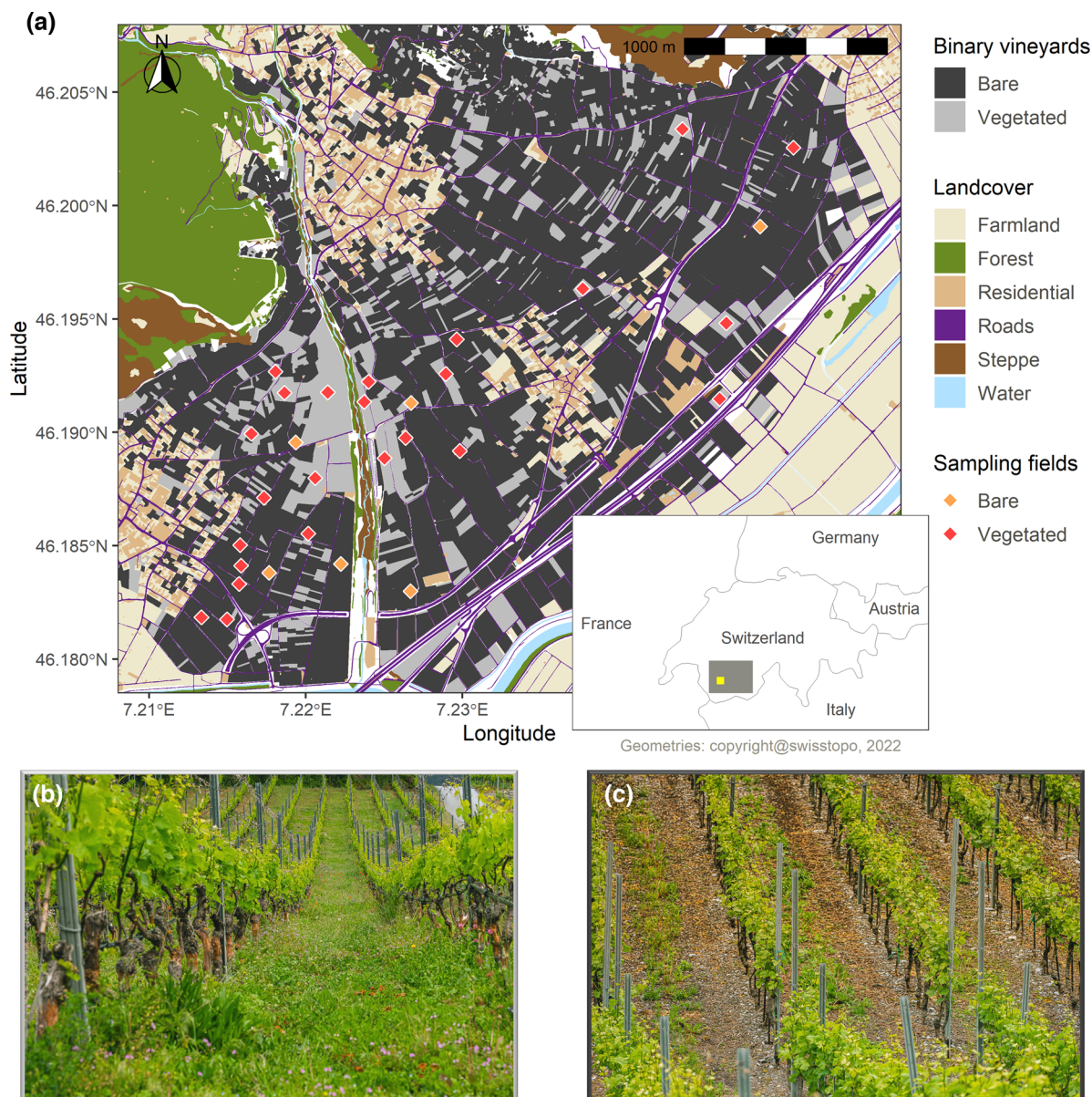


FIGURE 1 Example of the study area with (a) a zoom-in to two of our eight landscapes in our study area in SW Switzerland (Chamoson and Leytron), showing the sampling fields in vegetated (red points) and bare (orange points) vineyards, the binary nature of bare versus vegetated vineyard fields typical for the entire vineyard area in the region and the major surrounding land cover types. The inset map shows the location of the study area in Switzerland (grey box) and the zoom-in landscapes (yellow square). Farmland refers to agricultural area other than vineyards and mainly includes orchards and grasslands. The bottom images show typical examples of (b) vegetated and (c) bare ground vineyards (image copyright © C. Pfammatter and Naturpark Pfyn-Finges). A map of the full study area with sampling points is given in Figure S1.

(between 5 June 2016 and 29 June 2016), with a sampling duration of 3 days. Sampling was carried out with one pan trap per vineyard field, where one trap consisted of three coloured bowls with one blue, one yellow and one white bowl according to recommended sampling methods in the literature (Campbell & Hanula, 2007). The bowls were 13 cm in diameter and 12 cm deep, filled with soapy water and fixed on a wooden pole 1 m above ground. Out of 120 trap samples, four (3.3%) were damaged or missing and thus discarded from the dataset. We recorded the number of wild bee and leafhopper specimens in each trap and identified them to species level using identification guides (Amiet et al., 2001; Amiet et al., 1999; Biedermann

& Niedringhaus, 2004; Holzinger et al., 2003; Tables S4 and S5). Note that among wild bees, we grouped species belonging to the *Halic-tus simplex* group. Bowls belonging to the same trap were pooled for the analysis. As well as wild bees, we included domesticated honeybees (*Apis mellifera*) to detect potential different responses to vineyard management and landscape configurations as compared to wild bees. Similar as for ground beetles, we included habitat strictness and mean adult body size for leafhoppers (Biedermann & Niedringhaus, 2004; Holzinger et al., 2003), and pollen resources, and nesting location as traits for wild bees (Amiet et al., 1999, 2001, 2004, 2007, 2010) (see details in Table S2). No permits to sample

insects were needed and access to vineyards was kindly permitted by viticulturists.

2.5 | Environmental variables

At both pitfall and pan trap sample sites, vineyard ground vegetation density was visually estimated in 2015 and 2016 during the sampling sessions as the average vegetation density (%) across the entire vineyard field, that is including vine rows and inter rows (hereafter vegetation density; see Figures S2 and S3). To model habitat area and patch density as continuous predictors (rather than discrete classes used for the sampling design), and to allow a scale-explicit analysis from local to landscape scales, we quantified habitat area and patch density at 10 spatial scales ranging from 50 to 500 m in 50-m increments (Bosco, Wan, et al., 2019). Note that while ground vegetation density represents the mean vegetation density per vineyard field, habitat area (PLAND) represents the percentage of land area that was covered by vineyards that were classified as vegetated, irrespective of their within-field vegetation density.

2.6 | Statistical analyses

2.6.1 | Joint species distribution models

We analysed the data with Hierarchical Model of Species Communities (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017), a joint species distribution modelling framework (Warton et al., 2015). The advantages of HMSC include the fact that it allows observed variation in species occurrences and abundances to be partitioned into components related to environmental variation versus random processes (or unmeasured variation) at various spatial or temporal scales, ecological inference at both the species and community levels, and the modelling of relatively rare species (Ovaskainen et al., 2017), to name just a few.

The entire species dataset consisted of counts of 40 ground beetle species, 20 leafhopper species and 43 wild bee species (including honeybees). Because the study design and sampling effort differed between the three groups, we analysed them separately. We used the individual sampling sessions as the sampling unit, resulting in 105 ground beetle samples, and 116 unique leafhopper and wild bee samples.

Due to the zero-inflated nature of the response data, we modelled the occupancies and abundances of the species per insect group with a hurdle model structure, that is species occupancies were modelled with a presence-absence model (*probit* regression), and log-transformed species abundances within which each species was present were modelled with a normal model, after standardization to zero mean and unit variance. Within each insect group, we excluded species encountered in fewer than five samples (Trivellone et al., 2017), and thus retained $n_s = 15$ ground beetle species, $n_s = 8$ leafhopper species and $n_s = 11$ wild bee species in the presence-absence models. Many of these species had limited abundance variation across samples. Hence, we

applied the following criterion for species inclusion in the abundance models: apart from the most common abundance value (i.e. the mode), there had to be at least five other abundance values in the data. This resulted in the inclusion of eight ground beetle, nine leafhopper and seven wild bee species in the abundance models.

For each insect group, we preselected a single 'best' spatial scale of both, habitat area and patch density from the measured 10 spatial scales (McGarigal et al., 2016). To do so, we correlated each scale of habitat area and patch density with the first two axes of a principal coordinates analysis (PCoA) ordination of Bray-Curtis dissimilarity (*vegdist* and *cdmscale* functions in R package *vegan*; Oksanen et al., 2013; Tables S6–S8; Figure S5) and chose the best scale according to highest correlation values. These preselected scales of habitat area and patch density, and their interaction, were then combined with ground vegetation density as fixed effects in subsequent modelling. Vegetation density was modelled with a second-order polynomial function to allow for nonlinear responses.

We included several life-history and morphological traits to examine how much of the variation in species' responses to the covariates was explained by their trait differences (see above and Table S2). For leafhoppers, the trait data were included in the occurrence models only, because just two taxa were included in the abundance models. To examine whether closely related taxa respond more similarly to their environment than expected based on their traits, we assumed that the residual variation in species responses is potentially phylogenetically structured (Ovaskainen et al., 2017). Cladograms comprising various levels of taxonomic identifications were used as proxies of the phylogenetic relatedness (see Table S2). Equal branch lengths were assumed at each taxonomic level of the trees. For leafhoppers, the cladograms were used in the occurrence models only. To account for the fact that ground beetle samples were collected twice, we included the sampling month as a random effect, as well as a spatially explicit random effect modelling variation across sample locations. For leafhopper and wild bee data, all 116 samples were from unique locations, and we included a spatially explicit random effect only.

2.6.2 | Fitting the models

We fitted the occurrence and abundance models with the *Hmsc* 3.0 R package (Tikhonov et al., 2020) assuming the default prior distributions. We sampled the posterior distribution with four MCMC chains of 375,000 iterations, of which the first 125,000 were removed as burn-in. The iterations were thinned by 1000 to yield 250 posterior samples per chain, and thus 1000 posterior samples in total. For each model, we used the potential scale reduction factors (psrf) to explore model convergence. Approximate convergence is diagnosed when the upper limit of the psrf is close to 1. We examined the explanatory and predictive powers of the *probit* models through species-specific area-under-the-curve (AUC) values and coefficients of discrimination (Tjur R^2), which measure how well the model discriminates between occupied and unoccupied sampling units. The explanatory and predictive powers of the log-linear abundance models were measured by

coefficients of determination (R^2). To compute explanatory power, we calculated model predictions based on models fitted to all the data. To compute predictive power, we performed a fivefold cross-validation, assigning the sampling units randomly across sample sites to five folds. Predictions for each fold were based on a model fitted to data on the remaining four folds. To quantify the drivers of community structure, we partitioned explained variation among the fixed and random effects included in the model.

Predictions of expected species richness on each environmental gradient were generated by summing the predicted occurrence probabilities of all insect species at each of 20 uniformly distributed points along the gradient. The values of the non-focal environmental covariates were fixed at their observed mean value; hence, these represent marginal effects predictions. We predicted expected species richness for 1000 parameter values sampled from the posterior distribution, allowing us to visualize both the posterior mean prediction and its parameter uncertainty.

3 | RESULTS

The final datasets included a total of 698 ground beetle, 163 leafhopper and 450 wild bee individuals. On average, 7 ± 0.8 (mean \pm SE) ground beetle, 1.5 ± 0.2 leafhopper and 4 ± 0.4 wild bee individuals (range GB: 0–46; LH: 0–16; WB: 0–22), and 3 ± 0.2 ground beetle, 0.75 ± 0.1 leafhopper and 2 ± 0.2 wild bee species (range GB: 0–9; LH: 0–5; WB: 0–7) were caught per field. Among ground beetles, four species constituted >65% of the total counts (*Brachinus crepitans*, *Harpalus tardus*, *Calathus fuscipes* and *Harpalus honestus*), while for leafhoppers there was one predominant species (*Anacraga gallia ribauti*, >35%). Four species comprised >60% of the wild bee counts: *Ceratina cucurbitina*, *Lasioglossum tricinctum*, *H. simplex* and *A. mellifera* (Tables S3–S5).

For all three insect groups, a relatively broad-scale measure of patch density (450 m scale) was selected for inclusion in the HMSC models. This was combined with a fine-scale measure of habitat area in ground beetles (50 m) and leafhoppers (100 m) but a broader scale measure of habitat area (500 m) for wild bees (see Tables S6–S8 and Figure S5).

3.1 | Model convergence and fit

The MCMC convergence of the models was good, as indicated by potential scale reduction factors (psrf) for the β -parameters close to 1 for all three insect groups (ground beetle occurrences maximum psrf = 1.06, abundances = 1.02; leafhopper occurrences = 1.05, abundances = 1.03; wild bee occurrences = 1.03, abundances = 1.01). For the occurrence models, mean Tjur R^2 values were highest for leafhoppers, followed by ground beetles, then wild bees (Table 1), while AUC values were lower for ground beetles than the other two insect groups (ground beetles: 0.80 ± 0.09 , leafhoppers: 0.87 ± 0.11 , wild bees:

0.86 ± 0.08). The discriminatory ability of the occurrence models varied widely among species (Table 1). Predictive power based on fivefold cross-validation was highest for leafhopper occurrences (mean Tjur $R^2 = 0.09$, mean AUC = 0.74), but predictability of the occurrences of most ground beetle and wild bee species was very poor (mean Tjur R^2 and AUC values were 0.03 and 0.55 for ground beetles and 0.00 and 0.48 for wild bees, respectively). For species abundances, mean R^2 values based on cross-validation were also close to random expectation at 0.04, -0.12 and 0.03 for ground beetles, leafhoppers and wild bees, respectively. This implies that the distributions and especially the abundances of most species within these insect groups cannot be reliably predicted with the current environmental parameters alone (the best predicted species are listed in section 2.3 in the Supporting Information), while explanatory power was reasonably good.

3.2 | Effects of habitat area, fragmentation and ground vegetation density

For ground beetles and leafhoppers, the independent contributions of patch density to explained variance in both species occurrences and abundances were smaller than those of the other covariates. For wild bees, however, the mean contributions of each of the modelled covariates to explained variance, including the interaction between habitat area and patch density, were similar (Table 1; Figure 2).

3.2.1 | Species richness and overall abundance

Ground beetle species richness was predicted to increase with local vegetation density (Figure 3a), while ground beetle abundance did not show a consistent trend on any gradient. Leafhopper species richness peaked at intermediate to high vegetation densities and habitat area (Figure 3a,b), but was not influenced by patch density, or its interaction with habitat area. Within occupied sites, leafhopper abundances were not detectably related to either vegetation density or to the habitat structure variables. Overall species richness and abundance of wild bees were not detectably related to any of the tested variables (Figure 3), while there were several species-specific effects (Figure S8).

3.2.2 | Species-specific responses

The occurrences of eight ground beetle species and the abundances of six species were positively related to vegetation density. The occurrences and abundances of one ground beetle species were predicted to respond clearly to increasing habitat area (positive and negative relationships for occurrence and abundance, respectively). One beetle species showed a negative occurrence response to increasing patch density (see Figure S6). For one species (*Calathus fuscipes*), there was support for an interaction between habitat area and patch density on species occurrences, suggesting that the importance of absolute

TABLE 1 Explained variance quantified by Tjur R^2 for occurrence models (occ); R^2 for abundance models (abu) and variation among species given as standard deviation (SD) and value ranges per insect group

Group	Model	R^2	SD (range)	Fixed effects (%)				Random effects (%)	
				HA	PD	HA:PD	Vegetation	Site	Month
GB	occ	0.14	0.13 (0.03–0.50)	2.7	1.0	2.1	2.2	4.7	1.4
	abu	0.37	0.24 (0.11–0.79)	8.1	3.0	6.9	9.0	5.5	4.3
LH	occ	0.19	0.17 (0.05–0.51)	3.8	1.9	2.8	3.4	7.2	–
	abu	0.35	0.20 (0.20–0.49)	5.8	5	9.3	7.3	7.4	–
WB	occ	0.10	0.06 (0.02–0.18)	1.3	1.2	2.4	1.0	3.6	–
	abu	0.57	0.18 (0.36–0.88)	9.9	9.6	13.9	11.1	12.1	–

Note: Mean variance (%) explained by habitat area (HA), patch density (PD), their interaction and vegetation density, and random effects are given. See also Figure S2.

habitat area may decline as the number of habitat patches in the surroundings increases, and vice versa (Figure S9).

All leafhopper species were predicted to have higher occurrence probabilities at sites with higher vegetation density and for most species there was also support for the polynomial term, peaking at relatively high values (~50%). For one species (*Laodelphax striatella*), higher occurrence probabilities were also associated with a larger habitat area, and one species (*Neoliturus fenestratus*) showed a negative occurrence response to increasing patch density (Figure S7). Wild bees rarely showed strong associations with any of the environmental covariates. However, occurrences of *Hylaeus incongruus* and the abundance of *A. mellifera* were predicted to respond positively to local vegetation density (Figure S8).

3.2.3 | Species traits and phylogenetic relationships

The response of ground beetles to local vegetation density was dependent on body size, with the prevalence of smaller taxa being more likely to peak at intermediate vegetation densities than that of larger species (Figure S10), while leafhopper and wild bee distributions were not detectably related to the studied traits (i.e. <95% posterior probability).

Closely related beetle species abundances tended to respond similarly to the environmental covariates ($\text{Pr}(\rho > 0) = 0.92$; $E(\rho) = 0.74$; 95% confidence interval [CI] ($\rho) = 0.00$ – 1.00), reflecting similarity in the abundance responses to vegetation density of species belonging to the subfamily Harpalinae. A similar pattern was predicted for beetle species occurrence, but with weaker posterior support ($\text{Pr}(\rho > 0) = 0.45$; $E(\rho) = 0.75$; CI = 0.00 – 0.97). In wild bees, we detected a stronger signal of taxonomic structure in terms of species occurrence responses to the environmental covariates ($\text{Pr}(\rho > 0) = 0.96$; $E(\rho) = 0.79$; CI = 0.00 – 1.00), reflecting niche similarity in congeneric species within the genera *Lasioglossum* and *Ceratina*, than in the species abundance models ($\text{Pr}(\rho > 0) = 0.83$; $E(\rho) = 0.61$; CI = 0.00 – 1.00). There was no clear evidence of phylogenetic structure in leafhopper species occurrence distributions.

3.3 | Spatial and temporal variation

For several species in each insect group, a relatively high proportion of explained variance was captured by the site-level random effect (Figure 2). There was, however, limited residual covariance among species at the site level in any of the three insect groups, suggesting that residual spatial structure may be largely attributable to species-specific rather than common missing drivers.

Leafhopper species occurrences were strongly autocorrelated to a typical scale of c. 10 km (estimated $\alpha = 10,160$ m, posterior support for spatial signal = 1), but spatial autocorrelation was not consistently detected in wild bees or ground beetles. There was, however, evidence of temporal community turnover in ground beetles, with 70% of species captured at a higher abundance in May than in April. Sampling month explained on average 5.7% of their abundance variation.

4 | DISCUSSION

By combining a sampling stratification design (e.g. McGarigal & Cushman, 2002) with joint species distribution modelling and multiscale optimization (Bosco, Wan, et al., 2019; McGarigal et al., 2016), we have demonstrated variable effects of habitat area, fragmentation and ground vegetation density on three vineyard-inhabiting insect groups. For overall species richness and abundance, local vegetation density and fine scale habitat area are more important than fragmentation, but insects show fairly variable and species-specific responses. In general, ground beetles and leafhoppers showed the clearest responses to the three environmental predictors, while effects on wild bees were limited.

For wild bees, measured habitat area best predicted species distributions at a broader scale (500 m radius) than in less mobile leafhoppers or ground beetles (100 versus 50 m radii), following the concept of a positive species mobility - spatial scale relationship (Braaker et al., 2014; Concepción et al., 2015), while the selected best scale of fragmentation was relatively broad in all three insect groups (450 m).

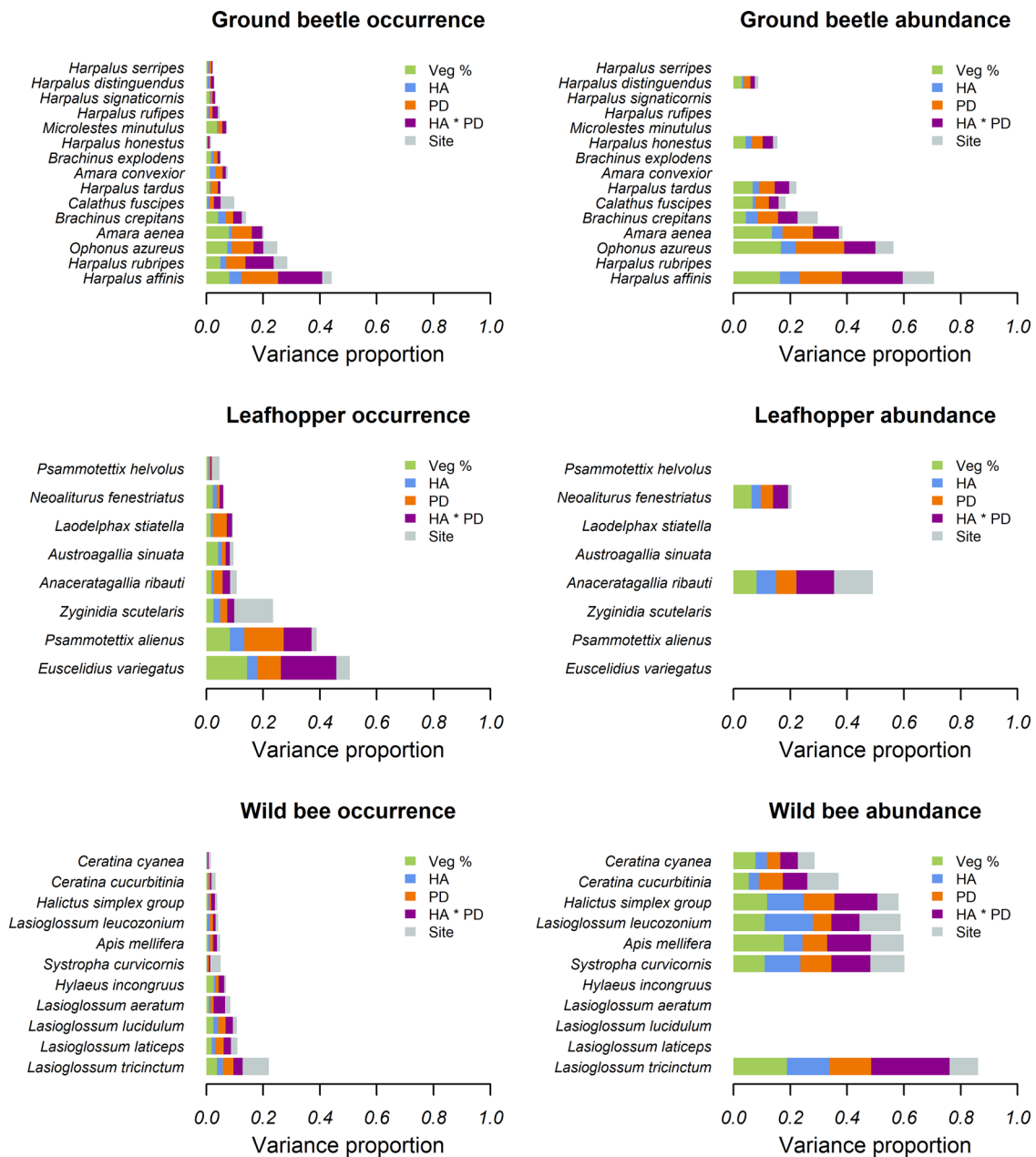


FIGURE 2 Variance partitioning among the explanatory variables (Veg % = ground vegetation density, HA = habitat area, PD = patch density) included in the models for the three insect groups (ground beetles a, b; leafhoppers c, d; wild bees e, f). The panels on the left show the results for the presence–absence models and the panels on the right for the abundance models. In both sides, the lengths of the bars correspond to the explanatory power achieved for each species, measured by Tjur R^2 for the presence–absence and R^2 for the abundance model. The species are ordered by increasing explanatory power.

Species richness of leafhoppers was positively related to vegetated habitat area (100 m radius) and species richness of both leafhoppers and ground beetles to within-field vegetation density, with an initially steep response to vegetation density plateauing once density exceeds c. 60% for ground beetles and showing a hump-shaped response for leafhoppers (optima at ~50%). This corroborates earlier findings demonstrating the importance of both increased field-specific vegetation density (Bosco, Arlettaz, et al., 2019) and the overall area of vegetated vineyards within short distances (Bosco, Wan, et al., 2019). The positive influence of habitat area and field vegetation

density detected here highlight the importance of farming practices that allow ground vegetation to grow in vineyards for promoting both the diversity and the overall abundance of invertebrates, as suggested previously (Bosco, Arlettaz, et al., 2019; Bosco, Wan, et al., 2019; Sáenz-Romo et al., 2019). This has cascading implications for other taxa, such as insectivorous predators (Bosco, Arlettaz, et al., 2019; Bosco et al., 2021; Guyot et al., 2017) and for key ecosystem services including pest control (Sáenz-Romo et al., 2019; Thomson & Hoffmann, 2009) and pollination (Maurer et al., 2020; Winter et al., 2018). The effects of local vegetation density appeared to be partially

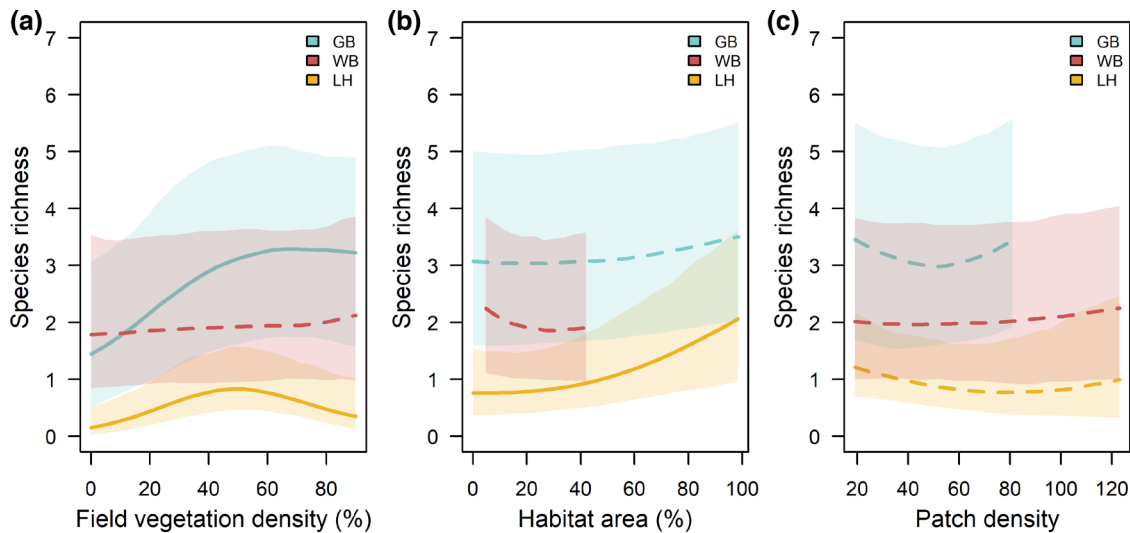


FIGURE 3 Predicted responses of the species richness of ground beetles (GB), wild bees (WB, including *A. mellifera*) and leafhoppers (LH) to vegetation density (%) (a), habitat area (%; percentage of landscape PLAND, measured at the 50 m scale for GB, 100 m scale for LH and 500 m scale for WB; b) and patch density (PD per 100 ha) at the 450 m scale (c). The lines represent the median posterior estimates. Continuous lines indicate substantial (>95%) posterior support and dashed lines <95% posterior support. Coloured areas show the credible intervals around the predicted means. Predictions are limited to the range of observed values per gradient and insect group, which is why ground wild bee predictions are lacking for habitat area >40% and beetle predictions are lacking for patch density >80.

linked to the body size of ground beetles, with smaller species showing hump-shaped responses more frequently than larger species. Smaller ground beetle species may face a stronger trade-off between maximizing food resources, which likely increase with higher vegetation densities (Bosco, Arlettaz, et al., 2019) and locomotion, which may be more costly at higher vegetation densities (Ribera et al., 2001).

No community-level responses were detected for wild bees, suggesting that environmental factors other than the ones tested here may drive community structure. The availability of nectar and pollen resources are obvious candidate drivers that are likely to affect the distributions and diversity of wild bees (Kratschmer et al., 2019; Scheper et al., 2015) and their pollination-related ecosystem services (Albrecht et al., 2020). A lack of effects of landscape structural parameters on wild bees has been reported previously (Kennedy et al., 2013). Although vineyard ground vegetation density can be a proxy for management intensity (Bosco et al., 2022), pesticide and herbicide application levels may vary considerably also among vegetated fields resulting in variable degrees of adverse top-down effects from agrochemicals (Masoni et al., 2017; Siviter et al., 2021) and bottom-up effects from herbicides leading to a vegetation layer of poorer quality for insects (Fried et al., 2019; Winter et al., 2018).

Overall, limited effects of fragmentation emerged from our insect community analyses, except for a few responses among ground beetles and leafhopper species. This contrasts with earlier findings suggesting strong negative effects of fragmentation either alone (on insect abundances: Bosco, Wan, et al., 2019) or in interaction with habitat area (bird distribution: Bosco, Arlettaz, et al., 2021; bumble bee colony performance: Maurer et al., 2020), but corroborates the habitat amount hypothesis (Fahrig, 2013). Integrating the present findings with earlier research on other taxa or biological measures, we can nonetheless conclude that, in general, increased field-scale vegetation

density, resulting from more nature-friendly farming practices—usually involving a renunciation from herbicide applications—along with a higher habitat area at local scales favours more diverse and abundant insect communities, while fragmentation effects are rare, highly variable and species specific. In addition, our results underline the fact that less mobile insects, such as ground beetles, will particularly benefit from simple ground greening measures, whereas pollinators, such as wild bees, are likely stronger influenced by nectar and pollen availability and diversity, perhaps at scales broader than those considered in this study (Ollerton et al., 2014; Scheper et al., 2015).

AUTHOR CONTRIBUTIONS

Laura Bosco, Samuel Cushman and Alain Jacot conceived the ideas and designed the methodology. Laura Bosco and Valentin Moser collected the data. Valentin Moser, Sonja Gerber and Roel Van Klink identified the insects. Laura Bosco, Mirrka Jones, Øystein Opedal and Otso Ovaskainen analysed the data. Laura Bosco led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.7092921> (Bosco et al., 2022).

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PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Fig. S1. Map of the study area in SW Switzerland, with the 120 sampling locations in the 8 municipalities

Table S1. Final sample sizes (original without discarded ones) per class/month for ground beetles in 2015 (April and May), and leafhopper and wild bees in 2016 (June)

Fig. S2. Boxplots showing the estimated ground vegetation proportion per vineyard field among the ground beetle sample fields in 2015 for the 5 classes separately, highlighting the binary distribution of bare (grey box) vs vegetated (green boxes) fields.

Fig. S3. Boxplots showing the estimated ground vegetation proportion per vineyard field among the leafhopper and wild bee sample fields in 2016 for the 5 classes separately, highlighting the binary distribution of bare (grey box) vs vegetated (green boxes) fields

Fig. S4. Boxplots showing the distribution of fields with included (status = yes) or discarded (status = no) pitfall trap samples in relation to a) ground vegetation %, b) fragmentation, c) habitat area, and d) sampling location and month (4 = April, 5 = May)

Table S2. Description of data on species occurrences and abundances, species traits (range and mean for continuous or number per factor level), taxonomic levels and environmental covariates for the final, analysed datasets (i.e. after excluding damaged traps and rare species) of ground beetles (GB), leafhopper (LH) and wild bees (WB)

Table S3. Total abundances, occurrence and the traits body size and habitat strictness for all 40 ground beetle species in the 105 analyzed traps, ordered by highest abundances

Table S4. Total abundances for all 20 leafhopper species in the 116 analyzed traps, ordered by highest abundances. 12 species were excluded due to < 5 occurrences in the data, and only 2 were retained for the abundance models (in brackets)

Table S5. Total abundances for all 43 wild bee species in the 116 analysed traps, ordered by highest abundances

Table S6. Pearson correlations (R) between ground beetle PCoA axes 1 and 2 and habitat area (PLAND) and patch density as a measure of fragmentation (PD) at each of the original measurement scales

Table S7. Pearson correlations (R) between leafhopper PCoA axes 1 and 2 and habitat area (PLAND) and patch density as a measure of fragmentation (PD) at each of the original measurement scales

Table S8. Pearson correlations (R) between wild bee PCoA axes 1 and 2 and habitat area (PLAND) and patch density as a measure of fragmentation (PD) at each of the original measurement scales

Fig. S5. Scale sensitivity analyses for PLAND and PD (Tjur R2 and R2 for the occurrence and abundance conditional on presence models per insect group) with ground beetles on top row, leafhoppers in the middle and wild bees in bottom row

Fig. S6. Species-specific responses of ground beetles to habitat area (%) at 50 m scale (top panels), patch density (patches/100 ha) at 450 m scale (middle panels), and field vegetation density (%; bottom panels) for predicted species prevalence (left row) and abundance (right row)

Fig. S7. Species-specific responses of leafhoppers to habitat area (%) at 100 m scale (top panels), patch density (patches/100 ha) at 450 m scale (middle panels), and field vegetation density (%; bottom panels) for predicted species prevalence (left row) and abundance (right row)

Fig. S8. Species-specific responses of wild bees to habitat area (%) at 500 m scale (top panels), patch density (patches/100 ha) at 450 m scale (middle panels), and field vegetation density (%; bottom panels) for predicted species prevalence (left row) and abundance (right row)

Fig. S9. Predicted probability of occurrence for the ground beetle *Calathus fuscipes* from pitfall trap samples illustrating the interaction between various degrees of habitat area (20%, 50% and 80%, measured at 50 m scale) and patch density (measured at 450 m scale), as illustrated by posterior mean probability values

Fig. S10. Gamma plot showing that the response of ground beetles to ground vegetation density (Veg) was dependent on the trait body size (log transformed), for both the linear and quadratic term. Red indicates significant positive and blue negative responses.

Table S9. Sampling fields with x and y coordinates (in CH1903/LV03, EPSG = 21781), unique ID's, municipality, sampling year, field size, and insect groups sampled

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