



Ground greening in vineyards promotes the Woodlark *Lullula arborea* and their invertebrate prey

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Received: 18 November 2018 / Revised: 8 February 2019 / Accepted: 8 April 2019
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Abstract

Vineyards are intensively managed monocultures, constituting homogeneously cultivated landscapes. They often have a mineral appearance, not only because they occur mostly in xeric biomes but also as a result of the herbicide treatments used to combat ground vegetation. However, new vineyard management practices are being developed that tolerate more vegetation cover on the ground, potentially having positive impacts on biodiversity. We have investigated the effects of ground greening on habitat preferences of the Woodlark (*Lullula arborea*), an emblematic, insectivorous passerine typical of vineyards in central and southern Europe. We first investigated the role of ground vegetation cover and plant species richness on habitat use by Woodlarks, while accounting for various additional habitat characteristics. Second, we assessed whether the dependence of Woodlarks on ground vegetation cover could be mediated by an increased occurrence of invertebrate prey. Ground-dwelling invertebrates were sampled with pitfall traps placed in vineyard fields visited by Woodlarks (presence fields) and in adjacent vineyards where Woodlarks had not been observed (pseudo-absence fields). We show that increased ground vegetation cover, plant species richness and wider inter-rows were the main drivers of Woodlark occurrence. Overall invertebrate prey abundance increased with ground vegetation cover. Similarly, the abundance and number of beetle and spider families were primarily driven by increased ground vegetation cover, plant species richness or wider inter-rows. We conclude that less intensive management, which involves the restricted use of herbicides and concomitantly favors a diverse plant community, promotes Woodlarks and their invertebrate prey, thus having a positive impact on vineyard biodiversity at multiple trophic levels.

Keywords Ground vegetation · Habitat preferences · Herbicides · Plant species richness

Zusammenfassung

Begrünte Weinberge fördern die Heidelerche *Lullula arborea* und ihre Beute

Weinberge sind intensive genutzte Monokulturen, welche oftmals homogen bewirtschaftete Landschaften prägen. Sie haben meist ein mineralisches Erscheinungsbild, nicht nur, weil sie vor allem in trockenen Biomen vorkommen, aber auch durch die regelmässigen Herbizid-Anwendungen zur Abtötung der Bodenvegetation. Es werden jedoch zunehmend neue Bewirtschaftungsweisen entwickelt, welche eine Bodenbegrünung zulassen – was positive Effekte auf die Biodiversität haben kann. Wir haben die Effekte der Bodenbegrünung auf die Habitatansprüche der Heidelerche (*Lullula arborea*) erforscht, eine typische, insektivore Singvogelart der zentral- und südeuropäischen Weinberge. In einem ersten Schritt untersuchten wir die Rolle der Bodenbegrünung und ihrer Artenvielfalt auf die Lebensraumnutzung der Heidelerche, wobei wir verschiedene

Communicated by T. Gottschalk.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10336-019-01666-7>) contains supplementary material, which is available to authorized users.

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zusätzliche Habitatvariablen berücksichtigten. In einem nächsten Schritt wollten wir verstehen, ob die Präferenz der Heidelerchen für begrünte Weinberge möglicherweise durch eine erhöhte Beutedichte erklärt wird. Bodenlebende Wirbellose wurden mit Bodenfallen gefangen, welche wir in zwei unterschiedlichen Kategorien von Weinbergen platzierten: Solche, die von Heidelerchen besucht wurden (Präsenz Parzellen) und angrenzende Parzellen, in welchen wir keine Heidelerchen beobachteten (Pseudo-absenz Parzellen). Wir zeigen, dass hauptsächlich eine erhöhte Bodenbegrünung, Anzahl an Pflanzenarten und breitere Fahrgassen zwischen den Reblinien die Vorkommenswahrscheinlichkeit der Heidelerche beeinflussten. Die totale Abundanz der Wirbellosen war ebenfalls höher in begrünten Weinbergen. Auch die Abundanz und Anzahl der Käfer- und Spinnenfamilien konnten entweder durch eine erhöhte Bodenbegrünung, Pflanzenvielfalt oder breitere Fahrgassen erklärt werden. Wir schliessen daraus, dass eine weniger intensive Bewirtschaftungsweise, welche den Herbizideinsatz vermindert und dadurch eine vielfältige Pflanzengesellschaft ermöglicht, die Heidelerche und ihre Beute fördert und somit positive Effekte auf die Biodiversität auf mehreren trophischen Ebenen hat.

Introduction

The so-called “green revolution” of the past century has resulted in a rapid intensification of most cultivated systems, leading to widespread declines in farmland biodiversity (Mendenhall et al. 2014; Heldbjerg et al. 2018), including bird populations (Benton et al. 2002; Hallmann et al. 2014). Options to counteract this decline have consisted of measures to increase the heterogeneity of cultivated landscapes, ranging from the delineation of protected areas to more sustainable ways of farming, from both a biodiversity and productivity perspective (Vandermeer and Perfecto 2007; Fischer et al. 2008; Tscharrnke et al. 2012; Vickery and Arlettaz 2012; Viers et al. 2013). Less intensive management practices have thus been developed with the aim to provide current and future generations with solutions that trade off food security for a growing human population and environmental sustainability (Fischer et al. 2008; Foley et al. 2011).

Vineyards are one such crop system that underwent strong farming intensification (Altieri and Nicholls 2002; Schmitt et al. 2008) and thus contributed to the destruction, degradation and fragmentation of natural and semi-natural ecosystems, posing a serious threat to biodiversity (Viers et al. 2013). Consequently, there is an increasing interest in optimizing in-field ‘biodiversity-friendly’ production practices and maintaining and restoring natural and semi-natural habitats in the wider vineyard surroundings (Gillespie and Wratten 2012; Assandri et al. 2016, 2017a; Buehler et al. 2017), as well as integrating synergistic approaches to favor biodiversity and ecosystem services (Brambilla et al. 2017; Assandri et al. 2018). Depending on the viticultural management practice, vineyards may harbor rare bird species (Assandri et al. 2017a, b; Guyot et al. 2017), while traditional, extensively managed vineyards typically show higher biodiversity and often lower pest vulnerability than conventionally, intensively managed vineyards (Altieri and Nicholls 2002; Schmitt et al. 2008; Trivellone et al. 2014).

In south-western Switzerland (Valais) around 80% of all vineyards have a mineral appearance due to widespread, systematic herbicide application, with thus only a minor fraction of the overall vineyard area harboring ground vegetation cover. Guyot et al. (2017) have shown that the avifauna of Valais vineyards is richer and more abundant in areas with a good ground vegetation cover. Terrestrially feeding, insectivorous birds typically show a preference for habitat mosaics, where ground vegetation and bare ground alternate at a fine scale (e.g. vine-row vs. inter-row). This preference is most likely due to ground vegetation promoting invertebrate prey supply, whereas bare ground increases prey accessibility for the birds (Schaub et al. 2010; Vickery and Arlettaz 2012). Therefore, prey availability—which is abundance modified by accessibility—may operate as a major driver of both territory settlement and foraging habitat selection (Benton et al. 2002; Atkinson et al. 2005; Traba et al. 2008).

The Woodlark (*Lullula arborea*) is a terrestrially feeding, mostly insectivorous bird that occurs throughout the Western Palearctic. In Switzerland, it is classified as vulnerable by the Swiss Red List and also as a species that necessitates specific recovery programs (Keller et al. 2010a, b). The European Union considers it to be a priority species being subject to specific conservation measures (EU Annex I, Birds Directive 2009/147/CE; The European Parliament and the Council of the European Union 2010). However, the species is not endangered globally (Burfield et al. 2004), and some populations are even growing, such as those in the UK (Conway et al. 2009), Italy (Campedelli et al. 2015), France and the Netherlands (Burfield et al. 2004). The species breeds in a variety of habitats, including semi-natural heathland (Mallord et al. 2007; Praus et al. 2014), but also in traditional, low-intensity agricultural systems (Brambilla and Rubolini 2009; Brambilla et al. 2012), wooded pastures (Schaefer and Vogel 2000), coniferous tree plantations (Bowden 1990) and olive groves (Castro-Caro et al. 2014) and vineyards (Arlettaz et al. 2012; Pithon et al. 2016;

Buehler et al. 2017). Around half of the Swiss Woodlark population occurs in Valais, where it mostly breeds in vineyards on the south-facing foothills along the Rhône valley (Arlettaz et al. 2012). There, Woodlarks select foraging habitats consisting of alternating vegetated and bare ground patches (Arlettaz et al. 2012) that are likely to enhance prey accessibility (Menz et al. 2009; Schaub et al. 2010; Guyot et al. 2017). However, other considerations than mere foraging site selection probably drive habitat selection decisions, of which the most notable would likely be the availability of favorable breeding opportunities. Woodlarks often build their nests in dense and tall vegetation patches to enhance nest concealment (Harrison and Forster 1959; Mallord et al. 2007; Buehler et al. 2017). Trade-offs between foraging and nest site selection may, therefore, be achieved only via a higher order of habitat selection, i.e. where both conditions are spatially fulfilled.

The aim of the study reported here was to answer the following questions: (1) What are the effects of vineyard ground vegetation, plant species richness and other environmental variables on the habitat use of Woodlarks? (2) What are the effects of vineyard ground vegetation, plant species richness and other vineyard habitat variables on invertebrate communities? and (3) Is invertebrate prey more abundant in fields where Woodlarks are present? To obtain the answers to these questions, we first assessed vineyard habitat preference patterns of Woodlarks during territory establishment and habitat use in the spring, with a special focus on the availability of ground vegetation cover and richness of plant species. Second, we studied the links between invertebrate prey abundance, vineyard habitat features and Woodlark occurrence.

Materials and methods

Study area

The study was carried out in 2012 (Woodlark habitat use part of study) and 2013 (invertebrate prey part of study) in two nearby areas in the upper Rhône Valley, in Valais, southwestern Switzerland: Leytron/Chamoson (46°20'N, 7°21'E) with a vineyard surface area of 4.5 km² and Salgesch/Varen (46°32'N, 7°58'E) with a vineyard surface area of 2.7 km². In both areas, vineyards are the predominant land-use type where they constitute a mosaic consisting of approximately 80% intensively-managed vineyards—by means of moderate to high herbicide applications—interspersed with a few vegetated vineyards (approx. 20% of the surface area). Most vineyards are located on the south-facing slopes north of the Rhône river and border on patches of dry forest and rocky steppes (climatic grasslands typically occurring in the driest areas of the inner

Alps). The removal of the grass layer in dry vineyard areas serves primarily to prevent competition between the vines and natural ground vegetation, notably for nutrient and water resources. However, there is an ongoing trend towards more ground greening in Valais, although even in vegetated vineyards, ground coverage is almost always restricted to the inter-rows, as the vine rows themselves are kept bare, either chemically or mechanically, leading to a within-field mosaic of vegetated and bare ground. While intra-annual variation (spring vs. summer vs. autumn) in ground vegetation cover and plant species composition are expected to be high due to vegetation cycles in temperate zones, inter-annual variation within a field is low given that the management practices remain stable over years. This is partly due to agricultural legislation related to long-term contracted subsidies in Switzerland. Given the relatively stable management practice in a given vineyard field, we believe that variation in invertebrate abundance between sampling sites is repeatable among years and that combining invertebrate and Woodlark data is therefore a valid strategy, even though the sampling did not occur in the same year (e.g. Strebel et al. 2015). We distinguished between different vineyard fields based on their management, such that a field represents a uniformly managed vineyard, usually with ground vegetation structures and cultivation practices that are distinct from those of neighboring fields, making the delimitations obvious. The size of a field is highly variable in the area and ranged from 0.03 to 1.5 ha in our sample, with a general trend to be small, with an average size of 0.24 ha. The management modes with respect to fertilizer and pesticide inputs vary considerably among farmers. Nonetheless, it is mainly herbicides and fungicides that are applied several times between March and July. Some farmers fertilize their fields with solid manure, pomace, compost or green manure, whereas synthetic fertilizers are used less frequently. During our study, there were no certified organic regimes within our study areas.

Woodlark transect surveys

The study on habitat use was based on repeated surveys performed along two transects (Leytron/Chamoson 7.3 km long; Salgesch/Varen 5 km long; Electronic Supplementary Material [ESM] 1), both having an observational buffer of 250 m at each side. This buffer was chosen based on an antecedent pilot study showing that Woodlarks can be well detected acoustically within a distance of 250 m. The transects were selected because they are located in regions consisting of wide-ranging vineyard areas, representing the mosaic of bare versus vegetated fields and harboring relatively large Woodlark populations (after Sierro and Arlettaz 2003). In total, four surveys per transect were conducted during March

2012, i.e. two surveys per week. This survey period was chosen as Woodlarks show their highest (singing) activity right after they return to their breeding grounds in late February and early March, settle their territories and begin breeding; hence, they are easier to detect at this time. All surveys were performed within 4 h of sunrise, i.e. during peak singing activity (Sirami et al. 2011), and there was little variation in weather conditions between surveys (no precipitation, no or little wind). Observations were restricted to exact locations of Woodlarks that were either displaying territorial behavior (singing on the ground or on a perch) or landing onto a precise spot after performing an extended song flight.

As management practices and hence ground vegetation structures vary strongly from field to field, we surmised that there is a selection process likely to happen at this scale. We thereafter compared fields harboring bird observations (presence fields, i.e. used habitat) to all those directly surrounding a presence field, where no observations were obtained (pseudo-absence fields, i.e. unused but available habitat; according to Guyot et al. 2017). This approach, where presence fields were compared to the vineyard habitat conditions directly surrounding it (i.e. all adjacent pseudo-absence fields) resulted in a non-balanced design as the number of pseudo-absence fields varied considerably among the different presence fields (number of pseudo-absences per presence field: range = 1–12; mean = 4). Based on the field status (i.e. presence vs. pseudo-absence), we considered a presence field with its adjacent pseudo-absence fields as a spatially dependent study “unit” (ESM 2). Although a given vineyard presence field could have harbored more than one Woodlark observation throughout the surveys, it was entered into the analysis only once.

Invertebrate sampling

The Woodlark survey data from 2012 served as a basis to select fields for invertebrate prey sampling, which was conducted in 2013. This approach was chosen in order to first compare invertebrate communities between Woodlark presence and pseudo-absence fields and second to assess the effect of ground vegetation structure and other habitat variables on invertebrates. Hence, among all Woodlark presence fields identified in 2012, we chose 15 in each of the two transect areas based on Woodlark observations in or close to those sampling fields in the spring of 2013 (field observations). As such, we can thus infer that our prey sampling was performed in bird territories that were also active in 2013. Per presence field, a subset of three adjacent pseudo-absence fields was selected randomly; the latter served as controls. In total, invertebrates were thus sampled from 30 presence fields and 90 pseudo-absence fields (from an original 57 presence and 231 pseudo-absence fields in 2012).

As Woodlarks feed terrestrially and have been described as generalist insectivores (Glutz von Blotzheim and Bauer 1985; Bowden 1990), we used pitfall traps to catch the ground-dwelling invertebrate prey that are likely to make up the bulk of their diet. The traps (diameter 7.5 cm), which were filled with 200 ml of a mixture of water and ethylene glycol, as well as with a scentless detergent to decrease water surface tension, were active for 8 days in the second week of May (between 7 May 2013 and 17 May 2013), matching the peak of Woodlark chick provisioning activity (Buehler et al. 2017). As we compared one presence field against three pseudo-absence fields, we installed three traps per presence field and one trap per pseudo-absence field, which enabled a 3:3 comparison per sampling unit (i.e. a presence field with all its adjacent pseudo-absence fields; ESM 2). The traps were buried in the middle of a field, along the vine rows to avoid interfering with farming operations and edge effects from adjacent fields. Of the 180 traps, 23 were destroyed by machines or removed, resulting in a total of 81 trap samples in presence fields and 76 in pseudo-absence fields. In the laboratory, invertebrates were identified to order level, with beetles (Coleoptera) and spiders (Aranaea) identified to family level.

For the analyses, total invertebrate abundance and specifically beetle and spider abundance were used as response variables. In addition, we analyzed the number of spider and beetle families, as higher taxonomic richness has repeatedly been established to be a good surrogate for species richness for several plant and animal taxa in different biomes (Williams and Gaston 1994; Balmford et al. 1996; Biaggini et al. 2007).

Habitat variables

The same habitat variables were mapped in all fields in the second week of April 2012 for the Woodlark habitat use part of the study and again during pitfall sampling sessions in 2013 for the invertebrate prey part (Table 1). Ground vegetation cover was visually estimated over the whole vineyard field as the mean coverage of all inter-rows and vine rows. In addition to quantitative aspects of ground vegetation, we estimated plant species richness as an index of ground vegetation quality. Plant species richness was determined by counting the number of plant species present in two randomly chosen, vegetated inter-rows within every field. To standardize the sampling effort, we invested 15 min per field in counting the number of different plant species (e.g. Archaux et al. 2006). Vineyard plantation and management structure were measured as follows: (1) inter-row type, indicating whether all inter-rows had the same ground cover management or not within a field; (2) inter-row width, which is the distance between vine rows; (3) whether the field was on a terrace system; and (4) whether the vine plants were

Table 1 Vineyard field variables derived from a geographic information system or field assessments and used as predictors for the modeling

Category	Covariate	Description	Data source
Topography	Slope	Mean field slope (°) (range 1.57°–30.47°; mean ± SD 7.56 ± 6.07)	DEM 25 m
	Aspect	Mean aspect (°) (range 78.69°–251.57°; mean ± SD 176.72 ± 40.93)	DEM 25 m
Vineyard structure	Inter-row type	Management of inter-rows (categorical: 1 = all equal, 2 = VBV, 3 = VBBV, 4 = VBBBV) ^a	Recorded in the field
	Terraced	Field structure (categorical: 1 = not terraced, i.e. continuous slope; 2 = terraced)	Recorded in the field
	Wire	Attachment of wine plants (categorical: 1 = on wires; 2 = on poles with Gobelet system)	Recorded in the field
	Inter-row width	The distance between the rows (in cm) (if inter-rows had variable widths, the mean value was calculated)	Recorded in the field
Ground vegetation	Vegetation	Mean ground vegetation cover (%), visually estimated for the whole field (continuous, in 5% steps; range 0–80%; mean ± SD 23.56 ± 23.71)	Recorded in the field
	Plant species richness	Number of plant species recorded in two rows for 15 min (continuous; range 0–12; mean ± SD 3.43 ± 3.18)	Recorded in the field

SD Standard deviation; DEM digital elevation model

^aV, Vegetated inter-row; B, bare inter-row. VBV, VBBV, VBBBV stand for the order of inter-row management in a field. In many vineyard fields vegetated inter-rows (V) are interspersed with 1–3 bare inter-rows (B) due to herbicide application

fixed on horizontal metal wires between distant poles or aligned on single-stand poles (Gobelet system). Mean aspect and slope steepness of vineyard fields were estimated from a digital elevation model (QGIS Development Team 2018).

Statistical analyses

For both the Woodlark habitat use and the invertebrate prey parts of the study, we used a model selection approach, applying a similar protocol and including the same habitat predictors in both parts (see Table 1). To answer the first question on habitat use, field status (i.e. presence vs. pseudo-absence) entered the logistic linear regression models as response variable ('glmer' R package 'lme4'; Bates et al. 2015), fitting a binomial distribution. The variable unit (i.e. presence field with all its adjacent pseudo-absences) was entered into the models as a random factor, but as the variance explained was zero, it was discarded from the resulting generalized linear model (GLM). For the invertebrate prey analysis (second question), overall invertebrate abundance, and beetle and spider abundance as well as the number of families, were entered into the linear regressions as response variables. We applied either generalized linear mixed effect models ('glmer' R package 'lme4'; Bates et al. 2015) with a Poisson distribution (for total invertebrate abundance and number of spider and beetle families) or linear mixed effect models 'lme4' with a Gaussian distribution (for spider and beetle abundance, which were both log-transformed due to right-skewness of the data). Overdispersion of the count data was tested using the function 'dispers_glm' (R package 'blme4'; Korner-Nievergelt 2015), and an observation-level random effect was then included if necessary (Gillies

et al. 2006; Bolker et al. 2009). The variables unit and field identification, to control for the three spatially clumped traps within a presence field, were always included as random variables, except when the explained variance was low ($p < 0.0001$) and model fits were worse. To address the third question (Is invertebrate prey more abundant in fields where Woodlarks are present?), we modeled all invertebrate variables against field status (i.e. presence field vs. pseudo-absence field) in the linear regression models described above.

For the model selection approach used for question 1 and 3, all environmental predictors were transformed when necessary: arcsin-square-root transformation for proportional data and log-transformation for count data or variables that were strongly right-skewed. Variables were then standardized to enable comparison between model estimates and improve convergence of the model algorithm. Collinearity between continuous variables was then calculated using Spearman rank correlation tests. Among intercorrelated variables with $|r_s| > 0.7$, the variable with the lower Akaike information criterion (AIC) in univariate model testing was retained (Dormann et al. 2012). Special interest was focused on the effects of ground vegetation cover and plant taxonomic richness on our response variables. However, as plant taxonomic richness increased significantly with increasing ground vegetation cover ('lm': estimate ± standard error [SE] = 0.0886 ± 0.0053; $t = 16.845$; $p < 0.001$), we had to control for ground vegetation when testing the effects of plant richness. Given their marked collinearity (Spearman correlation $|r_s| = 0.72$) they could not be tested together as such in the same multivariate models. We instead used the regression residuals (Graham 2003) of taxonomic richness

Table 2 Competitive models ($\Delta\text{AICc} < 2$) for Woodlark (*Lullula arborea*) occurrence, invertebrate abundance, beetle and spider abundance and number of their families

Rank	Model	<i>df</i>	logLink	AICc	ΔAICc	Model weight
Woodlark occurrence						
1	Residual plant richness + inter-row.log	3	-135.08	276.25	0	0.71
2	Inter-row.log + vegetation.as	3	-135.98	278.05	1.8	0.29
Invertebrate abundance						
1	Inter-row.log + vegetation.as	6	-733.06	1478.67	0	0.40
2	Residual plant richness + vegetation.as	6	-733.28	1479.12	0.44	0.32
3	Vegetation.as	5	-734.48	1479.36	0.69	0.28
Beetle abundance						
1	Residual plant richness	5	-219.82	450.04	0	0.51
2	Vegetation.as	5	-220.50	451.40	1.36	0.26
3	(Null)	4	-221.71	451.67	1.64	0.23
Number of beetle families						
1	Inter-row.log + vegetation.as	5	-283.47	577.3	0	1
Spider abundance						
1	Residual plant richness	5	-173.92	358.2	0	1
Number of spider families						
1	Residual plant richness + inter-row.log	5	-270.72	551.84	0	0.42
2	Residual plant richness + vegetation.as	5	-270.81	552.02	0.18	0.38
3	Residual plant richness	4	-270.54	553.35	1.51	0.20

df, Degrees of freedom; AICc, Akaike information criterion with a correction for small sample sizes; ΔAICc , change in AICc

Inter-row width was log-transformed (.log) and ground vegetation arcsin-square-root transformed (.as), as shown by their name extensions. See section [Statistical analyses](#) for a more detailed description

on ground vegetation cover, which then served as a substitute for plant taxonomic richness (hereafter “residual plant taxonomic richness”), while ground vegetation cover was entered into all models as the original variable.

Further, only variables with $p < 0.1$ in the univariate models were included for the next analytical step to avoid model overfitting, especially given the relatively small sample sizes. Also, linear and quadratic univariate models for the retained variables were tested (R function ‘poly’) and ranked based on their AIC value. For all models, the linear term was chosen, as all variables performed better linearly. On that basis, a full model with all retained variables was built and a model selection approach applied using the ‘dredge’ function (R package ‘MuMIn’, using ‘rank’ = AICc [AIC for small sample sizes]; [Bartón 2016](#)). Among competitive models with $\Delta\text{AICc} < 2$, we performed model-averaging for variable estimates (function ‘model.avg.’ R package ‘MuMIn’; [Bartón 2016](#)).

To visually illustrate occurrence probability in relation to the various significant effects, we plotted model-averaged functions estimated from a Bayesian approach, in which samples were drawn from joint posterior distributions with the function ‘sim’ (‘arm’ R package; [Gelman and Su 2015](#)). All statistical analyses were performed with the open-source software R (R Development Core Team [2018](#)).

Results

We collected 136 Woodlark visual observations with territorial behavior (Leytron/Chamoson: $n = 88$; Salgesch/Varen: $n = 48$). As there were multiple observations at some vineyard fields, we had a total of 57 Woodlark presence fields and 231 pseudo-absence fields at the end of the study (see ESM 1 for additional details).

In total, we sampled 7406 invertebrates (mean \pm standard deviation [SD] 47.17 ± 35.53 specimens per pitfall trap). These belonged to 19 different taxonomic orders, of which beetles were the most abundant (Coleoptera, $n = 3726$; 50%), followed by spiders (Araneidaea, $n = 974$; 13%) and flies (Diptera, $n = 691$; 9.3%). We identified 19 beetle families and 13 different spider families (see ESM 3 for additional details).

Woodlark habitat use

For the model selection approach, among the eight environmental covariates, three (inter-row width, ground vegetation cover, residual plant taxonomic richness) were entered into the full model, while the others were discarded due to collinearity or low effects in the univariate models (Table 2). Model averaging showed that Woodlark presence responded significantly and positively to wider inter-rows and higher

Table 3 Model-averaged conditional estimates, standard errors, z or t values, and lower and upper 2.5% confidence intervals for Woodlark occurrence, total invertebrate abundance, beetle and spider abundance and number of their respective families

Term	Estimate	Standard error	z or t value	2.5% confidence interval	97.5% confidence interval
Woodlark occurrence					
(Intercept)	-1.510	0.161	9.292	-1.82	-1.186
Residual plant richness	0.327	0.154	2.113	0.024	0.63
Inter-row.log	0.475	0.154	3.076	0.172	0.778
Vegetation.as	0.25	0.152	1.640	-0.049	0.548
Invertebrate abundance					
(Intercept)	3.511	0.078	44.791	3.358	3.665
Inter-row.log	0.135	0.078	1.722	-0.019	0.289
Vegetation.as	0.208	0.078	2.652	0.054	0.362
Residual plant richness	0.124	0.08	1.542	-0.034	0.281
Beetle abundance					
(Intercept)	2.593	0.122	21.173	2.353	2.833
Residual plant richness	0.285	0.11	2.587	0.069	0.500
Vegetation.as	0.246	0.105	2.335	0.040	0.453
Number of beetle families					
(Intercept)	1.081	0.047	22.959	0.986	1.171
Inter-row.log	0.116	0.049	2.346	0.019	0.213
Vegetation.as	0.161	0.051	3.170	0.062	0.261
Spider abundance					
(Intercept)	1.662	0.068	24.49	1.525	1.797
Residual plant richness	0.211	0.068	3.11	0.077	0.344
Number of spider families					
(Intercept)	0.957	0.05	19.020	0.859	1.056
Residual plant richness	0.155	0.051	3.015	0.054	0.255
Inter-row.log	0.095	0.05	1.896	-0.003	0.193
Vegetation.as	0.098	0.052	1.849	-0.006	0.201

Variables with significant effects are set in bold

residual plant taxonomic richness (Table 3; Fig. 1). Woodlark presence also tended to be positively influenced by the amount of ground vegetation cover, but this effect was statistically non-significant.

Vineyard fields with Woodlark presence had, on average, 1.5-fold more invertebrates than the pseudo-absence fields (mean \pm SD; 55.86 ± 36.15 vs. 37.91 ± 32.60 ; 'glmer' estimate: 0.52 ± 0.16 , $z = 3.272$; $p = 0.001$; Fig. 2a). Beetle and spider abundance as well as number of the respective families were also considerably higher in Woodlark presence fields than in pseudo-absence fields (beetle abundance: 0.56 ± 0.23 , $t = 2.47$, $p = 0.02$; number of beetle families: 0.39 ± 0.1 , $z = 3.91$, $p < 0.001$; spider abundance: 0.50 ± 0.14 , $t = 3.67$, $p < 0.001$; number of spider families: 0.32 ± 0.1 , $z = 3.16$, $p = 0.002$; Fig. 2b–e).

Invertebrate prey communities

To analyze total invertebrate abundance, we entered the same three variables as for the Woodlark habitat use into the full model (Table 2). In the top three models, ground

vegetation cover was always present and was significantly and positively related to overall invertebrate abundance (Table 3; Fig. 3). Residual plant richness and inter-row width both included zero in their 95% confidence intervals, denoting an absence of a statistically significant effect (Table 3).

With respect to beetle abundance, the top models only included residual plant taxonomic richness and ground vegetation, both of which were found to have significant positive effects (Table 2; Fig. 4a, b). However, the null model was also included among the three competitive models (Table 3). Ground vegetation cover and inter-row width were retained in the full model when testing for the number of beetle families (Table 2). There was only one top model, with both predictors having significant positive effects on the number of beetle families (Table 3; Fig. 4c, d).

Inter-row width, ground vegetation cover and residual plant taxonomic richness were entered into the model selection for spider abundance, while only residual plant taxonomic richness was present in the only competitive model, being positively related to spider abundance (Table 2; Fig. 5a). Again, residual plant taxonomic richness, inter-row

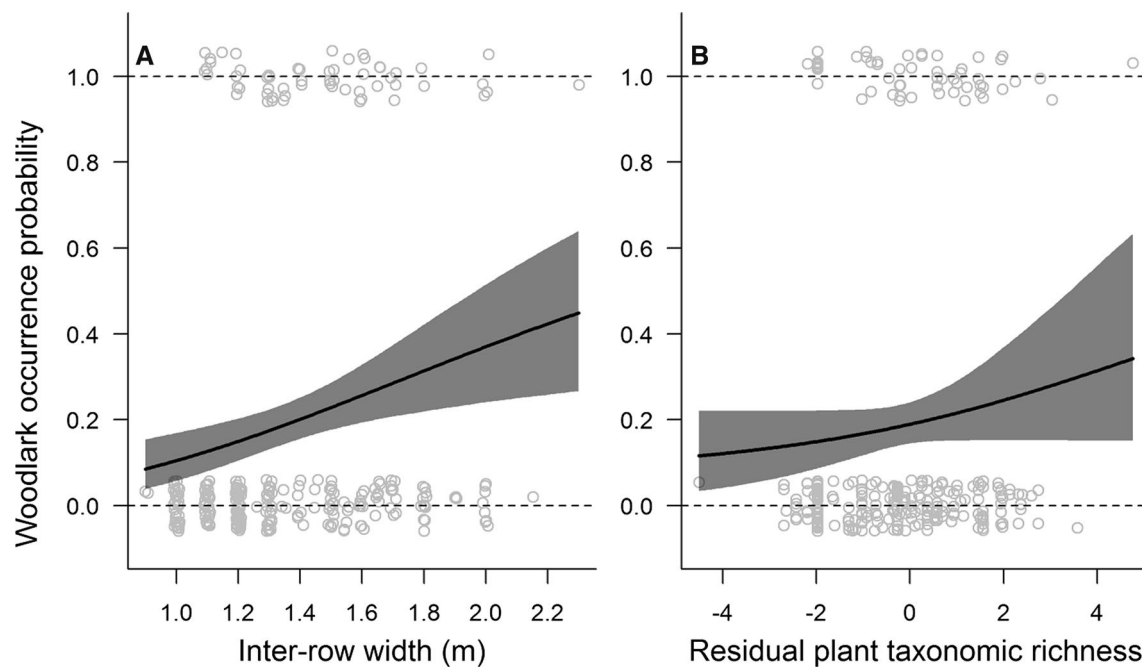


Fig. 1 Model-averaged relationships from binomial regression models between Woodlark (*Lullula arborea*) occurrence probability and the two significant predictors, i.e. inter-row width (a) and residual plant taxonomic richness (b). All variables present in the top models, with the exception of the one under consideration, were fixed at

their respective mean values for appropriate visualization. Gray shading denotes 95% Bayesian credible intervals. Light-gray circles show raw data. Both of the variables were found to have substantial positive effects on the probability of Woodlark occurrence

width and ground vegetation were present among the top three models (Table 2), while residual plant taxonomic richness was the only significant predictor, positively influencing the number of spider families (Table 3; Fig. 5b).

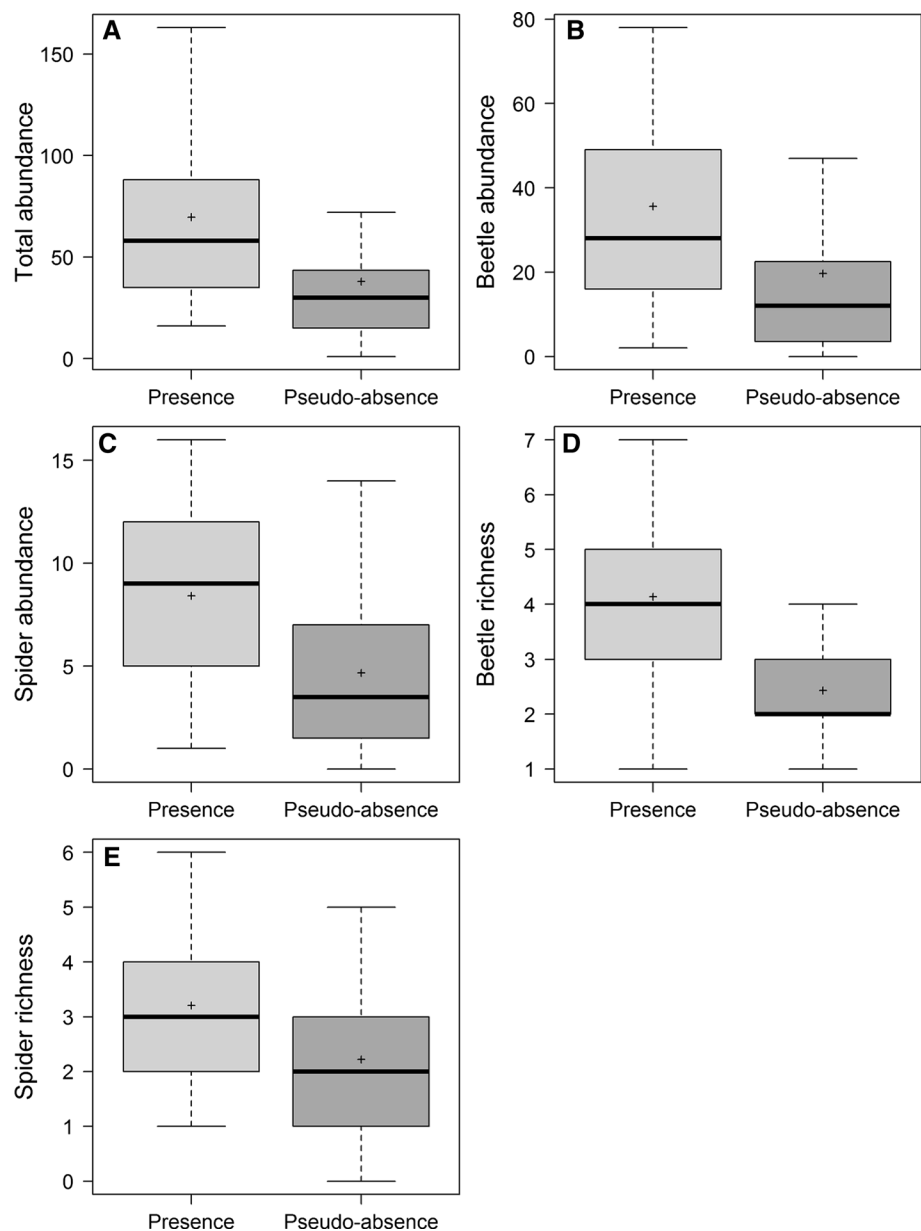
Discussion

In line with previous findings (e.g. Altieri and Nicholls 2002; Arlettaz et al. 2012; Assandri et al. 2017b; Guyot et al. 2017), the results of our study provide evidence that extensively managed vineyards benefit biodiversity at various trophic levels, ranging from primary herbivorous consumers up to insectivorous birds. Woodlark presence and their prey supply were principally explained by enhanced plant taxonomic richness, ground vegetation cover and wider inter-rows, all likely to be good proxies for ground vegetation management intensity.

The preference of Woodlarks for vegetated vineyards during the reproductive season corroborates the results from earlier studies (Arlettaz et al. 2012; Buehler et al. 2017), while the positive effect exerted by a rich flora is a novel finding: we show that habitat use in spring correlated with plant taxonomic richness, with which prey abundance was also positively related. This result indicates that Woodlarks may assess the quality of breeding grounds either directly

from ground vegetation or indirectly from prey supply. However, based on our study results we are not able to identify the causal relationships between Woodlark presence, ground vegetation and prey supply. It is therefore possible that their preference for vegetated vineyards could be driven by prey abundance and richness per se, prey accessibility during foraging but also by favorable micro-habitat conditions and concealment for breeding and protection against predators. Only future experimental work may enable the disentangling of these two effects, but we can assume that a diverse flora not only offers more ecological niche opportunities to invertebrates but also boosts their overall abundance (e.g. Thomson and Hoffmann 2009; Caprio et al. 2015; Puig-Montserrat et al. 2017), thereby enhancing the foraging efficiency of food provisioning by Woodlark parents (Searcy 1979). Woodlark presence also increased markedly with inter-row distance. This can be explained, first, by a correlation between ground vegetation cover and inter-row width ('lm': estimate \pm SE = 0.004 ± 0.001 , $t = 7.114$, $p < 0.001$). In most less intensively managed vineyards, the inter-rows are set wide and vines are guided on wires to allow access to (mowing) machinery, which usually favors a permanent ground vegetation cover. Second, it might also reflect the preference of Woodlarks for semi-open habitats (Bowden 1990), where the vertical structures, i.e. vine plants and

Fig. 2 Boxplots of invertebrate abundance (a), beetle abundance (b), spider abundance (c), number of beetle families (spider abundance, d) and number of spider families (beetle richness, e) in relation to vineyard field status (presence fields vs. pseudo-absence fields). Increased abundance and richness are shown in Woodlark presence fields compared to pseudo-absence vineyard fields. Horizontal black lines depict the median, boxes the upper and lower quartiles, antennas the minimum and maximum and crosses depict the mean values



poles in this case, are arranged less densely than in fields with narrow inter-rows.

We found significantly greater invertebrate abundances in general and number of beetle and spider families in particular occurring in Woodlark presence fields than in pseudo-absence fields. This finding mirrors the observation that presence fields also had considerably denser ground vegetation cover than did fields where there were no Woodlark observations. Although we did not study the diet of Woodlarks in vineyards, this species has been described as a generalist insectivore (Bowden 1990), contrary to several terrestrial foraging insectivorous farmland birds, such as the Hoopoe (Arlettaz et al. 2010; Guillod et al. 2016) or

the Wryneck (Coudrain et al. 2010). We therefore infer that its reproductive success might be higher in vineyards with ground vegetation where prey supply abounds. Invertebrates furthermore formed more abundant and richer communities among vegetated vineyards that also exhibited richer plant communities, which has implications not only for invertebrate assemblages and Woodlark prey supply but likely also for key ecosystem services such as pest control (e.g. Thomson and Hoffmann 2009; Burgio et al. 2016). However, given that invertebrates were not sampled the same year as the Woodlark surveys were conducted, the link between Woodlark habitat preferences and invertebrate prey supply must be interpreted cautiously. Even though vineyard management

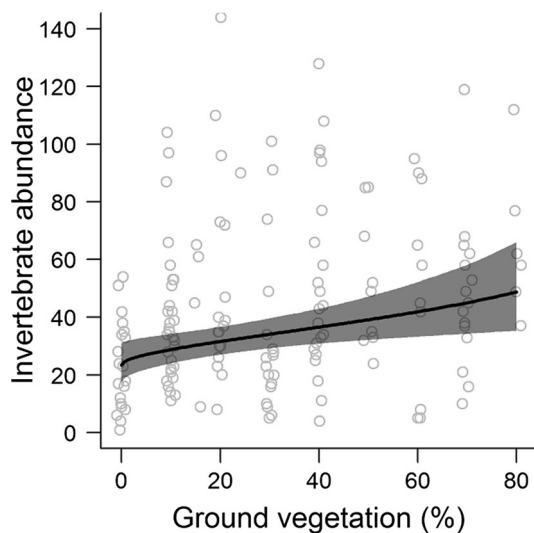


Fig. 3 Model-averaged relationships between invertebrate abundance and ground vegetation cover. All predictors present in the top models, with the exception of the one under consideration with significant effects, were fixed at their respective mean values for appropriate visualization. Gray shading denotes 95% Bayesian credible intervals. Light-gray circles show raw data

regimes tend to remain stable over years and thus similar ground vegetation conditions in different years are likely to mirror stable invertebrate prey abundances, vineyards can potentially be affected by varying meteorological conditions, changes in pesticide treatments and/or other extreme events, such as pest outbreaks (Benton et al. 2002).

Compared to vineyards with a mostly mineral appearance, fields with increased ground vegetation cover promote more diverse and abundant plant and invertebrate communities favoring insectivorous predators such as the Woodlark. This calls, at a landscape scale, for a tremendous reduction in the number of vineyards treated with herbicides. Special incentives and outreach activities under the auspices of the state should be envisioned to operate a major paradigmatic shift from conventional viticulture practices towards a sustainable, ‘biodiversity-friendly’ management. Based on our results, it appears that further promoting wider inter-rows, which is sought for improving grape and wine quality, would be a first obvious measure for boosting vineyard biodiversity. At a field scale, the presence of diverse plant assemblages as vegetation in the inter-row spaces should be promoted. This can be accomplished either by actively sowing site-adapted

Fig. 4 Model-averaged relationships between beetle abundance and number of families versus their significant predictors. **a** Beetle abundance vs. ground vegetation, **b** beetle abundance vs. residual plant taxonomic richness, **c** number of beetle families vs. ground vegetation, **d** number of beetle families vs. inter-row width. For both response variables, all predictors present in the top models, with the exception of the significant ones depicted here, were fixed at their mean values. Gray shading denotes 95% Bayesian credible intervals. Light-gray circles show raw data

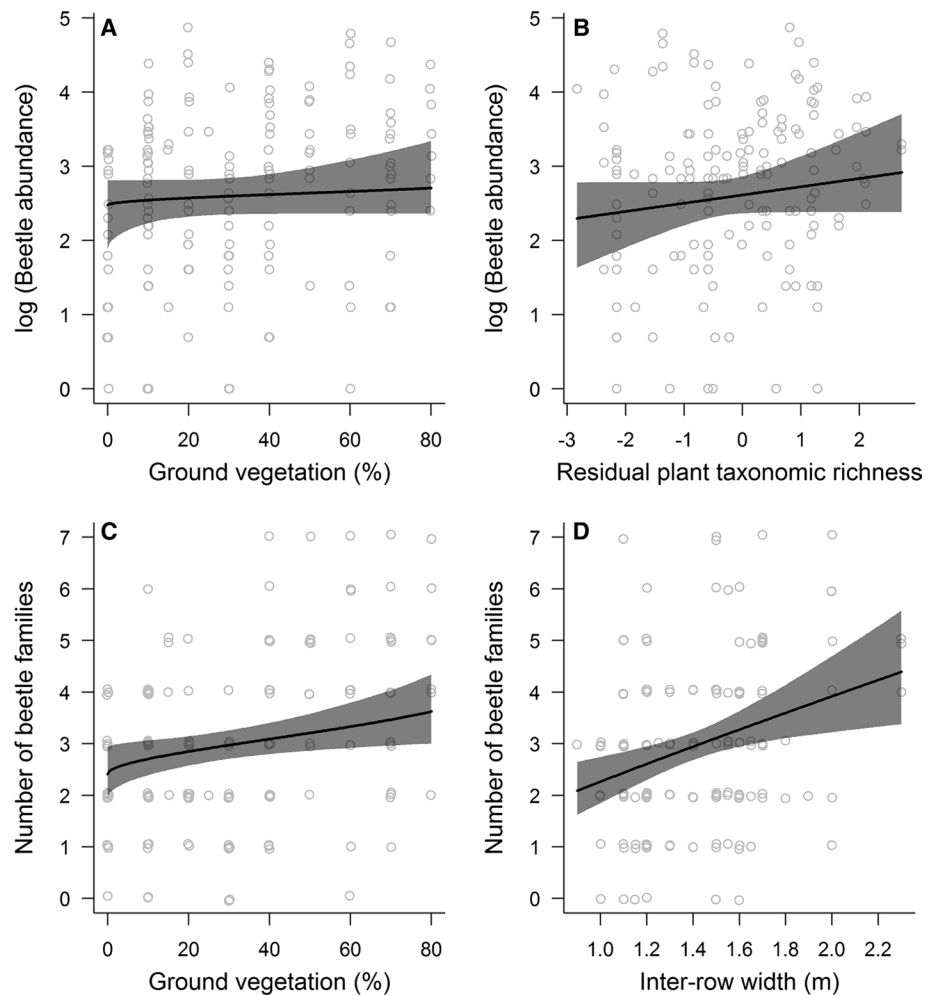
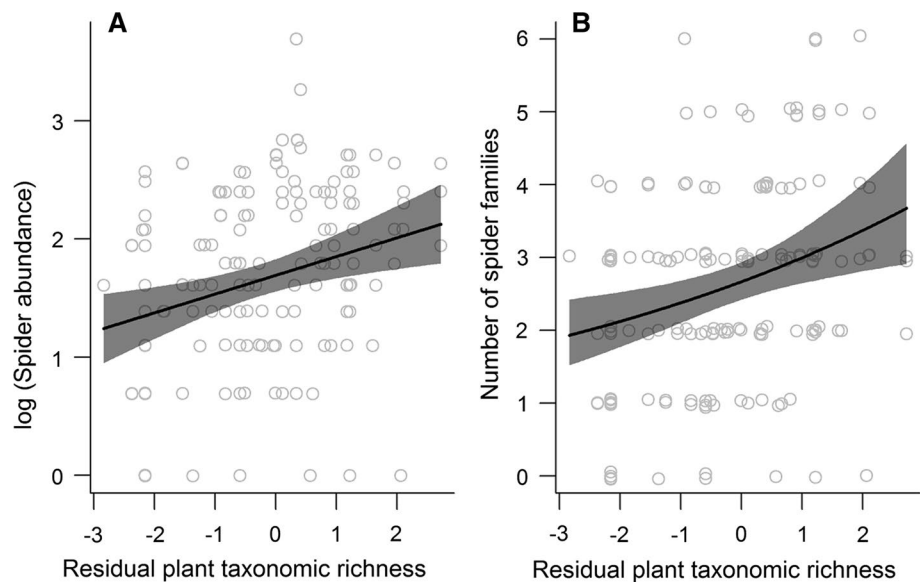


Fig. 5 Model-averaged relationships between spider abundance and number of families versus their significant predictors. **a** Spider abundance vs. residual plant taxonomic richness, **b** number of spider families vs. residual plant taxonomic richness. For both response variables, all predictors present in the top models, with the exception of the significant ones depicted here, were fixed at their mean values. Gray shading denotes 95% Bayesian credible intervals. Light-gray circles show raw data



seed mixtures or by allowing a spontaneous growth of the autochthonous vegetation. Overall these steps would contribute to the reinstatement of a heterogeneous habitat mosaic among vineyards, with heterogeneity being a key element in Woodlarks habitat selection (Campedelli et al. 2015; Sirami et al. 2011), and to the enrichment of general farmland biodiversity and ecosystem services (Benton et al. 2003; Vickery and Arlettaz 2012; Campedelli et al. 2015), while maintaining production requirements (Viers et al. 2013).

Acknowledgements We thank all vine growers and the Valais association for viticulture (VITIVAL) for their support and collaboration, and for providing access to their vineyards. We are grateful to Livio Rey for field and lab assistance and Antoine Sierro for helping with site selection.

Author contributions All authors contributed equally to this paper.

Funding This study was supported by the Swiss National Science Foundation, Grant 31003A_149780 to Alain Jacot.

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interest.

Ethical statement The experiments conducted in this study comply with the current laws of the country in which they were performed.

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