


Separating the effects of habitat amount and fragmentation on invertebrate abundance using a multi-scale framework

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Abstract

Context Herbicide treatments in viticulture can generate highly contrasting mosaics of vegetated and bare vineyards, of which vegetated fields often provide better conditions for biodiversity. In southern Switzerland, where herbicides are applied at large scales, vegetated vineyards are limited in extent and isolated from one another, potentially limiting the distribution and dispersal ability of organisms.

Objectives We tested the separate and interactive effects of habitat amount and fragmentation on

invertebrate abundance using a multi-scale framework, along with additional environmental factors. We identified which variables at which scales were most important in predicting patterns of invertebrate abundance.

Methods We used a factorial design to sample across a gradient of habitat amount (area of vegetated vineyards, measured as percentage of landscape PLAND) and fragmentation (number of vegetated patches, measured as patch density PD). Using 10 different spatial scales, we identified the factors and scales that most strongly predicted invertebrate abundance and tested potential interactions between habitat amount and fragmentation.

Results Habitat amount (PLAND index) was most important in predicting invertebrate numbers at a field scale (50 m radius). In contrast, we found a negative effect of fragmentation (PD) at a broad scale of 450 m radius, but no interactive effect between the two.

Conclusions The spatial scales at which habitat amount and fragmentation affect invertebrates differ, underpinning the importance of spatially explicit study designs in disentangling the effects between habitat amount and configuration. We showed that the amount of vegetated vineyards has more influence on invertebrate abundance, but that fragmentation also contributed substantially. This suggests that efforts for augmenting the area of vegetated vineyards is more beneficial for invertebrate numbers than attempts to connect them.

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Introduction

The conversion of natural landscapes into intensively modified systems, such as urban areas, industrial estates and high-intensity farmland, has destroyed, degraded, and fragmented habitats and led to tremendous biodiversity losses (Krebs et al. 1999; Foley et al. 2011; Mendenhall et al. 2014). Farmland landscapes in Europe often provide extreme cases of habitat loss and fragmentation, with extensive areas of intensively cultivated land interspersed with few natural habitat remnants. Because habitat fragmentation in cultivated landscapes is almost always associated with habitat loss, it is difficult to disentangle these two conceptually distinct processes (Debinski and Holt 2000; McGarigal and Cushman 2002; Fahrig 2003). This hampers understanding the mechanisms that drive biodiversity loss in intensively managed agricultural landscapes (Lawton 1995) and hinders the provision of evidence-based guidance for biodiversity conservation and agro-environmental management (e.g., Pedro and Simonetti 2015; Haddad et al. 2017).

Fahrig (2013) proposed the “habitat amount hypothesis” which asserts that the area of available habitat is a more important driver of species diversity than its spatial configuration and that, given the dominant effects of habitat amount relative to fragmentation, research should focus on habitat amount analyses and does not need to evaluate the effects of patch size and isolation. Several study outcomes have supported this hypothesis. For example, Seibold et al. (2017) found that saprophytic beetle species richness was mainly explained by habitat amount while the spatial arrangement seemed unimportant. Also, for predicting species richness of small mammals, habitat amount was the most important single predictor (Melo et al. 2017). Conversely, Haddad et al. (2017) have shown experimentally that, in addition to habitat amount, fragmentation was a key determinant of plant and invertebrate species richness. Furthermore, simulation studies have shown that species extinction probability increases with habitat fragmentation, but only when habitat amount is low (Rybicki and Hanski 2013; Hanski 2015). These contrasting results suggest

the need for more studies on a broader range of study ecosystems and taxa and including additional response variables, such as species abundances, so as to provide sound guidance for biodiversity management. Specifically, studies on invertebrates, especially within agroecosystems, have been scarce, but provide an excellent focus to separate the effects of habitat amount and fragmentation. The high-contrast nature of agricultural systems and the rapid responses and fine scaled population dynamics of invertebrates collectively make them more tractable for studying both field and landscape level patterns of population responses to area and fragmentation (McGarigal and Cushman 2002).

The observed relationship between a biological response and environmental variables or processes, such as habitat loss and fragmentation, are highly dependent on the scale of analysis (Wiens 1989; Wu and David 2002; McGarigal et al. 2016; Miguet et al. 2016). Hence, the scale of analysis must be matched to the objectives and organisms under question if accurate results are to be obtained (Levin 1992; Wu and David 2002). Currently, the most common approach (McGarigal et al. 2016) to identify the characteristic scale in habitat relationship modeling is a two-step procedure in which the optimal scale for each covariate is determined univariately, after which the scale optimized covariates are combined into a single multi-scale, multi-predictor model (e.g., Zeller et al. 2014; Laforge et al. 2015; Wan et al. 2017). There has been an increasing number of multi-scale habitat modeling studies, but few of them separated the effects of habitat amount and configuration (e.g., Schüepp et al. 2014; Pedro and Simonetti 2015; Seibold et al. 2017).

In this study, we aimed to disentangle the effects of habitat amount (i.e. total area of vegetated vineyards) and fragmentation (i.e. number of separate, vegetated vineyard patches) on invertebrate abundance in a vineyard system in Switzerland. We used a factorial design to select patches for sampling invertebrates, assuring that we captured a large proportion of the gradient of habitat amount and fragmentation in our study system. To gain a holistic understanding about the drivers of invertebrate abundance patterns in this vineyard ecosystem and to avoid possible confounding effects, we also included a suite of potentially important environmental variables in addition to habitat area and fragmentation in the analysis. With

a multi-predictor, multi-scale modeling approach we sought to answer the following questions: (i) does the fragmentation and habitat amount of vegetated vineyards affect invertebrate abundance and if so, are their effects dependent on each other? (ii) what is the relative importance of area versus fragmentation of vegetated vineyards on invertebrate abundance? (iii) which topographic, climatic and land use variables at which scale have the strongest effect on invertebrates? (iv) does the multi-scale, multi-predictor model provide stronger inference than a single-scale, multi-predictor model? Responses to these questions bear an important relevance in the context of biodiversity conservation in farmland.

Methods

Study area

The study was carried out in eight different landscapes in the canton of Valais, southern Switzerland (Fig. 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. Vineyards represent the predominant agricultural land use type on the foothills, covering a surface of roughly 50 km² in Valais. They are mainly located on south facing slopes and are interspersed with small remnants of dry and deciduous forest and rocky steppe (Arlettaz et al. 2012). About 80% of the vineyards are intensively managed and support virtually no ground vegetation cover due to regular herbicide application, whereas the remaining 20% are cultivated by a minority of farmers who have adopted more environmentally friendly management practices, which promote the growth of ground vegetation (Arlettaz et al. 2012). At the landscape level, these two management regimes represent a near binary system (bare ground vs. vegetated vineyards, Fig. 1), with few natural and semi natural elements present (e.g., trees, stone walls, hedges). This quasi-binary system of bare versus vegetated vineyards therefore presents a system well suited to evaluate the effects of habitat area and configuration.

Factorial sampling design to separate habitat amount and fragmentation

We used a factorial, stratified sampling design to separate the effects of habitat amount and fragmentation and to ensure that invertebrate sampling was well distributed across these two gradients, as suggested by McGarigal and Cushman (2002). A raster depicting all Valais vineyard fields (“field type”) classified into vegetated and bare was used for this purpose. To distinguish between vegetated and bare fields, we used the normalized difference vegetation index (NDVI) produced from high resolution satellite imagery (WorldView-2, Space Imaging GmbH EUSI, 2 × 2 m resolution, source: Swiss Federal Office of Topography). The recording is best done before the sprouting of the vine leaves (Mid-April in 2012 in Valais). Hence, satellite pictures for Valais were recorded on April 1 2013, ensuring that the calculated NDVI was not influenced by leaves of the vine plants. While intra-annual variation in ground vegetation cover, and subsequent NDVI, was expected to be high due to vegetation cycles in temperate zones, inter-annual variation was low given that the management modes remain stable over years. This is partly due to agricultural legislations related to long-term contracted subsidies in Switzerland. We set a threshold of NDVI = 0.28 to differentiate between bare and vegetated vineyard conditions, which was based on correlations with field estimates of ground coverage also collected in spring 2013. Fields with NDVI > 0.28 represented permanent ground cover, while those with NDVI < 0.28 showed remains of spontaneous winter greening and would be treated with herbicide later in the growing season. Hence, this threshold reflects the two management modes of bare (herbicide treated) and vegetated vineyards.

Habitat amount and fragmentation in our stratified sampling design were quantified with FRAGSTATS (McGarigal et al. 2012) using a moving window of 150 m radius. With this approach, we calculated class level patch density as a measure of fragmentation (PD; the number of patches per 100 ha) and class level proportion of landscape (PLAND) as a measure of habitat amount. Patch density was chosen as our indicator of fragmentation following a series of research that assessed the redundancy and behavior of landscape metrics (e.g., Neel et al. 2004; Cushman et al. 2008) and explicitly evaluated the relationships



Fig. 1 Zoom to one of our sampling landscapes showing the binary nature of bare versus vegetated vineyard fields. The smaller map in the right corner shows the location of our study area (black line) in the canton of Valais (grey surface), southern Switzerland

between landscape metrics and species responses to habitat heterogeneity and connectivity (e.g., Grand et al. 2004; Chambers et al. 2016). Furthermore, it fulfils the criteria that fragmentation measures should be interpretable intuitively, should not require much data input and be as simple as possible from a mathematical point of view (Jaeger 2000). Lower and upper 40% of PD and PLAND values were used to represent low and high levels of habitat area and

fragmentation respectively, creating four classes (Table 1). In addition to these four classes, we included the matrix around the vegetated patches as sampling fields (i.e. bare fields with < 40% ground vegetation cover), to be able to detect field-scale effects mainly driven by the difference between vegetated versus bare management modes. We tried to select three fields per class and landscape, resulting in 15 fields per landscape. But, as it was not possible to

Table 1 Factorial sampling design to separate the effects of habitat amount and fragmentation, both measured at a 150 m scale

| Habitat amount (PLAND 150 m): 0.04–81% | Habitat fragmentation (PD 150 m): 14–1233 patches/100 ha | |
|--|--|----------------|
| | Low (0–40%) | High (60–100%) |
| Low (0–40%) | 28 | 34 |
| High (60–100%) | 18 | 16 |

Value ranges for habitat area and fragmentation, and number of replicates for each class are reported. Additionally, 24 fields of bare ground vineyards (matrix), were included. In total, numbers add up to 120 sampling fields

find enough replicates for all combinations in all landscapes, we had to use a non-balanced design with varying replicates per class (Table 1). Across 8 landscapes we sampled 120 fields in total. We also a priori controlled for habitat variables such as slope and aspect to make sure that our samples would be evenly distributed among classes (ANOVA on linear model with aspect: $P = 0.102$; with slope: $P = 0.465$).

Invertebrate sampling

Invertebrate sampling was conducted in 2015 and 2016. Four landscapes (60 fields) were sampled in 2015 and another four landscapes (60 fields) in 2016. We sampled invertebrates during two sessions (late April and late May) each year, with a sampling duration of 1 week per session. Sampling fields were generally small, ranging from 0.015 to 1.5 ha in size, with an average size of 0.42 ha. Sampling was carried out with two pitfall traps per field (500 ml plastic cup), each being a quarter filled with a mixture of water and ethylene glycol (1:1) and a scentless detergent to lower water surface tension. After each trapping session, we collected the traps from the fields and stored the trapped specimens in 70% ethanol. Out of 240 trap samples, 29 (12%) were damaged or missing and thus discarded from the dataset. We recorded the number of specimens in each trap and sorted them by taxonomic order (see supporting material). Ants were excluded from the dataset due to their spatially clumped aggregations if colonies were nearby a sampling point. Traps belonging to the same field were pooled for the analysis.

Environmental variables

We selected a suite of topographic, climatic and compositional variables (Table 2) that were potentially important in predicting invertebrate abundance patterns in addition to habitat amount and fragmentation of vegetated fields. All topographic (3 variables) and climatic (2 variables) variables were computed based on a digital elevation model DEM raster (25 m \times 25 m, source: Swiss Federal Office of Topography) using the Geomorphometry and Gradient Metrics Toolbox (Evans et al. 2014) in ArcGIS (ESRI 2015). The compositional variables included the NDVI raster from 2013 and a landcover raster which was reclassified into six classes representing the

major land cover categories in our study area (Table 2). All raster layers were resampled to 5 m resolution, projected to the same coordinate system and clipped to the same extent prior to all analyses. We analyzed 10 spatial scales of environmental variation, ranging from 50 m to 500 m radii in 50 m increments.

For the topographic, climatic and the NDVI rasters, we calculated focal means across the 10 spatial scales using the focal statistics tool in ArcGIS, which calculates the mean of that variable within a circle of a specified radius around the center pixel. For the landcover rasters, we calculated six different metrics (4 landscape level and 2 class level) with FRAG-STATS (McGarigal et al. 2012) that were chosen following previous work showing that they were strong indicators of fragmentation effects on habitat suitability (e.g., Grand et al. 2004; Chambers et al. 2016) and connectivity (Cushman et al. 2013) influencing species distribution patterns: (1) class level PLAND; (2) class level correlation length, a measure of habitat extensiveness (GYRATE_AM); (3) landscape level PD; (4) landscape level contrast weighted edge density, which weights the length of edges by standardizing the contrasts between different habitat classes to a per unit area basis (CWED); (5) landscape level Shannon diversity index, as a measure for habitat type diversity (SHD); and (6) landscape level aggregation index, which gives the frequency with which cells of the same patch type are adjacent (AI). We also calculated class level PLAND and PD of vegetated vineyard fields at the same 10 spatial scales as proxies for habitat amount and fragmentation of vegetated vineyard fields for the multi-predictor, multi-scale modeling.

Scale optimization and covariate pre-selection

There were two steps in the scale optimization process. First, univariate models for all scales were fitted to identify the best scale per covariate, based on lowest AICc (Burnham and Anderson 2002). We used generalized linear mixed effect models (*glmer* R package *lme4*, Bates et al. 2015) with a Poisson distribution and field ID as a random factor. Overdispersion was tested (using the function *dispers_glmer*; R package *blmeco*, Korner-Nievergelt 2015) and if necessary an observation level random effect OLRE was included (Bolker et al. 2009). Second, collinearity among the scale-optimized variables was tested with

Table 2 All initial covariates, their description, data types, metrics calculated and best scales based on scale optimization (univariate models) are shown

| Category | Covariate | Description | Data type | Metric | Best scale (m) |
|--------------------|--------------------------------|------------------------------|------------------------------------|--------------------|----------------|
| Topographic | Slope | Slope | DEM 25 m | FocalStatistic | 450 |
| | Slope pos | Slope position index | DEM 25 m | FocalStatistic | 300* |
| | Rough | Roughness | DEM 25 m | FocalStatistic | 100 |
| Climatic | CTI | Compound topographic index | DEM 25 m | FocalStatistic | 450 |
| | Solrad | Solar radiation index | DEM 25 m | FocalStatistic | 500* |
| Compositional | NDVI | Mean NDVI | Satellite images (2013, 2 × 2 m) | FocalStatistic | 50 |
| | Field type | Vegetated versus bare fields | Vineyard shapefile and NDVI raster | PLAND | 50* |
| | | | | PD | 450* |
| | LC | Landcover on landscape level | Landcover shapefile | SHD | 50 |
| | | | | CWED | 100 |
| | | | | AI | 50 |
| | | | | PD | 50 |
| | | | | PLAND | 500 |
| | Resid | Residential area | Landcover shapefile | PLAND | 500 |
| | | | | Correlation length | 450* |
| | Roads | Roads, railways | Landcover shapefile | PLAND | 200* |
| | | | | Correlation length | 150 |
| | Agri | Managed green surfaces | Landcover shapefile | PLAND | 500* |
| Correlation length | | | | 100* | |
| Vine | Vineyards | Landcover shapefile | PLAND | 50 | |
| | | | Correlation length | 50 | |
| Steppe | Steppe, rocky and bare grounds | Landcover shapefile | PLAND | 150* | |
| | | | Correlation length | 500 | |
| Forest | Forests and groves | Landcover shapefile | PLAND | 100 | |
| | | | Correlation length | 300 | |

PLAND percentage of landscape, *SHD* Shannon diversity of patch types, *CWED* contrast-weighted edge density, *AI* aggregation index, *PD* patch density

Only the variables with an asterisk (*) were included in the final multi-scale model. Correlation length area-weighted mean of radius of gyration (extensiveness)

Spearman correlation. For pairs of intercorrelated variables with $|\text{rl}| > 0.7$ (Dormann et al. 2012) the variable with the lower AICc in the univariate model was retained in the modelling. To avoid overfitting of the final model relative to the sample size, we reduced numbers of covariates by selecting only those with a $P < 0.1$ in the univariate models. This resulted in a total of nine final variables for the modelling. To account for potential non-linear relationships, we

compared linear and quadratic univariate models among the final covariates and selected the better function according to lower AICc values (R function *poly*, package *stats*, R Development Core Team 2018). All final variables performed better using the linear term except for PLAND of vegetated vineyard fields, which entered the full model with the linear and quadratic terms. Spatial autocorrelation between invertebrate sampling locations was tested by first

creating a neighborhood list (function *dnearneigh* r package *spdep*, Bivand and Piras 2015; using a raw distance of 500 m) and subsequently a spatial weights matrix (function *nb2listw* package *spdep*). Moran's I (Legendre and Legendre 1998) test detected no significant spatial autocorrelation of the residuals (function *moran.test* package *spdep*).

Multi-scale model selection

All variables were standardized before entering the multi-scale model by subtracting the mean and dividing by the standard deviation to improve convergence of the model fitting algorithms and to provide meaningful comparisons based on the magnitude of standardized regression coefficients. We fitted a full *glmer* model (function *glmer*, R package *lme4* Bates et al. 2015) including all final variables at their characteristic scales, field ID and OLRE as random factors and using a Poisson distribution. Using the *dredge* function (R package *MuMIn*, Bartón 2016, using $rank = AICc$) the most competitive models with a $\Delta AICc < 2$ were selected and we produced model averaged coefficient estimates and SE, confidence intervals, relative variable importance and P values (function *model.avg* R package *MuMIn*, Bartón 2016). Finally, we estimated relative importance for each variable present in the top model using a leave-one-out-jack-knife procedure, where one variable at a time was dropped from the top model and the subsequent drop in AICc ($\Delta AICc$) was calculated. To show effect plots of all significant terms, we calculated model averaged predictions using a Bayesian framework, where we drew samples from the joint posterior distribution with the function *sim* (*arm* R package, Gelman and Su 2015). Additionally, we tested whether effects of fragmentation and habitat area of vegetated fields are interdependent. To do so, we used the best scale of each variable from the univariate scale optimization and produced an interaction model (PLAND*PD) using a *glmer* model with a Poisson distribution and field ID and OLRE as random factors.

Single-scale models

The same final variables in the multi-scale model were used for single-scale modeling, in which the scale across all variables was held constant such that a full single-scale model was produced at each of the 10

spatial scales described above (e.g., Wan et al. 2017). We used the same analytical approach for the single-scale models as for the multi-scale models (i.e. using a *glmer* with field ID and OLRE as random factors and a Poisson distribution). The best scale was selected based on the lowest AICc for a given scale and model selection was performed using dredge and model averaging for all competitive models with the $\Delta AICc < 2$ rule.

All models were run on a sample size of 211 trap samples and all statistical analyses were performed with R (R Development Core Team 2018).

Results

We collected a total of 13,979 invertebrates (ants excluded) across all replicates over all sessions and both years (4089 in April 2015, 3819 in May 2015, 3126 in April 2016 and 2945 in May 2016). On average, 66.25 ± 34.54 individuals were caught per field (range 15–205).

Optimized scales and variable selection

The scale optimization showed strong variation in best scales among the variables (Table 2), with climatic and topographic variables having generally broad-scale effects. The habitat amount of vegetated vineyards was most important at a field scale (50 m), while fragmentation had broad-scale effects (450 m) with no significant effects at finer scales. There was no significant interaction between PLAND and PD of vegetated fields at their optimal scales (PLAND 50 m*PD 450 m: estimate \pm SE = -0.04149 ± 0.04576 , $z = -0.91$, $P = 0.365$). For the landcover classes, habitat amount and correlation length performed best at intermediate to broad scales (Table 2).

Multi-scale model selection

Invertebrate abundance was strongly driven by PLAND of vegetated vineyards at a field scale (50 m radius), with a relative AICc importance of 35% (Table 3). PLAND of steppes was the second most influential variable, with relative AICc importance of 18.6%. The third and fourth most influential variables were solar radiation (relative AICc

Table 3 Model averaged estimates, standard errors, z values, 2.5% and 97.5% confidence intervals, relative importance (Δ AICc) and P values are given for all 9 covariates present inthe top models for the multi-scale approach and the only variable which was present in the top single-scale model with Δ AICc < 2

| Covariate | Estimate | SE | z value | 2.5% CI | 97.5% CI | Δ AICc (%) | P value |
|-----------------------------------|-----------|---------|---------|-----------|-----------|-------------------|---------|
| Multi-scale model | | | | | | | |
| (Intercept) | 4.07127 | 0.0339 | 119.382 | 4.004431 | 4.138112 | – | < 0.001 |
| PD fields 450 m | – 0.13021 | 0.03753 | 3.449 | – 0.2042 | – 0.05623 | 3.09 (7.7%) | < 0.001 |
| PLAND agri 500 m | 0.08883 | 0.03403 | 2.594 | 0.021718 | 0.15594 | 4.45 (11.1%) | 0.009 |
| PLAND fields 50 m | 1.99009 | 0.51423 | 3.848 | 0.976412 | 3.003777 | 14.11(35.3%) | < 0.001 |
| (PLAND fields 50 m) ² | – 1.1269 | 0.53082 | 2.111 | – 2.17331 | – 0.08048 | 3.2 (8%) | 0.035 |
| PLAND steppes 150 m | – 0.11953 | 0.03539 | 3.357 | – 0.18931 | – 0.04975 | 7.45 (18.6%) | < 0.001 |
| Slope position 300 m | 0.0774 | 0.03521 | 2.185 | 0.007985 | 0.146821 | 3.02 (7.5%) | 0.029 |
| Solar radiation 500 m | 0.09831 | 0.03552 | 2.751 | 0.028267 | 0.168344 | 4.68 (11.7%) | 0.006 |
| PLAND roads 200 m | 0.08738 | 0.03543 | 2.452 | 0.017523 | 0.157246 | – | 0.014 |
| Single-scale model at 50 m | | | | | | | |
| (Intercept) | 4.0729 | 0.1094 | 37.001 | 3.857118 | 4.288598 | – | < 0.001 |
| PLAND fields 50 m | 1.7386 | 0.5445 | 3.174 | 0.664972 | 2.812161 | 9.21 (82%) | 0.002 |
| (PLAND fields 50 m) ² | – 1.1638 | 0.5654 | 2.046 | – 2.27863 | – 0.04896 | 2 (18%) | 0.041 |

Variable importance was calculated as the drop in Δ AICc when the respective variable was removed from the top model and relative importance is given in brackets (no value for PLAND roads as it was not present in the top multi-scale model)

importance = 11.7%) and PLAND of agricultural land (11.1%). Patch Density of vegetated vineyards had a relative AICc importance of 7.7%.

Invertebrate abundance peaked when there was approximately 60% cover of vegetated surfaces within 50 m and decreasing slightly if PLAND was above 60% (Table 3, Fig. 2a), while areas with high PD at a 450 m scale supported lower number of invertebrates (Table 3, Fig. 2b). Also, PLAND of steppes was negatively related to abundance, even with only small proportions of steppe habitats being present within 150 m scale (0–9%; Fig. 2c). Higher solar radiation and PLAND of agricultural area, both at 500 m scale, enhanced abundance (Fig. 2d, e) and also slope position index at 300 m and percentage of roads at 200 m had positive effects (Fig. 2f, g). The top model had a conditional $R^2 = 0.495$.

Single-scale models

The best scale for the full single-scale modeling was at 50 m with an AICc of 2006.5 ranging up to 2012.7 at a 250 m scale, thus being considerably higher than the full multi-scale model (AICc = 1979.84; Fig. 3). At this scale (50 m) only PLAND of vegetated vineyards

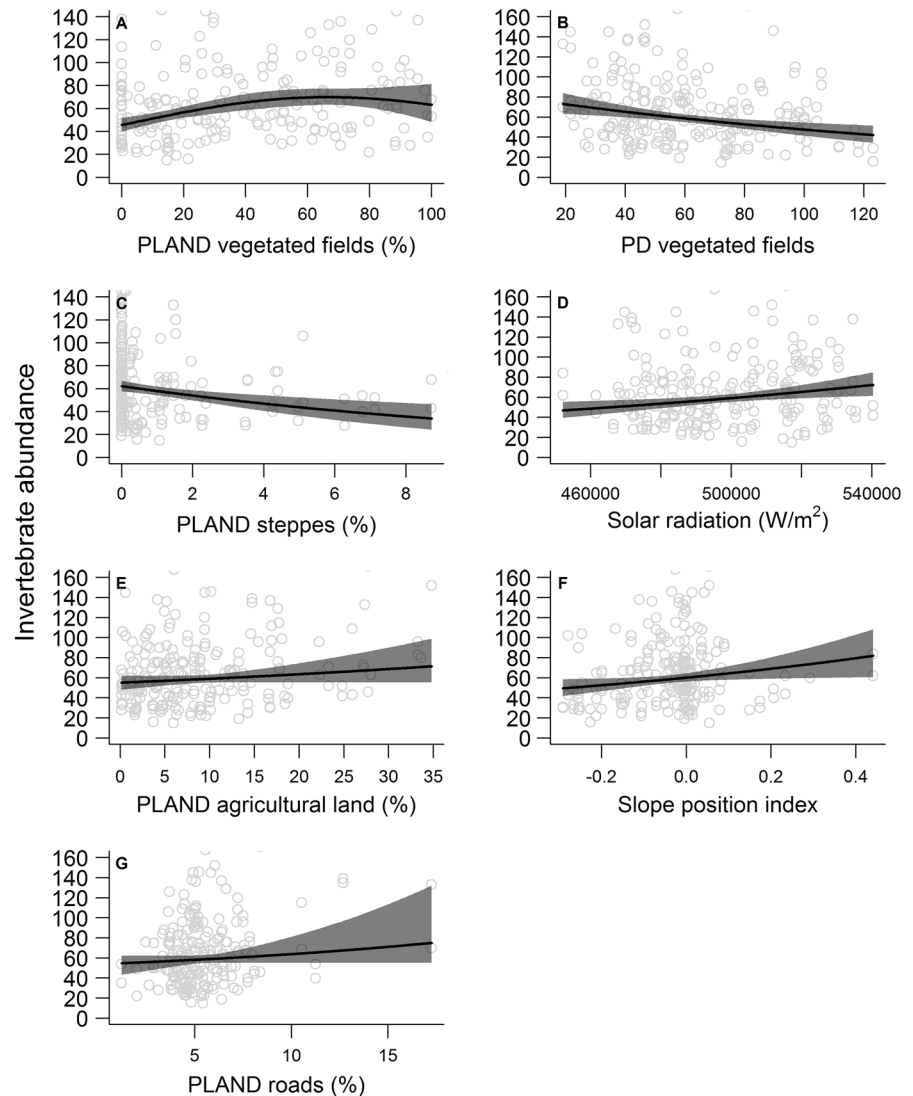
(linear and quadratic term) among the final nine variables was present in the two top models with Δ AICc < 2 after model selection, while all other predictors were discarded. PLAND of vegetated fields had a strong positive linear and negative quadratic effect on invertebrate abundance (Table 3) and the top model at this scale had an AICc of 1996.67.

Discussion

The innovative aspect of this study is that it used an a priori sampling stratification design to separate habitat amount and fragmentation effects in combination with multi-scale optimization modeling, which, although suggested more than 15 years ago by McGarigal and Cushman (2002), is still rarely seen in the literature. Thus, by relying on a quasi-experimental approach, we were able to achieve landscape-level replication across controlled gradients of area and fragmentation, which McGarigal and Cushman (2002) argue is essential to obtain strong inferences about fragmentation effects.

Our first research question was focused on whether habitat area or fragmentation affect invertebrate

Fig. 2 Model averaged abundance predictions from Poisson regression models with 95%—Bayesian credible intervals (grey areas) are shown for the seven significant variables based on multi-scale modeling. a Habitat amount (PLAND) of vegetated vineyards at 50 m scale. b Fragmentation (PD) of vegetated vineyards at 450 m scale. c PLAND of steppes within 150 m scale. d Solar radiation within 500 m scale. e PLAND covered by agricultural land at 500 m scale. f Slope position index within 300 m scale. g PLAND of roads within 200 m scale. All variables present in the top models, except the one under consideration, were fixed at their mean values for projections. Lightgrey circles show raw data



abundance more strongly. Similar to previous studies focusing on various diversity metrics (Fahrig 2013; Melo et al. 2017; Seibold et al. 2017), our results revealed, that habitat amount is more important than fragmentation in explaining invertebrate abundance. The second question was about their relative importance and if there was an interaction between habitat area and fragmentation. Based on AICc, the relative importance of habitat amount was estimated to be about seven times greater than the fragmentation degree, although the latter still showed significant and substantial negative effects on invertebrate abundance. Thus, consistent with results for species diversity measures (Fahrig 2003) habitat area appears

more important than fragmentation in our study system as well. Yet, contrary to the assertion of Fahrig (2013), habitat fragmentation additionally was an important and significant predictor in explaining abundance patterns. Importantly, we did not detect an interaction between area and fragmentation of vegetated vineyards, which suggests that for invertebrate abundance there is not a pattern of increasing effect of fragmentation with decreasing habitat area, as has been seen in a number of previous studies (e.g., Flather and Bevers 2002; Rybicki and Hanski 2013; Hanski 2015).

In our study, fragmentation showed negative effects at a rather broad scale (450 m scale), which is

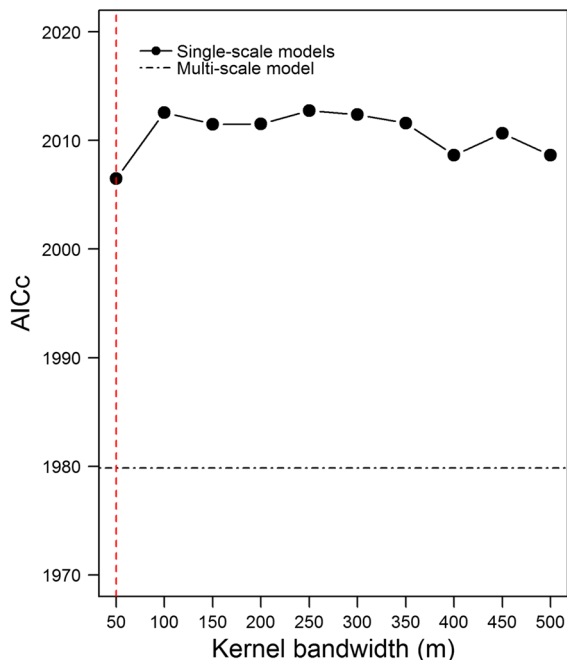


Fig. 3 AICc values for the full models are shown for all 10 single-scale models (black circles) and the full multi-scale model (horizontal dashed line at AICc=1979.84), showing that among the single-scale models the one at 50 m performed best having an AICc of 2006.5 (vertical red line) and that the full multi-scale had best model performance compared to any single-scale model. (Color figure online)

consistent with other invertebrate studies. For example, edge effects on beetle abundance were strongest beyond a 250 m scale (Ewers and Didham 2008) and positive connectivity effects on invertebrates inhabiting green roofs were observed within 200–400 m scales (Braaker et al. 2014). Thus, in line with those previous findings, this study shows that negative effects of fragmentation on ground dwelling invertebrate abundance at broad scales may act on a population rather than an individual level, possibly due to increased edge effects if fragmentation is high, resulting in a loss of dispersing individuals within the hostile matrix.

Habitat amount had much stronger effects than fragmentation and influenced invertebrate abundance most strongly at a fine scale of 50 m radius. At this scale, an effect of habitat amount can mainly be explained by the binary partition of management modes into vegetated and bare vineyard grounds (i.e. habitat and matrix fields) and underpins the positive effect of ground vegetation in vineyards at field scales

(Winter et al. 2018). For ground dwelling invertebrates, which we mainly caught with pitfalls, ground vegetation may only be a limiting factor within small areas, as small bodied and less mobile invertebrates have smaller home ranges and dispersal radii (e.g., Bowman et al. 2002). Studies on a wide range of other animal taxa have stressed the importance of habitat amount over fragmentation, while most of these studies focused on forest birds (e.g., Trzcinski et al. 1999; Radford and Bennett 2007) and some on rodents (Mortelliti et al. 2011) and herbivorous insects (Holland and Fahrig 2000).

Overall, this study shows that identifying the scale of effect for habitat configuration patterns on a biological response is crucial to detect potential adverse effects (Martin and Fahrig 2012; McGarigal et al. 2016). We only detected negative fragmentation effects on invertebrate abundance at a broad scale of 450 m, whereas habitat amount was most important at field scales (50 m), implying that such relationships could have remained undetected if measured at a single or inappropriate scales (Holland et al. 2005; Fahrig 2013). Drawing conclusions from this finding, we argue that previous contrasting results debating about whether habitat amount or fragmentation is more important, to a certain degree, may also be a matter of scale. We propose to consider both effects in future research (e.g., Schüepp et al. 2014; Haddad et al. 2017), given that their “scales of effect” (Martin and Fahrig 2012) are tested within a multi-scale framework.

Our third research question focused on identifying which environmental variables, in addition to area and fragmentation of vegetated vineyards, affect invertebrate abundance. Indeed, a number of other environmental variables were also influential. For example, solar radiation index at the broadest scale (500 m) was a strong predictor and had a significant and positive impact on invertebrate abundance, indicating that warmer soil and ambient temperatures potentially promote greater net primary productivity, faster growth and maturation of invertebrates, thus boosting their abundance (e.g., Coxwell and Bock 1995). Also, the proportion of roads in the landscape at a 200 m scale had a positive effect, indicating that with increasing number and area of roads within a 200 m distance, invertebrates increased in numbers. Dirt (non-asphalted) tracks are the most abundant road type in vineyards and their positive effect is therefore most

likely driven by “more natural” areas and adjacent herbaceous vegetation along the margins of dirt tracks, which are less frequently used by cars than asphalted roads. Hence they do not represent a highly artificial feature, fragmenting the habitat, as shown in other studies (e.g., Eigenbrod et al. 2008; Fahrig and Rytwinski 2009). In contrast, the amount of steppe habitat had negative effects on invertebrate abundance at a 150 m scale, and this at very low proportions (0–10%). In our study area, steppe habitats represent the most unproductive natural (climactic) habitat remnants. Their intrinsic low primary productivity may not only explain why they were not converted into vineyards but also why they harbor so little entomofauna. Overall, our results show that, while the area of vegetated vineyards is particularly important, invertebrate abundance is further driven by a number of abiotic and anthropogenic factors, each at their characteristic scale. This suggests that habitat analyses and in particular studies on the effects of habitat amount versus fragmentation should adopt a scale-explicit, multi-predictor approach, rather than relying on a binary conceptual model (e.g., Cushman et al. 2010).

Our fourth research question focused on whether multi-scale optimization across several predictor variables improved predictions of invertebrate abundance, as has been found by many other researchers (e.g., McGarigal et al. 2016). Multi-scale modeling confirmed that testing the characteristic scale for each covariate and subsequently analyzing species habitat relationships using a multi-scale framework resulted in better model performance and clearer inferences compared to single-scale modeling. Specifically, the scale optimized model had full AIC weight in comparison to any of the single-scale models ($\Delta\text{AIC} > 25$), indicating that the scale optimization was essential to obtain a good model about the environmental drivers of invertebrate abundance. This study, therefore, adds to the considerable and increasing evidence that species habitat relationships are fundamentally scale dependent, and that multi-scale optimization approaches are needed to obtain clear predictions of species response to landscape characteristics—in this case invertebrate abundance in agricultural systems as function of extent and configuration of different management regimes, abiotic and anthropogenic factors.

Conclusions

Our research provides three main insights. First, field-scale habitat amount in vineyards has much greater influence on invertebrate abundance than does fragmentation. Second, landscape-scale fragmentation (PD at 450 m), however, provides significant and substantial improvement to our models. Thus, assessing habitat amount without fragmentation is not sufficient to study biological responses. Third, invertebrate abundance is strongly influenced by a set of different variables in addition to habitat amount and fragmentation of vegetated vineyards, each acting at characteristic scales. Thus, multi-scale optimization modeling is critical to obtain clear insights into the ecological and environmental drivers of invertebrate abundance, and simplistic binary representations of habitat versus non-habitat as categorical mosaics is inappropriate. The main management implication suggests that efforts to increase the practice of vegetated vineyards are likely a good strategy to enhance invertebrate numbers in this agroecosystem, while focus should be centered on augmenting the fraction of ground-vegetated vineyards within the landscape while enhancing their connectivity appears to be less important.

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