

Fragmentation effects on woodlark habitat selection depend on habitat amount and spatial scale

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Abstract

Habitat loss and fragmentation are key drivers of biodiversity loss. However, they are usually confounded, making it difficult to separate fragmentation effects from those of habitat loss. In addition, it has been shown that often fragmentation negatively affects biodiversity only below a certain threshold of habitat amount. We investigated the separate and interactive effects of habitat amount and fragmentation on habitat selection of the woodlark at 10 spatial scales. In southern Switzerland this passerine mainly breeds in ground-vegetated vineyards, which therefore represent the focal habitat type in this study. Additionally, we investigated land cover, topographic and climatic variables at the same 10 scales to obtain a holistic picture of species-habitat associations. Habitat selection was analyzed at two hierarchical levels: home range selection within the study area and habitat use within home ranges. Home range selection was strongly driven by an interactive effect of habitat amount and fragmentation: woodlarks avoided fragmented areas if habitat amount was below 20% but exhibited a preference for fragmented areas if habitat amount exceeded this threshold. Both habitat amount and fragmentation most strongly affected habitat use at the 100 m scale. We did not find such interactive effects for habitat use within home ranges. At this level, habitat amount at a 50 m scale influenced woodlark presence positively with no significant effects of fragmentation. Furthermore, woodlarks preferred evenly sloped landscape mosaics interspersed with steppes and groves. Two main insights emerge from our study. First, these results highlight the necessity of studying scale explicit and interactive effects of habitat amount and fragmentation when addressing ecological questions, such as habitat selection in birds. Second, we provide management recommendations for farmers: more vineyards should be vegetated and arranged as disjunct patches where their surface covers more than 20% of the landscape but be aggregated where vegetated area is lower.

Introduction

Habitat loss and fragmentation are key drivers of the biodiversity crisis (Haddad *et al.*, 2015) and affect the abundance of populations and the diversity of communities (e.g. Tschamtko *et al.*, 2002; Fahrig, 2003), such that both community structure and interactions of species with their biotic and abiotic environment can be profoundly altered when habitat is lost and fragmented (Lawton, 1995). In most cases, habitat fragmentation involves a simultaneous loss of habitat, complicating our ability to distinguish and disentangle these two separate processes (McGarigal & Cushman, 2002;

Fahrig, 2003; Tschamtko *et al.*, 2012). The effects of habitat amount and fragmentation have been widely studied, with equivocal support for several hypotheses. The habitat amount hypothesis (Fahrig, 2013) states that the area of available habitat is more important than its spatial configuration and that patch size and isolation effects do not need to be tested independently of habitat area. Several study outcomes supported this view. For instance, Seibold *et al.* (2017) found that saproxylic beetle species richness was mainly explained by habitat amount irrespective of habitat configuration, while Melo *et al.* (2017) similarly suggested that when predicting species richness of small mammals, habitat amount was the

most important factor. However, several recent studies have suggested that habitat amount and fragmentation are both key drivers of biodiversity responses (Schüepp *et al.*, 2014; Hanski, 2015; Haddad *et al.*, 2017; Lindgren & Cousins, 2017; Fletcher *et al.*, 2018), with often synergistic or interactive effects between the two. Simulation modelling studies have proposed that the extinction probability of a species is increased by fragmentation when habitat amount is low (<20–30%; e.g. With & King, 1999; Flather & Bevers, 2002), while the former has no or a reduced effect if habitat amount is high (Rybicki & Hanski, 2013; Hanski, 2015).

In birds, it has been established that the amount of habitat required for population persistence varies depending on the species response to landscape configuration (With & King, 2001), particularly when habitat amount is below the species-specific area threshold ensuring long-term population viability (Flather & Bevers, 2002). Therefore, understanding the interactive effects of habitat loss and fragmentation is of prime importance when it comes to defining thresholds of habitat amount below which the spatial configuration of the remaining habitat becomes crucial (Parker & Mac Nally, 2002).

Here our aim was to investigate the separate and interactive effects of habitat amount and fragmentation using the woodlark *Lullula arborea* as a focal species. This farmland passerine inhabits highly anthropogenically altered and fragmented vineyard landscapes in southern Switzerland, where it shows a clear preference for ground vegetated vineyard fields (Bosco *et al.*, 2019a). Hence, vegetated vineyards represent the focal habitat in this study and are generally surrounded by bare vineyards, considered as matrix (i.e. unsuitable habitat). Our main objective was to determine whether habitat fragmentation vs. amount influence woodlark habitat selection and to identify the scales of effect of the two factors. We distinguished between second-order habitat selection (home range settlement within the study area) and third-order selection (habitat use within the home range, *sensu* Johnson, 1980).

Given that species-habitat associations are highly dependent on the spatial scale (e.g. McGarigal *et al.*, 2016; Miguët *et al.*, 2016), we applied a widely used multi-scale analytical framework: after univariate determination of the optimal spatial scale for each environmental predictor, the scale optimized covariates are combined into a single multi-scale, multi-predictor model (e.g. Laforge *et al.*, 2015; McGarigal *et al.*, 2016; Bosco *et al.*, 2019b). This approach enabled us to determine scale-explicit habitat amount thresholds, above which fragmentation might become negligible. Additionally, we accounted for other environmental factors potentially influencing habitat selection to gain a more holistic understanding of woodlark habitat preferences. In line with recent findings (e.g. Schüepp *et al.*, 2014; Hanski, 2015; Haddad *et al.*, 2017; Lindgren & Cousins, 2017; Fletcher *et al.*, 2018), we hypothesized that responses of our study species to habitat fragmentation depend on (1) the amount of available habitat, such that fragmentation effects will be seen only when habitat area is low, and (2) the order of habitat selection, such that fragmentation may matter more in coarse

scale, that is, second-order, habitat selection. This is based on the assumptions that configurational aspects may be less important for within home range habitat use (i.e., selection at the vineyard field scale) and that fragmentation may affect abundance of invertebrate prey more strongly at broader scales (e.g. Bosco *et al.*, 2019b).

Materials and methods

Study area and species

The study was carried out in the upper Rhône valley in Valais, Switzerland (between Leytron 46°20'N, 7°21'E and Varen 46°32'N, 7°58'E). In the study region, vineyards are the predominant land use type and are arranged in a mosaic of intensively managed, bare vineyards (~80%), interspersed with fewer ground-vegetated vineyards (~20%). Valais vineyards are mainly located on the south-facing slopes north of the Rhône river and are interspersed with patches of dry forest and rocky steppe, which are climatic grasslands typical of the driest areas of the inner Alps. Individual vineyards can easily be distinguished based on their characteristic ground cover management, the grape variety or their attachment type (on wires or poles) and will hereafter be referred to as 'fields'. The two management types – ground-vegetated versus bare-ground vineyards – nearly form a binary system (Fig. 1). For the entire Valais vineyard perimeter one can find a wide range of fragmentation degree and area covered by vegetated fields, which are embedded within otherwise intensively used, bare fields. This offers a suitable system to investigate the effects of habitat amount and fragmentation upon a nationally endangered bird species.

The woodlark is an insectivorous passerine classified as vulnerable on the Swiss Red List (Keller *et al.*, 2010). Within its Palearctic distribution range, it occurs in a variety of different breeding habitats, including semi-natural heathland (Praus *et al.*, 2014), olive groves (Castro-Caro *et al.*, 2014) and vineyards (Arlettaz *et al.*, 2012; Buehler *et al.*, 2017; Bosco *et al.*, 2019a). In the latter habitat, it shows a pronounced preference for ground-vegetated fields (Arlettaz *et al.*, 2012; Buehler *et al.*, 2017; Bosco *et al.*, 2019a) which offer not only better prey supply (e.g. Thomson & Hoffmann, 2009; Bosco *et al.*, 2019b), but also cover for their terrestrial nests (Buehler *et al.*, 2017).

Woodlark data collection

We captured 49 woodlarks, ringed (ring size N, SEMPACH HELVETIA) and equipped them with VHF radio-transmitters (Holohil BD-2, 0.9g, 60p/min, Canada) using leg harnesses (Naef-Daenzer, 1993, 12 birds in 2014; 21 in 2015; 16 in 2016; see Table A1). Birds were captured from early March and until early May. We used the homing-in technique to locate the birds, as this method has successfully been used in previous studies on woodlarks in this region (Schaub *et al.*, 2010; Arlettaz *et al.*, 2012) and the localizations are predicted to be more precise using hand-held antennas for birds regularly sitting on the ground (Naef-Daenzer, 1993).

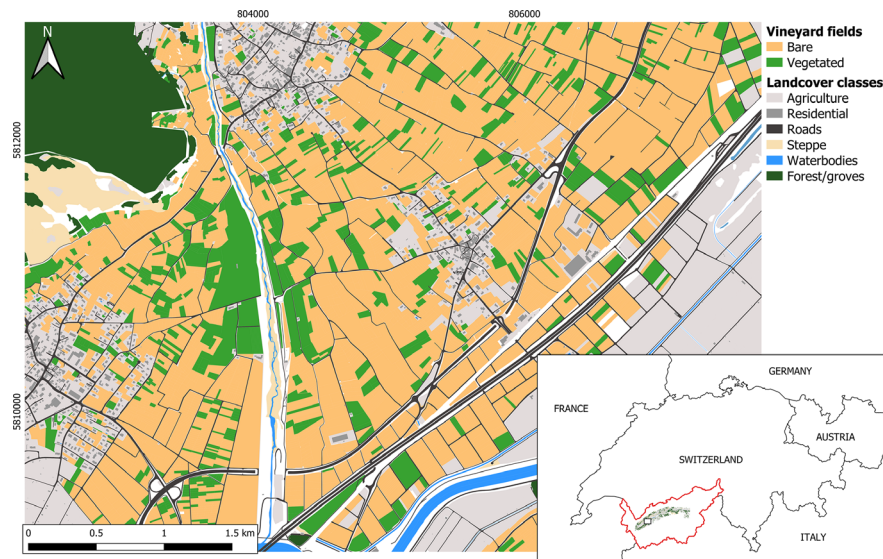


Figure 1 Location of the study area in SW Switzerland (Valais; red outline), with a zoom onto a vineyard area where the mosaic of bare (orange) and ground-vegetated (green) vineyard fields are depicted in a dichotomous way. The most abundant landcover classes in addition to vineyards are shown (see color legend). [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

Between two relocations we waited for at least 10 min to limit temporal dependency. On average, we recorded 4.6 relocations/bird/day while the number of tracking days ranged from 7–19 per bird (mean \pm SD = 12.08 \pm 4.6). Only birds with a minimum of 30 relocations ($n = 36$) were used for the analysis. All homing-in locations were digitized using the software QGIS (QGIS Development Team, 2018). In three cases, we captured and radio-tracked both sexes of a woodlark pair, resulting in huge overlaps of locations and home ranges between the partners. For each such pair, we thus only included data from males in the analyses to avoid the overlaps. We chose males because they had more locations and the data were temporally more evenly distributed than those of females that were involved in incubation. To account for potential sex bias, we tested sex-specific differences in habitat use by contrasting the sex of the birds with all environmental variables (Table 1) univariately. Univariate models were run in the R software environment (R Development Core Team, 2018) using the *glmer* function (package *lme4*, Bates *et al.*, 2015) with a binomial distribution and bird identity as random effect.

Environmental variables

For all environmental predictors, we investigated 10 spatial scales, ranging from 50 m to 500 m radii in 50 m increments. The smallest scale (50 m) corresponds approximately to half of the smallest woodlark home range radius, while 500 m is almost twice the largest home range radius observed in our population (home range size range: 4–30 ha based on 95% kernel density estimations from radio bearings, unpublished data). The increments (50 m) were chosen based on the expectation that during the breeding season woodlark habitat use is strongly shaped by the abundance

and density of invertebrates (Bosco *et al.*, 2019a). The activity range of less mobile, ground-dwelling arthropods is rather small, and effects of habitat configuration and amount on these important prey species have been shown to peak at 50 m (habitat amount) and 450 m (fragmentation) radii (Bosco *et al.*, 2019b).

To distinguish between vegetated and bare vineyard fields, we calculated the normalized difference vegetation index (NDVI), using high-resolution satellite imagery from 2013 (recorded on April 1, 2013, 2×2 m resolution, satellite: WorldView-2, Space Imaging GmbH EUSI, source: Swiss Federal Office of Topography). Intra-annual variation in ground vegetation cover is expected to be high due to vegetation cycles in temperate zones, whereas inter-annual variation within a field is low given that the management practices often remain stable over years. This is partly due to long-term contracted subsidies in Switzerland. Thus, with a relatively stable management practice per vineyard field, the satellite image from 2013 gave a realistic picture for subsequent years during which we measured woodlark habitat use. Mean NDVI values were extracted per field, resulting in a raster layer classifying all Valais vineyard fields into vegetated (value = 1) and bare (value = 0).

We quantified habitat amount and fragmentation of vegetated vineyards with FRAGSTATS (McGarigal *et al.*, 2012). Specifically, 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 for all 10 spatial scales. Patch density has been shown to be a good proxy to study species responses to habitat heterogeneity and connectivity (e.g. Grand *et al.*, 2004; Chambers *et al.*, 2016). Also, it can be interpreted intuitively, it does not require much data input and is simple from a mathematical point of view (Jaeger,

Table 1 Topographic, climatic, habitat resource and landcover predictors that were considered in our two habitat selection models (second and third order) for woodlarks inhabiting SW Swiss vineyards

Category	Covariate	Description	Resource data type	Metric	Best scale (m) second order	Best scale (m) third order
Topographic	Slope position	Slope position index	DEM 25 m	FocalStatistic	250*	150*
	Roughness	Terrain roughness	DEM 25 m	FocalStatistic	50	50
Climatic	Solrad	Solar radiation index	DEM 25 m	FocalStatistic	250*	50*
Habitat resources	NDVI	Mean NDVI	satellite images 2 m	FocalStatistic	50	50
	Vegetated fields	Vegetated vineyard fields	vineyard shapefile and NDVI raster	GYRATE_AM PLAND PD	150 100* 100*	50 50* 50
Landcover	Landcover AI	Landcover classes at landscape scale	Landcover raster	AI	50	100*
	Residential	Residential, built areas	Landcover raster	PLAND GYRATE_AM	100* 50	50* 50
	Roads	Roads, railways	Landcover raster	PLAND GYRATE_AM	350 250*	50 50
	Agricultural	Cultivated surfaces	Landcover raster	PLAND GYRATE_AM	50 50*	50 50*
	Vineyards	Vineyards (bare and vegetated)	Landcover raster	PLAND GYRATE_AM	50* 200	50 50*
	Steppes	Steppes, rocky and bare grounds	Landcover raster	PLAND GYRATE_AM	50 450*	150* 150
	Groves	Small forests, hedges	Landcover raster	PLAND GYRATE_AM	100* 50	150 150*
	Edge vegetation	Edge vegetation e.g. road verges	Landcover raster	PLAND GYRATE_AM	50* 50	50* 50

Variables with an asterisk (*) were retained for the final multi-scale, multi-predictor models.

Abbreviations: AI, aggregation index; GYRATE_AM, area-weighted mean of radius of gyration (extensiveness); PLAND, percentage of landscape; PD, patch density.

2000). We also calculated area weighted mean radius of gyration of vegetated fields, also known as correlation length (GYRATE_AM; a measure of habitat extensiveness; McGarigal *et al.*, 2012, hereafter referred to as extensiveness) to obtain information about the effect of the linear extensiveness and contiguity of habitat patches.

In addition, a set of several topographic, climatic and landcover covariates were chosen based on prior information about woodlark habitat preference (e.g. Bowden, 1990; Arlettaz *et al.*, 2012; Bosco *et al.*, 2019a; Table 1). All topographic and climatic variables (slope position, terrain roughness and solar radiation) were computed from a digital elevation model (25 × 25 m; Swiss Federal Office of Topography) using the Geomorphometry and Gradient Metrics Toolbox (Evans *et al.*, 2014) in ArcGIS (ESRI, 2017).

All raster layers were resampled to a 5 × 5 m resolution, projected to the same coordinate system (CH1903/LV03; EPSG 21781) and clipped to the same extent. For the topographic, climatic and the NDVI rasters, we calculated means across the 10 spatial scales using the focal statistics tool in ArcGIS, which calculates the mean of that variable within a circle of the specified radius around the center pixel. The landcover layer was rasterized and reclassified into seven major land use classes present in our study area (Table 1). For the landcover raster, we incorporated three metrics calculated in FRAGSTATS: (1) PLAND per class type; (2) extensiveness per class type (GYRATE_AM), and (3) landscape

level aggregation index of the study area (AI; the frequency with which cells of the same patch type are adjacent, McGarigal *et al.*, 2012).

Orders of habitat selection

To analyze home range selection within the study area, we used the 100% minimum convex polygon (MCP), computed in QGIS for all woodlark individuals with a minimum of 30 relocations. To account for potential location errors, MCPs were buffered by 25 m (approximately twice the precision error of localizations, estimated from field surveys). We then generated a random sample of pseudo-absences in a 1:1 ratio with actual occurrences, outside the home range area. As most woodlarks of this population breed in vineyards and we only tracked birds breeding in this habitat type, we confined the reference area to the vineyard perimeter and simultaneously controlled that random pseudo-absences would not fall into home ranges of other woodlarks. Furthermore, pseudo-absences had a maximum distance to respective woodlark presence points of 500 m, corresponding to the mean maximum distance between two relocations observed during radio-tracking sessions, averaged across all tracked individuals (see Zeller *et al.*, 2017). This assured that pseudo-absence locations could theoretically be reached by the corresponding woodlark individual (i.e. representing unused but available habitat). For each presence and pseudo-

absence point, the mean value of every environmental predictor was measured at the 10 spatial scales.

To test for habitat-use within their home ranges, corresponding to third-order habitat selection, the same number of randomly distributed pseudo-absences as observed occurrences was generated for each radio-tracked bird within their buffered MCP areas. To account for potential location errors, pseudo-absences had a minimum distance to presence points of 25 m. Finally, for all presence and pseudo-absence locations, we measured the mean value of all environmental variables within the same 10 spatial scales as above.

Statistical analysis

Before building the full second- and third-order habitat selection models, we first fitted univariate models separately for each scale and predictor to select the optimal scale per environmental variable, based on their lowest AICc (see Fig. A5 & A6). For that purpose, we used mixed-effect logistic regressions (R function *glmer*) with a binomial distribution and bird ID as random factor. Second, collinearity among the 23 scale-optimized variables was tested with Spearman's rank correlation. For pairs of correlated variables with $|r_s| > 0.7$ (Dormann *et al.*, 2012), the variable with the lower AICc in the univariate model was retained. Furthermore, we compared linear and quadratic univariate models among the final covariates and selected the better function with reference to AICc values (R function *poly*, package *stats*, R Development Core Team, 2018), but quadratic terms were discarded if their 95% credible intervals included zero and the effect size of the squared effect was smaller than the effect size of the linear term. As we were especially interested in the combined effects of habitat amount and fragmentation of vegetated vineyards (metrics PLAND and PD), we tested for potential linear interaction effects whenever both variables were retained in the full model. We did not include quadratic effects of PLAND or PD of vegetated fields when the interaction between them was present in the model, as linear interactions are easier to interpret and allow the identification of potential cut-off values.

All covariates were standardized (mean = 0, SD = 1) before building the multi-scale, multi-predictor model to improve model convergence and provide meaningful comparison of effect sizes. We fitted a full *glmer* model including all final covariates at their characteristic scales, bird ID as random factor and using a binomial distribution. We used the *dredge* function in the *MuMIn* package in R (Bartón, 2016, using rank = AICc) to select the most competitive models with $\Delta\text{AICc} < 2$. We applied model averaging among those top models using the *model.avg* function in the *MuMIn* package to obtain conditional averages of variable estimates $\pm \text{SE}$ and confidence intervals. We calculated the area under the receiver operating characteristic (ROC) curve (AUC) using the *roc* and *auc* functions in the *pROC* R package (Robin *et al.*, 2011) to evaluate model performance for both sensitivity (the proportion of observed positives correctly predicted) and specificity (the proportion of observed negatives correctly predicted). The standardized pAUC values range between 0 and 1, where pAUC = 1 stands for a

perfect ROC curve and pAUC = 0.5 for a non-discriminant ROC curve (Robin *et al.*, 2011). Finally, we estimated the relative importance of each variable present in the final model using a leave-one-out-jack-knife procedure, where one variable at a time was dropped from the top model and the subsequent change in AICc (ΔAICc) was calculated.

To show occurrence probability 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 *sim* function in the *arm* R package (Gelman & Su, 2015). The same statistical protocol was applied for both second- and third-order habitat selection analyses and was performed in R (R Development Core Team, 2018).

Results

We recorded a total of 2116 woodlark locations from the 36 individuals (26 males, 10 females). On average, we obtained 55 radio bearings per bird. MCP home range sizes ranged from 1 ha to 31 ha (mean \pm SD = 8.8 ± 5.1 ha). Home ranges were larger for males than females (males: 9.8 ± 5.6 ha, females: 6.4 ± 2.7 ha; linear model *lm*, $P = 0.03$) but were non-significantly related to the number of relocations (*lm*, $P = 0.09$; note we used only birds with > 30 radio bearings). As we did not identify sex-specific habitat selection patterns for any environmental predictor, we pooled the data of both sexes for all subsequent analyses.

Second-order habitat selection

Patch density and extensiveness of vegetated fields were highly collinear ($|r_s| = 0.94$) such that only PLAND and PD entered the full model, both at a scale of 100 m radius, while extensiveness was discarded. Optimal scales among the final variables ranged from the finest (50 m) up to a coarse scale of 450 m radius (Table 1). Additionally, the interaction between habitat amount and patch density of vegetated vineyards was retained after model selection (field PLAND:field PD), which yielded two competitive models with $\Delta\text{AICc} < 2$ (see Supplementary material A1).

Home ranges were mainly located in areas with either low amounts of vegetated vineyards (PLAND < 20%) which were also unfragmented (negative effect of PD) or in areas with higher amounts of vegetated vineyards (PLAND > 20%) but subdivided into multiple patches (positive effect of PD; up to 60 patches per 100 ha). This denotes a strong interaction between habitat amount and fragmentation (Table 2; Fig. 2a,b). The effect of fragmentation changed from negative to positive between 10 and 30% of habitat amount, with near zero slope for fragmentation at a habitat amount of 20% (Fig. 2a). The predicted probability of woodlark occurrence was highest for home ranges located in relatively fragmented areas with high habitat amounts (Fig. 2b). Home range selection was further driven by steppe habitat and residential areas: extensive areas of steppes within 450 m radius (extensiveness of steppe) were preferred whereas residential areas (PLAND at 100 m) were avoided (Table 2). Woodlark presence areas comprised a maximum of only 10%

residential area (mean \pm SD = $0.9 \pm 1.4\%$), while extensiveness of steppe habitat ranged from 0 to 192 m (mean \pm SD = 56 ± 40 m). Home range selection within the study area was well explained by the top model with a pAUC of 0.86 ± 0.006 at a conditional R^2 of 0.76.

Third-order habitat selection

For the third-order habitat-selection analysis, the optimal scales of the predictors were at 50, 100 and 150 m radii. Fragmentation of vegetated patches (PD) was not present in the full model, that consisted of 10 variables (Tables 1 and 2). Habitat amount of vegetated vineyards and slope position, were both included with their quadratic terms in the full model. Model selection resulted in three top models with AICc < 2, with the best model including all variables from the full model, while the second and third model each dropped one variable (PLAND of residential area and extensiveness of agricultural surfaces; see Supplementary material A1).

Woodlark presence points were mainly located in valley or lower slope areas (optimum at slope position = 0 within

150 m radius; Fig. 3a) and with high amounts of vegetated vineyards within 50 m radius (PLAND of vegetated fields > 60%; Fig. 3b). Furthermore, woodlarks selected areas with continuous vineyard cover, irrespective of bare or vegetated (extensiveness of vineyards at 50 m; Fig. 3d) surrounded by extensive grove (extensiveness of groves at 150 m radius) and steppe patches (PLAND of steppes at 150 m radius; Table 2 and Fig. 3c,e). The top model had a pAUC of 0.69 ± 0.008 and a conditional R^2 of 0.32.

Discussion

Our results indicate that, depending on the hierarchical level and the spatial scale, both habitat amount and fragmentation are important factors that influence woodlark habitat selection, but that the relative impact of fragmentation is moderated by the amount of the focal breeding habitat. This highlights the importance of considering multi-scale and multi-level effects in the habitat amount vs configuration debate. Future research, especially conservation studies that aim at providing specific, spatially explicit guidance for biodiversity preservation and restoration, must, therefore, consider both

Table 2 Conditional averaged model estimates, standard errors (SE), z values, variable importance [indicated as the drop in AICc (Δ AICc) and its relative contribution (% in brackets)] as well as confidence intervals (CI) for all standardized covariates present in the competitive models for the second order (i.e. home range settlement within study area) and third order (habitat use within home ranges) habitat selection models

Covariate	Estimate	SE	z value	Δ AICc (%)	2.50% CI	97.50% CI
Second-order habitat selection model						
(Intercept)	-0.997	0.237	4.208	-	-1.461	-0.532
Extensiveness agricultural 50	-0.065	0.083	0.79	0.6 (0.04%)	-0.228	0.097
(Extensiveness agricultural 50) ²	0.104	0.056	1.848	1.2 (0.1%)	-0.006	0.215
Extensiveness of roads 250	0.621	0.089	7.006	48.8 (2.8%)	0.447	0.795
Extensiveness of steppes 450	0.882	0.078	11.365	138.4 (8.04%)	0.730	1.035
Vegetated field PD 100	-0.057	0.093	0.611	399.0 (23.2%)	-0.239	0.125
Vegetated field PLAND 100	-0.084	0.083	1.007	473.7 (27.5%)	-0.247	0.079
PLAND edge vegetation 50	-0.217	0.075	2.898	7.1 (0.4%)	-0.363	-0.070
PLAND groves 100	-0.423	0.066	6.431	40.1 (2.3%)	-0.551	-0.294
PLAND residential 100	-1.297	0.139	9.34	120.4 (7.0%)	-1.570	-1.025
PLAND vineyards 50	0.591	0.111	5.311	22.2 (1.3%)	0.373	0.809
Slope position 250	0.481	0.061	7.872	62.9 (3.7%)	0.362	0.601
Solar radiation 250	0.246	0.088	2.802	6.1 (0.34%)	0.074	0.418
Field PD 100: field PLAND 100	1.120	0.076	14.729	400.4 (23.3%)	0.971	1.269
Third-order habitat selection model						
(Intercept)	0.019	0.116	0.164	-	-0.208	0.246
Extensiveness agricultural 50	-0.095	0.045	2.100	2 (0.5%)	-0.183	-0.006
Extensiveness of groves 150	0.396	0.064	6.169	37.6 (10%)	0.270	0.522
Extensiveness of vineyards 50	0.340	0.061	5.574	29.4 (7.9%)	0.221	0.460
Landcover AI 100	0.172	0.053	3.248	8.4 (2.2%)	0.068	0.276
Vegetated field PLAND 50	0.328	0.057	5.745	52.4 (14%)	0.216	0.440
(Vegetated field PLAND 50) ²	0.234	0.042	5.517	30.2 (8.1%)	0.151	0.317
PLAND edge vegetation 50	-0.124	0.059	2.095	3 (0.8%)	-0.240	-0.008
PLAND residential 50	-0.097	0.049	1.992	1.9 (0.5%)	-0.193	-0.002
PLAND steppes 150	0.332	0.061	5.465	29.3 (7.8%)	0.213	0.450
Slope position 150	0.308	0.054	5.700	95.6 (25.5%)	0.202	0.414
(Slope position 150) ²	-0.408	0.051	8.007	68.4 (18.3%)	-0.507	-0.308
Solar radiation 50	0.243	0.057	4.229	16.3 (4.4%)	0.130	0.356

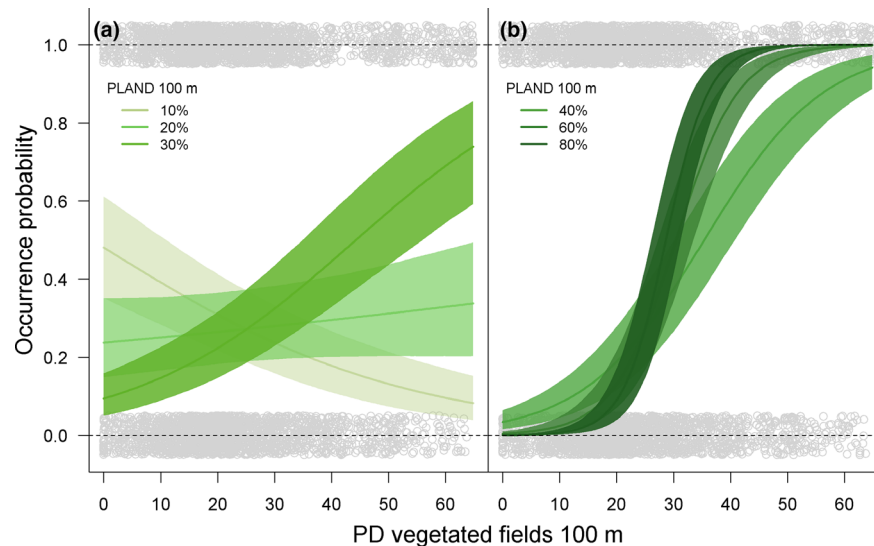


Figure 2 Predictions of woodlark occurrence probability (absence: $\gamma = 0$; presence: $\gamma = 1$) from 2nd order habitat selection model with 95%-Bayesian credible intervals (shaded areas) showing the significant interaction between various degrees of habitat amount (PLAND; a: 10–30%; b: 40–80%) and fragmentation (PD), at a characteristic scale of 100 m radius for both predictors. PLAND within 100 m radius ranged from 0–89%. All variables present in the competitive models, except the two under consideration, were fixed at their mean values for these projections. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

factors separately and interdependently and at multiple hierarchical levels.

Fragmentation effects change with habitat amount

In line with our first hypothesis, we found negative fragmentation effects only in areas with low habitat amount during woodlarks home range selection. But interestingly the effect of fragmentation became positive in the context of higher habitat amount (Fig. 2a). This corroborates earlier studies showing that woodlarks, and farmland associated species generally, prefer heterogeneous habitat arrangements and variegated landscape mosaics (e.g., Fahrig, 2003; Vickery & Arlettaz, 2012; Campedelli *et al.*, 2015; Fahrig, 2017; Leroux *et al.*, 2017). When selecting their home ranges, woodlarks are ecologically more constrained in high-intensity vinicultural areas where vegetated vineyard fields are rare. Under these circumstances, they may be forced to compensate for a lack of suitable habitat in the wider landscape by selecting areas with aggregated ground-vegetated patches, where food supply and nesting opportunities are locally greater (Arlettaz *et al.*, 2012; Buehler *et al.*, 2017; Bosco *et al.*, 2019b). In contrast, in areas with higher amounts of habitat, woodlarks prefer a heterogeneous distribution of vegetated vineyards among disjunct fields which are likely to be characterized by differing managements of ground coverage. In our study area, one encounters large differences in the way vegetated vineyard fields are managed, which leads to variable vegetation composition and structure. This spatiotemporal habitat heterogeneity is known to be beneficial to biodiversity in other agroecosystems, such as hay meadows where mowing operations can generate contrasted habitat heterogeneity in space and time

(Benton *et al.*, 2003; Vickery & Arlettaz, 2012; Buri *et al.*, 2013). It is known that complex agricultural landscapes are more likely to provide a more stable palette of resources that species require to fulfill their life cycle, compared to homogenized farmlands such as extensive monocultures (e.g. Rundlöf *et al.*, 2008; Tschamtko *et al.*, 2012). The optimal scales of habitat amount and fragmentation at 100 m indicate that the birds are considering extents of around 3 ha when selecting their home ranges. Such extents comprise on average 50 vineyard fields (mean field size in the study area = $612 \text{ m}^2 \pm 1410 \text{ m}^2$) and represent one third of an average woodlark home range of c. 9 ha. Thus, even though this selection is at a fine scale, it shows that spatial configuration and composition of vineyard fields are important aspects in woodlark home range selection. Natural elements in the wider landscape also played a role in woodlark occurrence probability at the second-order selection. Extensive areas of steppe within a 450 m radius (i.e. c. 64 ha; 7 woodlark home ranges) were important, exemplifying woodlark preference for semi-open, arid habitats in the wider landscape (Bowden, 1990). A small fraction of the local woodlark population breeds in steppe habitats on south-exposed, shallow slopes. Human settlements were avoided at the 100 m radius scale (PLAND residential area), supporting the view that woodlarks are non-synanthropic and generally need unsealed land covered by a mixture of extensive agricultural area and semi-natural habitats (Campedelli *et al.*, 2015).

Habitat amount shapes habitat use at a fine scale

As hypothesized, habitat fragmentation did not influence woodlark presence when habitat selection was investigated at

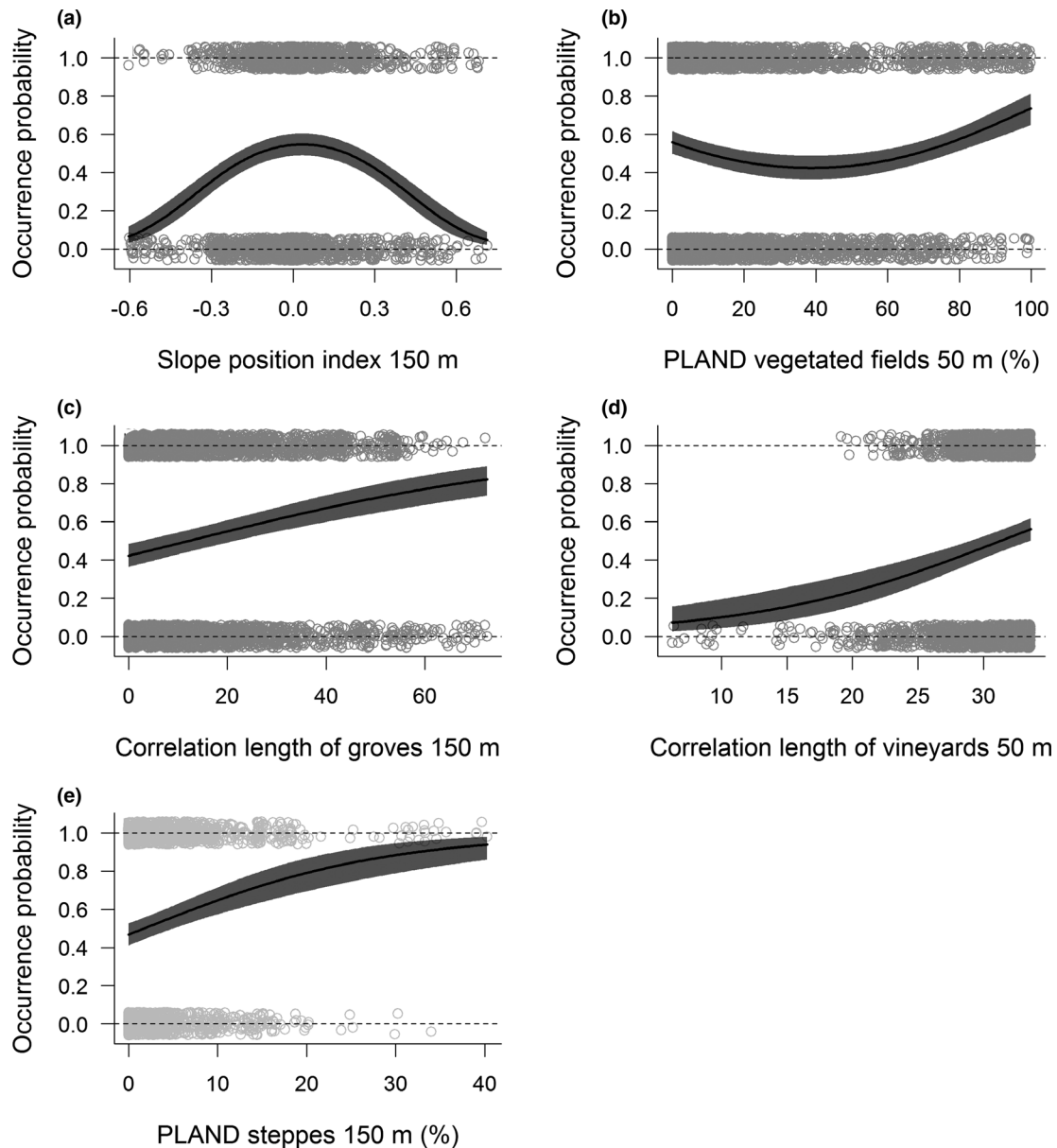


Figure 3 Model-averaged predictions of woodlark occurrence probability (absence: $\gamma = 0$; presence: $\gamma = 1$) from 3rd order habitat selection model with 95%-Bayesian credible intervals (shaded areas) showing the five most important variables. All variables present in the competitive models, except the ones under consideration, were fixed at their mean values for these projections. (a) Negative quadratic effect of the slope position index within 150 m radius; (b) positive quadratic effect of habitat amount of vegetated vineyards within 50 m radius (PLAND); (c) extensiveness of groves at 150 m scale; (d) extensiveness of vineyards within a 50 m radius; (e) habitat amount of steppes (PLAND) within 150 m radius.

a finer scale, while habitat amount was again a major predictor, but now at a smaller scale of 50 m radius (c. 1 ha). These differing results for the two orders of habitat selection are likely explained by the fact that, for within home range habitat use, woodlarks often seem to show strong site fidelity throughout the breeding season (based on field observations). Thus, we assume that irrespective of their spatial configuration, at this level the birds mainly select extensive vegetated fields at a scale of around 1 ha, corresponding to groups of

c. 15 fields. Woodlark occurrence probability strongly increased if areas had more than 60% ground-vegetation cover. These results are consistent with previous findings at finer scales about woodlarks foraging- and nest-site selection in vineyards (fourth order of habitat selection, Arlettaz *et al.*, 2012; Buehler *et al.*, 2017).

Slope position was a main determinant of woodlark habitat use within their home ranges (third order) and revealed selection for valley or lower slope areas within a 150 m radius

scale, which corresponds roughly to a mean woodlark home range (c. 7 ha). Hence, even though this variable influences within home range habitat use, woodlarks respond to topography at a broader scale. Slope position was positively related to ground vegetation cover (NDVI within 50 m radius), indicating that evenly sloped landscapes are more likely to be vegetated and are thus (indirectly) used more often. At this scale, woodlarks were also found in areas that had a mosaic of grove patches and steppes, again demonstrating a preference for heterogeneous landscapes within the home range (Campedelli *et al.*, 2015), in particular where grove edge length is increased (Brambilla & Rubolini, 2009).

Conclusions

Our results corroborate previous findings supporting the habitat amount hypothesis (e.g. Fahrig, 2013; Melo *et al.*, 2017; Seibold *et al.*, 2017), and those stating that habitat configuration also has important effects when studying biodiversity responses (e.g. Schüepp *et al.*, 2014; Hanski, 2015; Haddad *et al.*, 2017; Lindgren & Cousins, 2017; Fletcher *et al.*, 2018). Furthermore, we not only highlight the necessity of considering interactive effects between habitat amount and fragmentation but also support the so-called 20% habitat amount rule (Flather & Bevers, 2002; Rybicki & Hanski, 2013), below which fragmentation effects are predicted to become adverse. In addition, given that the spatial scales at which our predictors showed their strongest influence were dependent on the hierarchical level of analysis, we stress the importance of applying scale-explicit analyses at different levels of habitat selection in order to improve predictions and accuracy about species-habitat relationships (e.g. McGarigal *et al.*, 2016).

From a species conservation perspective, our findings suggest increasing the number of vegetated vineyard fields at a landscape scale. Further, ground-vegetated fields should be arranged in disjunct patches when vegetated vineyards cover more than 20% in the wider landscape. In contrast, in areas where habitat amount is limited (below 20%), vegetated fields should be aggregated. Different agricultural policies, such as subsidized connectivity projects, can be used as tools to manage the spatial configuration of vegetated fields in viticultural landscapes. Additionally, natural elements such as steppes and groves must be preserved or restored to obtain a variegated mosaic. Such measures promoting vegetated vineyards embedded in heterogeneous landscapes will benefit woodlarks and likely also overall vineyard biodiversity.

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Supporting information

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

Data S1. Supplementary material