

**The effects of ground vegetation cover on vineyard
habitat use by the woodlark *Lullula arborea* and its
arthropod prey**

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THE EFFECTS OF GROUND VEGETATION COVER ON VINEYARD HABITAT USE BY THE WOODLARK *LULLULA ARBOREA* AND ITS ARTHROPOD PREY

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ABSTRACT

Vineyards are among the most intensively managed crop systems. They underwent rapid agricultural intensification in the past decades although more nature-friendly practices are emerging. Vineyards are widespread in southern Swiss landscapes. In the driest areas such as Valais, only a minor fraction of vineyards harbours ground vegetation cover. We investigated how ground vegetation contributes to enhance biodiversity within vineyards, focusing on the woodlark, an emblematic ground-foraging insectivorous passerine typical of this habitat. During the breeding season, we studied both the spatial patterns of habitat use by the bird and the effects of ground vegetation on ground-dwelling arthropods, its main prey. Birds' whereabouts were located by acoustic and visual surveys, and radio-tracking. Ground vegetation characteristics were assessed via field mapping and NDVI-based satellite imagery. Ground-dwelling arthropods were sampled with pitfall trapping. Habitat selection by the birds was approached at both territory scale and vineyard parcel scale. We found significantly higher arthropod abundance and species richness in parcels harbouring a greater cover of ground vegetation. Arthropod diversity (Shannon index) of beetles and spiders increased with vegetation cover. On both spatial scales, woodlark territories and vineyard parcels, areas used by the birds had more ground vegetation cover than neighbouring, unused areas and they also harboured greater arthropod abundance, biomass and species richness. Woodlarks thus select areas with a greater ground vegetation cover which harbour more diverse communities and more abundant populations of arthropods. The emerging farming practice of keeping more vegetation on the ground of vineyards thus benefits biodiversity.

KEYWORDS

Arthropod abundance and richness, bare ground, fragmentation, NDVI, territory and parcel scale, vineyard parcel

INTRODUCTION

Over the past six decades a rapid agricultural intensification has occurred in Europe and North America (Gardner 1996), leading to a widespread decline in farmland biodiversity, especially in bird populations (Krebs *et al.* 1999; Benton *et al.* 2003). Many different studies have claimed that in addition to the traditional protected areas, conservation of biodiversity depends on the way agricultural areas are managed (Vandermeer & Perfecto 2005; Tschamtker *et al.* 2012; Viers *et al.* 2013), meaning that agriculture should integrate conservation and production within heterogeneous landscapes (Vandermeer & Perfecto 2005; Fischer *et al.* 2008; Viers *et al.* 2013). Thus, nowadays new agricultural practices and policies are being established to counteract the negative impacts on global biodiversity, such as the introduction of agri-environment schemes in Europe (e.g. Kleijn & Sutherland 2003; Kleijn *et al.* 2006; McKenzie *et al.* 2013) as current and future generations demand from agriculture to find a trade-off solution between food security for the human population and environmental sustainability (Fischer *et al.* 2008; Foley *et al.* 2011).

Vineyards are one such crop system that underwent rapid intensification (Altieri & Nicholls 2002; Schmitt *et al.* 2008) and thus contributed to the conversion and fragmentation of formerly natural landscapes, posing a threat to biodiversity by occupying key habitats and simplifying the structure and composition of ecological communities (Viers *et al.* 2013). In Viers *et al.* (2013) the concept of “vinecology” is proposed, which is the integration of ecological and viticulture principles, with the aim for vineyards and biodiversity to coexist, by optimizing the in-field methods and by maintaining or restoring natural habitats surrounding the vineyards. Depending on the viticulture management, vineyards can harbour several rare species (Altieri & Nicholls 2002; Schmitt *et al.* 2008), where traditional, extensively managed vineyards show lower pest vulnerability and higher biodiversity (Altieri & Nicholls 2002).

In some parts of Europe there is an ongoing trend towards a more nature-friendly vineyard management with an accompanying reduction in the application of biocides (Arlettaz *et al.* 2012; Nascimbene *et al.* 2013), what promotes ground vegetation between the vine rows. These in-field methods which can be applied over the whole vineyard parcel seem very important, as biodiversity can benefit on large scales whereas under the concept of land sparing, biodiversity is only promoted on 5-7% of the surface. Different studies have demonstrated a positive effect of ground vegetation between or within the vineyard parcels, on e.g. the abundance and activity of natural enemies acting as pest control (Thomson &

Hoffmann 2009; Sanguaneko & Leon 2011); bird occurrence probabilities (Duarte *et al.* 2014; Siervo & Arlettaz 2003; Arlettaz *et al.* 2012); plant species richness (Sanguaneko & Leon 2011); soil fertility conditions, reduced erosion, improved soil tilth and microbiological functioning (Wolpert *et al.* 1993; Steenwerth & Belina 2008).

In Switzerland one-third of the viticulture area occurs in Valais, where it is located mainly on the south-facing slopes along the Rhône valley (Arlettaz *et al.* 2012) with about 90 percent of them being of mineral appearance, i.e. without ground vegetation. These different management types lead to a mosaic landscape of few parcels with ground vegetation and lots of parcels without. These spatial and structural variations in ground vegetation may directly influence arthropod species, as less mobile animals are more prone to fragmentation effects such as the connectivity between fragments (e.g. Gibb & Hochuli 2002; Fahrig 2003). The usage of pesticides in vineyards negatively affects the composition of arthropod species communities and their life strategies (e.g. Bruggisser *et al.* 2010; Trivellone *et al.* 2012) and the plant species richness (Nascimbene *et al.* 2013), thus vineyard parcels with some ground vegetation provide a habitat of higher quality to different species among different taxa, as in these parcels typically less or no pesticides are applied. In a study on the avifauna of these Valais vineyards, landscapes with high proportions of natural structures and ground vegetation cover as well showed high bird species diversities (Siervo & Arlettaz 2003), which might be explained through a preference for a mosaic of ground vegetation and bare ground, as a patchy vegetation increases prey accessibility (Schaub *et al.* 2010; Vickery & Arlettaz 2012). Other studies have demonstrated that increased bird abundance or diversity might be explained by higher abundance and accessibility of their arthropod prey (Benton *et al.* 2002; Atkinson *et al.* 2004; Atkinson *et al.* 2005; Traba *et al.* 2008) and further, how prey availability shapes the habitat selection based on a preference for a certain vegetation structure that optimizes food availability (Traba *et al.* 2008) especially for breeding males who defend food resources to maximize their breeding success (Searcy 1979).

One such species is the woodlark, a ground breeding mostly insectivorous farmland bird, which is classified as vulnerable in the Swiss Red List and belongs to the Swiss list of priority species for recovery programmes (Keller *et al.* 2010a; Keller *et al.* 2010b). Around one half of the Swiss woodlark population occurs in Valais, where it mostly breeds in vineyards and shows a clear preference for parcels with ground vegetation (Schaub *et al.* 2010; Arlettaz *et al.* 2012; Bosco 2012, unpublished data). More specifically, on a level of micro habitat

selection, the woodlark prefers foraging habitats with a proportion of ground vegetation cover around 40-60 percent and thus avoids vineyards with too dense or too little vegetation (Arlettaz *et al.* 2011). Also on a parcel level, woodlarks clearly prefer vineyards with more ground vegetation and higher plant species richness (Bosco 2012, unpublished data). In the UK, where woodlarks traditionally occurred in heathlands (Holloway 1996), they have colonized new areas such as clear-fell forestry habitats and farmlands (Sitters *et al.* 1996), showing as well a preference for foraging habitats consisting of sparse vegetation and bare ground (Harrison & Forster 1959; Bowden 1990; Mallord *et al.* 2007). During the breeding season their diet consists of caterpillars, beetles, spiders and other small arthropods and their larvae (Glutz & Bauer 1985; Rey 2013, unpublished data) and already Bowden (1990) stated that these prey are present in many different vegetation types, but the structure of the vegetation may be crucial for the ease with which woodlarks can find them.

In the present study we assessed the effects of vineyard ground vegetation cover and plant species richness on arthropod abundance and diversity, using pitfall traps, in order to see if this consequently may affect the woodlarks' habitat selection. We hypothesized that the overall arthropod species richness and abundance are higher in parcels with more ground vegetation, while there will be taxa specific reactions to the vegetation structure due to their different ecologies. In a second step we assessed the habitat mosaic of woodlark territories with an additional aspect on habitat fragmentation effects such as the connectivity between fragments. Using a combination of radio-tracking data and satellite picture derived Normalized Difference Vegetation Index (NDVI) values, we assessed the proportion and distribution of parcels with ground vegetation cover within the woodlark territories and their effects on the habitat use of woodlarks. Further, we compared woodlark territories to random, non-occupied territories (Traba *et al.* 2008; Arlettaz *et al.* 2012; Tagmann-Ioset *et al.* 2012) to see whether there are differences in terms of vegetation cover. We predicted that 1) woodlark territories have more ground vegetation cover compared to random territories, 2) fragmentation leads to an increase in territory size and 3) within a territory, larger and more connected parcels are visited more often than small and less connected parcels.

MATERIAL AND METHODS

Study sites

The study was carried out in 2013 at four different sites in the upper Rhône valley in Valais, namely Chamoson (Ch, 46°20'N, 7°21'E), Salgesch/Varen (S/V, 46°32'N, 7°58'E), Praveriaz (46°17'N, 7°31'E) and Loc (46°17'N, 7°30'E). In all four sites vineyards are the predominant landscape appearance and they are known to harbour relatively large woodlark populations (Sierra 2010). All four sites show a mosaic of many intensively managed vineyards with no or very little vegetation cover and few vineyards with ground vegetation. Still, the landscape differs between the sites, as in Chamoson most parcels are in the plain, whereas the other three sites are located on the south-facing hillside having more steep parcels and natural structures such as hedges, trees or drystone walls.

Satellite pictures and vineyard parcel characteristics

The vineyard parcels, which were used for arthropod samplings were mapped directly in the field in 2012 for the percentage of ground vegetation (estimate for the whole parcel) and the ground vegetation quality, by counting the number of plant species while walking through one vine row of the respective parcel. Additionally, the ground vegetation cover was mapped for a subsample of 100 vineyard parcels in 2013 in order to see whether the NDVI values are a reliable proxy for the amount of ground vegetation. Parcel slope and size were assessed from the satellite pictures using the software QGIS (QGIS Development Team 2014). For the NDVI values, the aim was to get an estimate of the ground vegetation cover of the viticulture area of all sites using satellite pictures. This is best done before the sprouting of the vine leaves (22nd of April in 2010 for Chasselas and Pinot Noir in Châteauneuf, S. Emery, pers. communication). Hence, satellite pictures for Valais were recorded on the 1st of April 2013 (WorldView-2, Swisstopo), which guarantees that the calculated vegetation index is not influenced by leaves of the vine plants. We calculated the NDVI value of each parcel with the GIS software QGIS (QGIS Development Team 2014) using the raster calculator. This index is derived from the red / near-infrared reflectance ratio:

$$[\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})],$$

where NIR is the amount of near-infrared light and RED the amount of red light (Pettorelli *et al.* 2005). The basis for this formula renders the fact that chlorophyll absorbs red light while

near-infrared light is reflected. NDVI values can range from -1 to +1, where negative values are related to a lack of vegetation (Pettorelli *et al.* 2005).

Arthropod sampling

Arthropods were sampled using pitfall traps (according to Britschgi *et al.* 2006) at two different sites (Chamoson and Salgesch/Varen). For the pitfall trap locations we chose for each site 15 parcels where we observed woodlarks based on the data of 2012 and for each woodlark parcel three surrounding parcels where we didn't observe woodlarks, as controls - resulting in a total of 30 woodlark and 90 control parcels for both sites together. In each woodlark parcel we burrowed 3 traps, having the middle trap in the middle row of the parcel, the ones right and left to it, each 4 meters apart and all three traps 15 meters away from the edge of the parcel to avoid spill-over effects. In each control parcel one trap in the middle row was installed, 15 meters away from the edge of the parcel. Of the 180 traps 22 got destroyed or were removed, having a total of 158 traps which were used for this study. The traps were 200ml plastic cups of 8cm height and 7.5cm diameter, filled with a mixture of water and ethylene glycol (1:1) and a scentless detergent to decrease the water surface tension. All traps were active for 8 days between 7.5.2013 and 17.5.2013 and have been protected from rain with small plastic roofs. Until the identification all the collected arthropods were stored in 70 percent ethanol in plastic tubes. We identified the arthropods to order, family or, if possible, to genus or species level, using reference guides (Roberts 1996; Stresemann & Klausnitzer 2011; Chinery 2012) and a binocular microscope (Leica M80, Germany). To get the arthropod biomass of each trap, we dried the samples for 72 hours at 60 degrees (Britschgi *et al.* 2006) and weighed them afterwards with a Mettler precision balance (precision 0.1 mg). In a first step we analysed the overall arthropod abundance and richness in relation to various vineyard parcel variables (see statistical analyses). In a second step we focused on beetle and spider abundance and richness separately, where we additionally analysed Shannon diversity (for beetles on a species level and for spiders on a family level).

Woodlark capturing and radio-tracking

We used mist nets and perch traps for the capturing and additionally tape-luring and a stuffed woodlark to attract the birds, especially the territorial males (according to Arlettaz *et al.* 2012). Capturing usually started early in the morning, as the singing activity of the birds is highest in the period of four hours after dawn (Sirami *et al.* 2011) and was most successful on days with no or only low wind and sunny weather, as the birds were more active under these

conditions. All 13 individuals were captured in March and April 2013, ringed (ring size N, SEMPACH HELVETIA) and equipped with a radio-transmitter (Holohil DB-2, 0.9g, 60p/min, Canada) using leg harnesses (Naef-Daenzer 1993). The homing-in technique was used 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 may be more precise using hand-held antennas for birds regularly sitting on the ground (Naef-Daenzer 1993). For each homing-in localization we mapped the exact parcel the bird was situated, on a map of high resolution in order to gain precise information about the habitat use of woodlarks. Between two localizations we waited for at least 15 minutes to avoid temporal biases and to be sure that the new homing-in point is not an artefact of flushing the bird away from the previous point. For accurate territory delineation we aimed to have a minimum of 50 points per bird, what was reached for 10 out of the 13 birds (see appendix Table A1). One bird lost his transmitter after 18 days and was not included in the analyses, as we gained too few locations. All homing-in points were digitalised using the software QGIS (QGIS Development Team 2014).

Territory selection

All territories were delineated based on the acquired homing-in points using the plugin “heatmap” in the software QGIS (QGIS Development Team 2014), which creates kernel density estimators - an accurate method for territory and home range boundary calculations (Naef-Daenzer 2000; Barg *et al.* 2005; Traba *et al.* 2008; Steiniger & Hunter 2013). Kernel bandwidths were determined using the least squares cross validation method (according to Barg *et al.* 2005) for each bird, i.e. each territory (package “kedd”, Guidoum 2013; function “h.ucv”, R Development Core Team 2013). Territory borders were established at the 90% density isopleth, according to other avian kernel-based studies (e.g. Borger *et al.* 2006), while the core areas, i.e. areas of high-use within the territories, were produced at the 40% density isopleth under the condition to have at least four locations on four different and non-consecutive days in order to avoid temporal autocorrelation.

We compared used to unused area on two spatial scales: Once on a larger scale with woodlark against random territories and then on a smaller scale with woodlark against control parcels within the territories. The territories delineated based on the woodlark homing-in locations are hereafter called ‘woodlark territories’, while ‘random territories’ refer to the adjacent dummy territories and likewise ‘woodlark parcels’ are all parcels which were visited during the radio

tracking sessions while ‘control parcels’ refer to all non-visited parcels within a territory, both belonging to the factor ‘parcel status’. To investigate the habitat choice of woodlarks on the territory scale, we compared woodlark territories against randomly chosen, non-visited areas, by generating five adjacent dummy territories per woodlark territory. To produce these adjacent dummy territories, we first draw a buffer around each woodlark territory, which was tenfold the area of the respective territory. Then in each buffer, five points were randomly allocated with the condition to be inside the vineyard area (i.e. no settlements, forests etc.) but outside the woodlark territories. Around these random points, circles of the same size of each respective woodlark territory were drawn, with the possibility to overlap together (modified after Arlettaz *et al.* 2012; Tagmann-Ioset *et al.* 2012). We investigated whether there were fragmentation effects on the territory selection and habitat use of woodlarks by focusing on the following aspects: 1) decrease of total green area within territories; 2) increasing number of green parcels (fragments) with 3) consequently a decrease in size of green parcels and 4) a decrease of connectivity between green parcels; where green means here vineyard ground vegetation cover above 40%.

For small-scaled analyses about the habitat use within the territories, we compared visited vineyard parcels (i.e. visited during radio-tracking sessions), which were considered as ‘woodlark parcels’, with all other parcels which were not visited within a territory, which served as pseudo-absences (according to Arlettaz *et al.* 2012; Bosco 2012, unpublished data). We investigated the habitat choice in relation to parcel size where we compared the size of visited parcels with the same number of randomly chosen parcels. To do so, we randomly allocated the same number of locations for each bird respectively within their territories in two different runs in order to test whether woodlark locations were non-random. Further, we compared NDVI values (as a proxy for ground vegetation), parcel respectively territory size, number of locations per parcel and the connectivity between visited parcels. The connectivity of the visited parcels was calculated using the “ftools” plugin in QGIS (QGIS Development Team 2014) with the function “distance matrix”. The output is the mean distance from the one parcel in question to all other parcels. The reciprocal of the mean distance then gave a connectivity value for each visited parcel in each territory. As parcels at the border of the territory are automatically less connected than those in the middle, we draw a buffer of 200 m around the territories in order to include all green parcels outside the territories but within this buffer.

Nest site selection

During the radio-tracking sessions, woodlark nests were searched in order to obtain information of woodlarks nest site selection and to investigate nestling diet in the frame of another study (see Rey 2013). Of six pairs we found their nests while of one pair we found the replacement clutch as well, after the first brood was predated. For the nest site selection analysis we mapped the ground vegetation cover, vegetation height and parcel slope on two different scales. First on a parcel scale, where we compared the ‘nest parcel’ to all neighbouring parcels as controls and then on a 1 m² scale where we compared one square meter around the nest to four randomly chosen square meters within the nest parcel in order to see if the birds prefer certain vegetation structures within the vineyard parcels.

Statistical analyses

As woodlark and adjacent control parcels, respectively woodlark and random territories are spatially dependent and hence form a unit, we defined it as a new variable called ‘unit’, which entered all models (glmmPQL; packages “nlme”, Pinheiro *et al.* 2012 and “MASS”, Venables & Ripley 2002) as random term. Woodlark occurrence probability (visited vs. non-visited parcels) with respect to ground vegetation cover was calculated using a glmer model with a binomial error distribution (package “lme4”, Bates *et al.* 2014) where the limits of a 95% confidence interval were obtained as the 2.5% and 97.5% quantiles of the posterior distribution (package “arm”, function “sim” with 5000 simulations, Gelman *et al.* 2014).

Arthropod Shannon diversities were analysed using the package “vegan” (Dixon 2003) and the function “diversity”. Regarding arthropod analyses we tested arthropod abundance and richness against: 1) vineyard parcel ground vegetation cover; 2) NDVI values; 3) number of plant species; 4) parcel status; 5) parcel size; 6) parcel slope and 7) site. First we used a univariate model approach and in a second step we did model selection (R package “MuMIn”, function “dredge”, Barton 2014) which is based on the best Akaike’s Information Criterion (AIC) values. Before the model selection we first assessed the correlation between predictors using Spearman’s correlation coefficient and excluded predictors if their coefficient $|r|$ was >0.7 (Arlettaz *et al.* 2012). As a quadratic relationship between arthropod abundance respectively woodlark presence and ground vegetation was possible, we as well included the square of the variable ground vegetation (Schaub *et al.* 2010; Arlettaz *et al.* 2012; Tagmann-Ioset *et al.* 2012). To test whether a treatment effect, i.e. the difference between woodlark and

control parcels, was present at all sites, we included the interaction between parcel status and site into the models.

We performed detrended correspondence analyses (DCA) using the package “vegan” (Dixon 2003) and the function “decorana”, for arthropod data sets to visualize whether there are community changes between the parcel status, the sites and the different amounts of vegetation cover. To do so, the variable ground vegetation cover was transformed from a linear variable (0-100%) to a factor with four levels (class 1: 0-10%; class 2: 11-30%; class 3: 31-50%; class 4: 51-100%). Classes were not distributed equally, as we were interested in vegetation management effects and thus assigned ‘class 1’ to a high pesticide application with no spontaneous greening; ‘class 2’ to pesticide application with moderate spontaneous greening; ‘class 3’ to spontaneous and permanent greening with moderate pesticide application and ‘class 4’ to spontaneous and permanent greening with low or no pesticide application. Then univariate, linear models were run using the variables parcel status, site and the vegetation classes as predictors for DCA1 and DCA2. All analyses were performed using the open source software R version 3.0.2 (R Development Core Team 2013).

RESULTS

We found a significant positive correlation between ground vegetation cover estimates and the NDVI values (estimate=0.001 ± 0.0001, $t_{122}=9.1$, $p<0.001$) as well as between ground vegetation cover and the number of plant species (estimate=0.02 ± 0.002, $t_{116}=10.78$, $p<0.001$).

Effects of vineyard parcel characteristics on arthropods

7409 arthropods were sampled and identified, of which 3964 were captured in Chamoson and 3445 in Salgesch. Mean number of arthropods per pitfall trap was 47.19 ± 35.5 , ranging from one to 167 items per trap and mean arthropod biomass was $0.012g \pm 0.02g$. In total 23 different orders were found, with beetles (N=3726, 50.3%), spiders (N=974, 13.2%), dipterans (N=691, 9.3%) and harvestmen (N=640, 8.6%) being the most abundant ones (see Appendix Fig. A4).

Both, arthropod abundance and richness (i.e. number of orders per trap) were significantly higher in parcels with more ground vegetation (abundance: 0.01 ± 0.002 , $t_{123}=4.48$, $p<0.001$;

richness: 0.004 ± 0.0008 , $t_{123}=4.99$, $p<0.001$) and higher NDVI values (abundance: 2.7 ± 1.08 , $t_{123}= 2.49$, $p=0.014$; richness: 1.26 ± 0.45 , $t_{123}=2.81$, $p=0.006$), but there was no difference in abundance or richness between the sites (abundance: -0.10 ± 0.13 , $t_{27}=-0.78$, $p=0.44$; richness: 0.05 ± 0.06 , $t_{27}=0.91$, $p=0.37$). Looking at the ground vegetation quality – while including ground vegetation as covariate - plant richness had no apparent effect on arthropod abundance (0.002 ± 0.001 , $t_{115}=1.48$, $p=0.14$) and on arthropod richness (0.05 ± 0.03 , $t_{115}=1.42$, $p=0.16$). Arthropod biomass was positively correlated with arthropod abundance (0.009 ± 0.001 , $t_{125}=6.61$, $p<0.001$), arthropod richness (0.14 ± 0.03 , $t_{125}=4.31$, $p<0.001$) and percentage of ground vegetation (0.006 ± 0.002 , $t_{122}=2.91$, $p=0.004$), while there was no difference between the sites (0.077 ± 0.14 , $t_{27}=0.57$, $p=0.57$). Regarding other parcel variables, we found that parcel size had no effect on arthropod abundance (-0.000001 ± 0.00002 , $t_{124}=-0.03$, $p=0.97$) and richness (0.00001 ± 0.00001 , $t_{124}=1.05$, $p=0.3$), but it was positively correlated with ground vegetation estimates (0.004 ± 0.0008 , $t_{121}=4.67$, $p<0.001$). The slopes of the parcels had no influence on ground vegetation cover, arthropod abundance and richness (all p values >0.5).

For the model selection approach, the variable ‘number of plants’ was excluded from the analyses as there was a strong positive correlation between ground vegetation cover and number of plant species (Spearman’s correlation coefficient: 0.73). The best model explaining arthropod abundance (model 60, Akaike weight: 0.4) included the following variables: Arthropod biomass, parcel slope, ground vegetation and its quadratic term. In Table 1 the best three models, with a delta AIC <2 , are shown. Arthropod biomass (0.57 ± 0.002 , $z_{141}=25.84$, $p<0.001$), parcel slope (0.01 ± 0.005 , $z_{141}=1.84$, $p=0.07$) and ground vegetation cover (0.03 ± 0.002 , $z_{141}=12.62$, $p<0.001$) all were positively related to abundance, while the quadratic term of ground vegetation showed a negative relationship (-0.0004 ± 0.00003 , $z_{141}=-11.67$, $p<0.001$), as arthropod abundance started to stagnate around 65% of ground cover (Fig. 1). For arthropod richness, arthropod biomass (0.13 ± 0.06 , $z_{141}=2.20$, $p=0.03$) and the quadratic term of ground vegetation (0.00005 ± 0.00002 , $z_{141}=2.22$, $p=0.03$, Fig.1) were involved in the best model (model 18), while this only had 17% likelihood to be the best one among the considered models (Table 1).

With regard to order specific preferences of the eight most abundant orders and all larvae, we found no effect of ground vegetation cover on abundance of harvestmen, isopods and larvae (harvestmen: 0.004 ± 0.004 , $t_{123}=1.04$, $p=0.30$; isopods: 0.004 ± 0.005 , $t_{123}=0.75$, $p=0.46$; larvae: -0.001 ± 0.005 , $t_{123}=-0.19$, $p=0.85$), while earwig abundance showed a significant

negative relationship with ground vegetation cover (-0.01 ± 0.004 , $t_{123}=-2.30$, $p=0.023$). The other five orders, namely beetles, spiders, dipterans, heteropterans and hymenopterans, all were positively correlated with ground vegetation for both, abundance and family richness (Table 2).

Looking at the arthropod composition on order level, there was no change of the community in relation to the vegetation classes, but a significant difference between the sites (DCA1: 0.31 ± 0.06 , $t_{155}=5.24$, $p<0.001$; DCA2: 0.25 ± 0.07 , $t_{155}=3.63$, $p<0.001$) with more isopods, earwigs and larvae in Salgesch/Varen and more harvestmen and dipterans in Chamoson (eigenvalue of DCA1=0.28 and DCA2=0.19). On a family level, the arthropod community composition of class 4 (51-100%) was significantly different from class 1 (DCA1: -0.34 ± 0.11 , $t_{147}=-3.02$, $p=0.003$; DCA2: 0.12 ± 0.11 , $t_{147}=1.05$, $p=0.3$) and class 2 (11-30%; DCA1: -0.27 ± 0.12 , $t_{147}=-2.25$, $p=0.025$; DCA2: 0.28 ± 0.12 , $t_{147}=2.35$, $p=0.02$, Fig. 2), while sites did not differ (eigenvalue of DCA1=0.38 and DCA2=0.31).

Vegetation effects on beetle and spider diversities

Among the 3726 beetles, we identified 41 different species in 19 families, with Carabidae being the most abundant family (N=2214, 59.42%). On species level, *Brachinus crepitans* was the most frequent carabid (N=1397), followed by *Opatrum sabulosum* (Tenebrionidae, N=848), *Nebria brevicollis* from the cryptic genus *Nebria* (Carabidae, N=594), the Silphidae species *Silpha obscura* (N=167), *Amara aenea* (Carabidae, N=54) and *Rhyssalus germanus* (Scarabaeidae, N=44). Shannon diversity was positively correlated with ground vegetation cover (0.006 ± 0.002 , $t_{109}=3.73$, $p<0.001$), while there was no effect of plant richness (0.004 ± 0.02 , $t_{101}=0.2$, $p=0.85$). Among the six most abundant species, all except for one (*Rhyssalus germanus*), showed a positive correlation with either ground vegetation quantity, plant richness or both (Table 3). Regarding community changes we found that ground vegetation classes 1, 2 and 3 all differed significantly from class 4 for DCA1 (class 1: 0.16 ± 0.05 , $t_{137}=3.43$, $p<0.001$; class 2: 0.24 ± 0.05 , $t_{137}=4.5$, $p<0.001$; class 3: 0.16 ± 0.06 , $t_{137}=3.01$, $p=0.003$, DCA 2: all p values >0.1) as several species only appeared in vegetation class 4 (e.g. *Silpha obscura*, *Dermestes lanarius*, *Agrypnus murinus*) while the other three classes harboured similar communities (eigenvalue DCA1=0.14 and DCA2=0.22).

Among the spiders, 13 different families were found, of which the following ones occurred most frequently and were therefore used for family specific analyses: Gnaphosidae (N=320),

Zodaridae (N=181), Lycosidae (N=157), Thomisidae (N=126), Salticidae (N=62) and Theridiidae (N=53). Shannon diversity (on family level) increased significantly with increasing ground vegetation cover (0.005 ± 0.002 , $t_{123}=2.99$, $p=0.003$) and plant richness (0.05 ± 0.02 , $t_{115}=2.71$, $p=0.008$), while the relationship with NDVI values was borderline significant (1.4380399 ± 0.7371817 , $t_{123}=1.950726$, $p=0.0534$). Zodaridae and Thomisidae both showed a positive relationship with ground vegetation cover (Zodaridae: 0.02 ± 0.006 , $t_{123}=3.27$, $p=0.002$; Thomisidae: 0.011 ± 0.004 , $t_{123}=2.45$, $p=0.02$), while there was no effect on the abundance of the other four families (all p values >0.2). Plant richness did not have any effect on the abundance of the spider families. Spider communities did not significantly change between vegetation classes but between sites (DCA1: 0.28 ± 0.1 , $t_{145}=2.74$, $p=0.007$; DCA2: 0.03 ± 0.11 , $t_{145}=0.26$, $p=0.8$) having more Theridiidae in Chamoson and more Salticidae in Salgesch/Varen (eigenvalue DCA1=0.47 and DCA2=0.42).

Woodlark habitat choice on a territory scale

Kernel density estimates of Woodlark territory size showed notable variation between individuals (mean \pm SD, 8.01 ± 4.54 ha, range 1.87-18.06 ha), what may be explained by the fact that both individuals with far the largest territories (18.06 and 14.04 ha) most likely were unpaired males. Core area size likewise varied considerably across individuals (mean= 0.89 ± 0.61 ha, range 0.17-2.21 ha) as being significantly correlated with the total territory size ($t_{10}=4.12$, $p=0.002$). The percentage of the territory size used as core areas was between 5.35-21.99% (mean= $11.27 \pm 4.92\%$) while the percentage of locations found within the core areas ranged from 20.33-54.23% (mean= $34.85 \pm 10.03\%$).

Comparing the NDVI for territory status and site, NDVI values were significantly higher in woodlark compared to random territories (0.02 ± 0.009 , $t_{59}=2.62$, $p=0.011$, Fig. 3a) while they did not differ between sites (0.02 ± 0.01 , $t_{10}=1.34$, $p=0.21$). NDVI values in core areas were not significantly different from the rest of the territory (Two sample t-test: $t_{21.28}=0.92$, $p=0.37$) but showed a positive correlation (0.74 ± 0.3 , $t_{10}=2.48$, $p=0.033$) as greener core areas were located in greener territories. Regarding fragmentation effects, we found that territory size was positively correlated with the number of green parcels found within the respective territory (2078.4 ± 495.9 , $t_{10}=4.2$, $p=0.002$) and negatively with its mean NDVI (-73071 ± 34179 , $t_{29}=-2.14$, $p=0.041$). There was neither a correlation between territory size and the mean size of all green parcels within a territory (-4.00 ± 6.44 , $t_{10}=-0.62$, $p=0.55$) nor with the relative green area (i.e. the sum of the sizes of all green parcels relative to the corresponding

territory size; -84.23 ± 630.128 , $t_{10}=-0.134$, $p=0.89$), although for both we found a negative trend.

Woodlark habitat use within territories

In total 978 parcels were analysed, of which 299 were visited by woodlarks and 679 were non-visited control parcels. Parcel size was positively correlated with NDVI (4193 ± 706 , $t_{814}=5.94$, $p<0.0001$) and woodlark parcels were larger compared to random parcels (1044 ± 99.4 , $t_{814}=10.51$, $p<0.0001$).

In a first step we compared visited versus non-visited parcels. For the occurrence probability curve we used the arthropod data set, as only there we had both information: parcel status (woodlark or control) and ground vegetation cover estimates. Woodlark occurrence probability increased significantly with increasing ground vegetation cover (0.04 ± 0.008 , $z=4.79$, $p<0.0001$), resembling a logistic curve with a slight flattening around 80% ground vegetation (Fig. 3b). NDVI values differed considerably between woodlark and control parcels (0.013 ± 0.005 , $t_{816}=2.75$, $p=0.006$) being significantly higher in woodlark parcels. In a second step we analysed visitation rate within woodlark parcels. The number of visits was positively related to NDVI values (3.34 ± 0.8 , $t_{287}=4.18$, $p<0.0001$) and to its parcel size (0.0002 ± 0.00001 , $t_{287}=10.39$, $p<0.0001$) where NDVI values again increased with increasing parcel size (8860 ± 1592 , $t_{287}=5.56$, $p<0.0001$). As the probability to encounter a bird in a parcel increases with its size, the same number of woodlark locations per territory were randomly allocated and simulated twice, to control for such a potential artificial size effect. For both runs we found again a positive correlation between number of visits per parcel and its size (0.0002 ± 0.00001 , $t_{287}=16.30$, $p<0.0001$ and 0.0002 ± 0.00001 , $t_{287}=17.8$, $p<0.0001$) and concomitantly also a positive effect in relation to NDVI values (2.75 ± 0.85 , $t_{287}=3.25$, $p=0.001$ and 4.14 ± 0.77 , $t_{287}=5.4$, $p<0.001$).

Regarding arthropod abundance, we found that there were considerably more arthropods in woodlark compared to control parcels (0.4 ± 0.11 , $t_{127}=3.4$, $p=0.001$, Fig. 3c) while the effect differed among sites (interaction parcel status * site: -0.65 ± 0.23 , $t_{126}=-2.88$, $p=0.005$). A post-hoc comparison within site shows that woodlark parcels had more arthropods in Chamoson (0.71 ± 0.15 , $t_{64}=4.6$, $p<0.0001$) but not in Salgesch (0.05 ± 0.17 , $t_{62}=0.32$, $p=0.75$). Arthropod richness was higher in woodlark parcels (0.16 ± 0.04 , $t_{127}=3.84$, $p=0.0002$), while there was neither a difference of arthropod richness nor of a parcel status effect between the sites ('site': 0.05 ± 0.06 , $t_{27}=0.91$, $p=0.37$; 'parcel status'*'site': $-0.15 \pm$

0.08, $t_{126}=-1.81$, $p=0.073$). There was a considerable difference between woodlark and control parcels regarding arthropod biomass, as in woodlark parcels, biomass was significantly higher (0.23 ± 0.1 , $t_{125}=2.35$, $p=0.02$) irrespective of site (0.08 ± 0.14 , $t_{27}=0.6$, $p=0.55$). Shannon diversity of both, beetles and spiders, was higher in woodlark compared to control parcels (beetles: 0.24 ± 0.08 , $t_{114}=2.99$, $p=0.003$; spiders: 0.22 ± 0.07 , $t_{127}=2.95$, $p=0.004$) irrespective of site (all p values >0.1). Arthropod communities did not differ between woodlark and control parcels for DCA1 and DCA2 (all p values >0.07) neither on order or family level nor for beetles or spiders.

Woodlark nest site selection

Woodlark nest parcels had significantly higher ground vegetation cover (-0.005 ± 0.002 , $t_{33}=-3.09$, $p=0.004$) and vegetation height (-0.01 ± 0.004 , $t_{33}=-2.76$, $p=0.01$, Fig. 4), than the surrounding control parcels, whereas these two variables were strongly inter-correlated (Spearman's correlation coefficient=0.65). On the 1 m² scale, woodlark nest sites again had higher amounts of vegetation cover (-0.005 ± 0.002 , $t_{26}=2.48$, $p=0.02$) and a considerably taller vegetation (-0.02 ± 0.004 , $t_{26}=-3.60$, $p=0.001$, Fig. 4) than the control points in the respective nest parcel. Parcel slope had no effect on either scale (p values >0.6).

DISCUSSION

We successfully demonstrate the positive effects of vineyard ground vegetation cover on biodiversity on different trophic levels, i.e. plant richness, arthropod abundance and diversity and woodlark occurrence. The arthropod community changes between the different amounts of ground vegetation indicate the sensitivity of arthropod species to a certain vegetation amount and structure. Further, we found considerable higher arthropod abundance, richness and biomass in woodlark than in the unused control parcels and consequently higher ground vegetation cover on both, the territory and parcel scale. This study, although only being correlative, highlights the importance of incorporating different trophic levels – especially for insectivorous bird species – in order to completely understand their habitat preferences and accordingly to successfully protect them by giving clear recommendations to the farmers.

Vegetation effects on arthropods

Here we demonstrate the positive effects of ground vegetation cover on overall arthropod abundance and richness and on spider and beetle diversity. These results are consistent with

other studies about arthropods in vineyards, who found for instance that with increasing pesticide use, the diversity of specific arthropod taxa decreased dramatically (Trivellone *et al.* 2012) and that there was an increase in abundance of natural pest enemies when vegetation was present in vineyards (Thomson & Hoffmann 2010). Looking at taxa specific reactions to ground vegetation cover, we found that abundance of harvestmen and isopods showed no reaction to ground vegetation, as these two orders are common in most types of habitats. Earwigs were more common in parcels with no or little ground vegetation cover as they showed a negative relationship with amount of ground vegetation, possibly because these omnivores rely on small stones to hide under during the day. Abundance and richness of beetles, spiders, dipterans, heteropterans and hymenopterans were higher in parcels with more ground vegetation, showing that pollinators, as the latter three orders are, simply depend on flowering plants as food sources. Among the beetles are many families which feed on plant material, seeds and grains (e.g. Tenebrionidae, Scarabaeidae), or which are omnivorous predators (e.g. Carabidae) and may therefore prefer habitats with more ground vegetation, as found in other publications (Roberts 1996; Braaker *et al.* 2014; Yanahan & Taylor 2014). When looking at spider family reactions to the vegetation, we only found a positive effect on Zodaridae and Thomisidae, while the other families showed no reaction to the amount of ground vegetation. Zodaridae might be more abundant in greener parcels, because they feed on ants exclusively, which in turn are indeed omnipresent in all types of habitats but many species may still have a preference for vegetated areas as they mainly feed on plant material and (sap-sucking) insects and their honeydew (Roberts 1996). Thomisidae exploit a wide variety of habitats but rely on flowering plants, which they use to wait camouflaged in the flowers lurking for their prey – mainly pollinating insects (Roberts 1996) and are hence more abundant in greener vineyard parcels.

We found a clear community change of arthropod families from vegetation class 4 to class 1 and 2, showing that the communities occurring in parcels with almost no vegetation cover are different ones from those living in dense ground vegetation. As our results showed a higher arthropod richness in greener vineyard parcels, the communities potentially have changed from low to high vegetation cover in terms of an increase of arthropod species. Nevertheless the species occurring in these mineral vineyards without vegetation cover may be very specialized ones, of which some may disappear in parcels with a dense vegetation cover. For the beetle species, we found a significant community shift from class 4 to the three other classes, as in the vineyards with high amounts of vegetation (51-100%) several new species

appeared which were almost not present in vineyards with little vegetation cover. For the spider communities we only found a difference between the sites, possibly due to different microclimatic conditions, whereas there was no difference between the vegetation classes. If we would have identified and analysed spiders on species level, differences may then have become visible, as specialized species were here not considered on family level.

Despite our very clear results, there was still some variation which could not be explained by the vegetation cover solely but maybe in combination with other environmental variables related to ground cover, such as soil moisture, soil type, vegetation structure, mowing of vegetation, pesticide application and habitat connectivity (Yanahan & Taylor 2014) which we did not consider here, but should ideally be incorporated in future studies.

Ground vegetation quality had no influence on overall arthropod abundance or richness, indicating that for most arthropod species we sampled, the presence and quantity of ground vegetation is crucial while the richness of plant species might be more important for specialized species. Further, we only considered ground dwelling arthropods with our pitfall traps, while flying, epiphytic and thus pollinating arthropods were underrepresented, and thus the importance of vegetation quality might be underestimated in our results. Other studies have demonstrated the positive effects of species-rich plant communities on pollinator diversity in vineyards (e.g. Gillespie & Wratten 2012; Kehinde & Samways 2014). We found no direct effect of plant richness on beetle diversity, even though there was a strong positive correlation between ground vegetation cover and plant species richness while diversity of spider families was positively correlated with the number of plant species. For future studies, plant species should be identified in order to analyse the plant community composition, with a focus on rare and specialized species, in relation to vegetation amount respectively vegetation type (i.e. spontaneous greening or seed mixtures). This would be a next step in completing the puzzle about the woodlarks habitat preferences, as plant species composition potentially has an effect on arthropod richness what then may cascade up along the food chain to the birds.

Woodlark habitat choice

Our results show that woodlarks choose areas with more ground vegetation cover when establishing their territories while there was no visible effect of the spatial arrangement of the green parcels. We hypothesized that there might be fragmentation effects, namely that more fragmented territories (i.e. less green area, more and smaller fragments, less connected fragments) should increase in size, to compensate for the lower territory quality. Here we only

found that larger territories do have more fragments and are less green, i.e. have lower NDVI values compared to smaller territories. Even though there was a trend showing a negative relationship between territory size and mean size of green parcels and relative green area, we were not able to show that these fragments are indeed significantly smaller in size and less connected. In further steps we will try to find a more adequate way to measure connectivity between fragments in vineyards in order to deepen the understanding of the differential habitat use of woodlarks in this habitat.

The linear occurrence probability curve only flattened slightly at 80% of vegetation cover, indicating a preference for parcels with high proportions of ground vegetation on parcel scale. In a previous study on small-scale foraging sites, Arlettaz *et al.* (2012) found a quadratic preference curve, peaking at around 40-60% ground vegetation cover. This difference is probably based on a scale-effect, as in their studies a different spatial scale was investigated as foraging sites of 5 m² were used exclusively, whereas in our study we focused on larger scales, i.e. territory and parcel scale. Thus we conclude, that the birds prefer green areas and parcels with 70-100% vegetation cover – as there are higher prey abundances – while for foraging they prefer open areas with a sparse vegetation (40-70%) within the green parcels, in order to increase prey accessibility. Other studies have shown how foraging sites differ from breeding and roosting sites within woodlark territories, as at foraging sites the presence of bare ground seems to be crucial for the accessibility of the prey (Bowden 1990; Mallord *et al.* 2007; Schaub *et al.* 2010; Arlettaz *et al.* 2012; Vickery & Arlettaz 2012) while for breeding and roosting, a denser vegetation cover might be advantageous to hide from predators (e.g. Harrison & Forster 1959; Bowden 1990; Mallord *et al.* 2007; Sirami *et al.* 2011). These results support our findings about the nest site selection, where we showed that nest sites had clearly more and taller ground vegetation than control sites, on both spatial scales, what is in line with other studies (Bowden 1990; Mallord *et al.* 2007). Hence, woodlarks seem to have various habitat requirements on different spatial scales which need to be fulfilled for a successful breeding, highlighting the importance of landscape heterogeneity, especially for farmland birds (Sirami *et al.* 2011).

Further, we found that greener and more connected parcels were visited more often, whereas this might be caused by the fact that woodlarks use the centre of their territories more intensively and consequently these centered parcels are better connected within the territories than those placed at the territory border. Here also we will try to find a better and more

realistic measurement for the connectivity of green parcels. Additionally we should compare the connectivity between green, visited parcels and green, non-visited parcels to prove that woodlarks indeed prefer green parcels which in addition are better connected with each other.

Still, the preference for connected green vineyard parcels may result from their dependency on arthropods, which form their main food sources during the breeding season. Our results clearly show that arthropod abundance, richness, biomass and Shannon diversity of beetles and spiders are significantly higher in woodlark than in the control parcels and that arthropod abundance and richness reached a peak in parcels with total greening. This indicates a potential positive selection by woodlarks of sites with more arthropods and thus consequently with more ground vegetation. Although for foraging there is a trade-off between prey abundance and accessibility such that foraging sites with a mixture of vegetation and bare ground are preferred (Schaub *et al.* 2010; Arlettaz *et al.* 2012; Tagmann-Ioset *et al.* 2012). As a next step we should investigate whether there are direct effects of the abovementioned fragmentation effects on arthropods living in vineyards, what could indirectly affect woodlarks and possibly their breeding success. Additionally we should look at epiphytic arthropods as well, as woodlarks seem to take its prey directly from the ground as well as from the plants (Bowden 1990, and pers. observations), for example by taking sweep net samples in these vineyards. Finally, arthropod nestling diet has to be investigated further in order to understand which arthropods are actually preferred during the breeding season (see Rey 2013).

Recommendations

We successfully showed that there are considerably more arthropods in terms of abundance and richness in greener vineyards and in parcels, which were used by woodlarks, which consequently seem to adapt their territory selection and habitat use on the availability and variety of its arthropod prey. Our study indicates, how the viticulture management can influence the abundance and diversity of animal species, cascading up to different trophic levels. We recommend the viticulturists to increase the number of green parcels in these study sites in order to preserve and promote local biodiversity and especially woodlark populations. More specifically, on a parcel scale ground vegetation should be around 70-100% while on a smaller scale, i.e. for foraging, the vegetation should be sparse (40-70%) and mixed with bare ground on several patches within such a green parcel. This implies that a moderate herbicide application to reduce vegetation denseness is reasonable and for ground feeding insectivorous

birds it can be even beneficial. On the other hand the vegetation management should depend on the soil type, as on a lean soil spontaneous greening should naturally not become too dense. Furthermore, there are taxa which prefer or are even specialized on bare ground with no or only very little ground cover, showing that a heterogeneous landscape of a mixture of green and mineral vineyards should be preserved. Still, there is a need for further studying the effects of fragmentation in this vineyard mosaic and considering possible effects of the different vegetation structures and plant species compositions on arthropods, in order to be able to give precise recommendations about the distribution of green parcels and the structure, quality and composition of ground vegetation with the eventual aim to integrate biodiversity and agriculture, based on the concept of vinecology.

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LITERATURE

- Altieri, M.A. & Nicholls, C.I. (2002). The simplification of traditional vineyard based agroforests in northwestern Portugal: some ecological implications. *Agroforestry Systems*, **56**, 185-191.
- Arlettaz, R., Maurer, M.L., Mosimann-Kampe, P., Nussle, S., Abadi, F., Braunisch, V. & Schaub, M. (2012). New vineyard cultivation practices create patchy ground vegetation, favouring Woodlarks. *Journal of Ornithology*, **153**, 229-238.
- Atkinson, P.W., Buckingham, D. & Morris, A.J. (2004). What factors determine where invertebrate-feeding birds forage in dry agricultural grasslands? *Ibis*, **146**, 99-107.
- Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallowin, J.R.B., Smith, R.E.N., Haysom, K.A., Ings, T.C., Asteraki, E.J. & Brown, V.K. (2005). Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. *Journal of Applied Ecology*, **42**, 932-942.
- Barg, J.J., Jones, J. & Robertson, R.J. (2005). Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology*, **74**, 139-149.
- Bartón, K. (2014). MuMIn: Multi-model inference. R package version 1.10.0. <http://CRAN.R-project.org/package=MuMIn>

- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. <http://CRAN.R-project.org/package=lme4>
- Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002). Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673-687.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182-188.
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393-1405.
- Bowden, C.G.R. (1990). Selection of foraging habitats by Woodlarks (*Lullula arborea*) nesting in pine plantations. *Journal of Applied Ecology*, **27**, 410-419.
- Braaker, S., Ghazoul, J., Obrist, M.K. & Moretti, M. (2014). Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, **95**, 1010-1021.
- Britschgi, A., Spaar, R. & Arlettaz, R. (2006). Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: lessons for overall Alpine meadowland management. *Biological Conservation*, **130**, 193-205.
- Bruggisser, O.T., Schmidt-Entling, M.H. & Bacher, S. (2010). Effects of vineyard management on biodiversity at three trophic levels. *Biological Conservation*, **143**, 1521-1528.
- Chinery, M. (2012). *Pareys Buch der Insekten : über 2000 Insekten Europas*. Kosmos, Stuttgart.
- Dixon, P. (2003). VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, **14**, 927-930.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487-515.
- Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J. & Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, **6**, 380-385.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Müller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockstrom, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. (2011). Solutions for a cultivated planet. *Nature*, **478**, 337-342.
- Gardner, B. (1996). *European agriculture : policies, production, and trade*. Routledge, London.
- Gelman, A., Su, Y.S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J., Zheng, T. & Dorie, V. (2014). Data analysis using regression and multilevel/hierarchical models. R Package Version 1.7-03. <http://CRAN.R-project.org/package=arm>
- Gibb, H. & Hochuli, D.F. (2002). Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biological Conservation*, **106**, 91-100.

- Gillespie, M. & Wratten, S.D. (2012). The importance of viticultural landscape features and ecosystem service enhancement for native butterflies in New Zealand vineyards. *Journal of Insect Conservation*, **16**, 13-23.
- Glutz von Blotzheim, U. N. & Bauer, K. M. (1985). *Handbuch der Vögel Mitteleuropas, Band 10/1. Passeriformes (1. Teil): Alaudidae – Hirundinidae, Lerchen und Schwalben*. Aula-Verlag, Wiesbaden.
- Guidoum, A.C. (2013). Kernel estimator and bandwidth selection for density and its derivatives. R package version 1.0.0. <http://CRAN.R-project.org/package=kedd>
- Harrison, C.J.O. & Forster, J. (1959). Woodlark territories. *Bird Study*, **6**, 60-68.
- Holloway, S. (1996). *The historical atlas of breeding birds in Britain and Ireland: 1875-1900*. Poyser, London.
- Kehinde, T. & Samways, M.J. (2014). Management defines species turnover of bees and flowering plants in vineyards. *Agricultural and Forest Entomology*, **16**, 95-101.
- Keller, V., Ayé, R., Müller, W., Spaar, R. & Zbinden, N. (2010a). Die prioritären Vogelarten der Schweiz: Revision 2010. *Der Ornithologische Beobachter*, **107**, 265-285.
- Keller, V., Gerber, A., Schmid, H., Volet, B. & Zbinden, N. (2010b). Rote Liste Brutvögel. Gefährdete Arten der Schweiz, Stand 2010. Bundesamt für Umwelt, Bern, und Schweizerische Vogelwarte, Sempach.
- Kleijn, D. & Sutherland, W.J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947-969.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tschirntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243-254.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999). The second silent spring? *Nature*, **400**, 611-612.
- Mallord, J.W., Dolman, P.M., Brown, A. & Sutherland, W.J. (2007). Nest-site characteristics of Woodlarks *Lullula arborea* breeding on heathlands in southern England: are there consequences for nest survival and productivity? *Bird Study*, **54**, 307-314.
- McKenzie, A.J., Emery, S.B., Franks, J.R. & Whittingham, M.J. (2013). Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *Journal of Applied Ecology*, **50**, 1274-1280.
- Naef-Daenzer, B. (1993). A new transmitter for small animals and enhanced methods of home-range analysis. *Journal of Wildlife Management*, **57**, 680-689.
- Naef-Daenzer, B. (2000). Patch time allocation and patch sampling by foraging great and blue tits. *Animal Behaviour*, **59**, 989-999.
- Nascimbene, J., Marini, L., Ivan, D. & Zottini, M. (2013). Management intensity and topography determined plant diversity in vineyards. *Plos ONE*, **8**, e76167.
- Pettorelli, N., Vik, J.O., Myrsetrud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, **20**, 503-510.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Development Core Team (2012). nlme: Linear and nonlinear mixed effects models. R Package Version 3.1-111.

- QGIS Development Team (2014). QGIS Geographic Information System. Open source geospatial foundation project. QGIS Version 2.4.0. <http://qgis.osgeo.org>.
- R Development Core Team (2013). R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria. <http://www.R-project.org/>.
- Roberts, M.J. (1996). *Spiders of Britain and Northern Europe*. Harper Collins Publishers, London.
- Sanguaneko, P.P. & Leon, R.G. (2011). Weed management practices determine plant and arthropod diversity and seed predation in vineyards. *Weed Research*, **51**, 404-412.
- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R. (2010). Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *Plos ONE*, **5**, e13115.
- Schmitt, T., Augenstein, B. & Finger, A. (2008). The influence of changes in viticulture management on the butterfly (Lepidoptera) diversity in a wine growing region of southwestern Germany. *European Journal of Entomology*, **105**, 249-255.
- Searcy, W.A. (1979). Female choice of mates – a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *The American Naturalist*, **114**, 77-100.
- Sierro, A. & Arlettaz, R. (2003). L'avifaune du vingoble en Valais central: évaluation de la diversité à l'aide de transects. *Nos Oiseaux*, **50**, 89-100.
- Sirami, C., Brotons, L. & Martin, J.-L. (2011). Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment. *Bird Study*, **58**, 99-106.
- Sitters, H.P., Fuller, R.J., Hoblyn, R.A., Wright, M.T., Cowie, N. & Bowden, C.G.R. (1996). The woodlark *Lullula arborea* in Britain: population trends, distribution and habitat occupancy. *Bird Study*, **43**, 172-187.
- Steenwerth, K. & Belina, K.M. (2008). Cover crops enhance soil organic matter, carbon dynamics and microbiological function in a vineyard agroecosystem. *Applied Soil Ecology*, **40**, 359-369.
- Steiniger, S. & Hunter, A.J.S. (2013). A scaled line-based kernel density estimator for the retrieval of utilization distributions and home ranges from GPS movement tracks. *Ecological Informatics*, **13**, 1-8.
- Stresemann, E. & Klausnitzer, B. (2011). *Exkursionsfauna von Deutschland, Band 2: Wirbellose: Insekten*. 11. Auflage, Spektrum Akademischer Verlag, Heidelberg.
- Tagmann-Ioset, A., Schaub, M., Reichlin, T.S., Weisshaupt, N. & Arlettaz, R. (2012). Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. *Acta Oecologica*, **39**, 25-32.
- Thomson, L.J. & Hoffmann, A.A. (2009). Vegetation increases the abundance of natural enemies in vineyards. *Biological Control*, **49**, 259-269.
- Thomson, L.J. & Hoffmann, A.A. (2010). Natural enemy responses and pest control: importance of local vegetation. *Biological Control*, **52**, 160-166.
- Traba, J., Morales, M.B., Garcia de la Morena, E.L., Delgado, M.-P. & Krištín, A. (2008). Selection of breeding territory by little bustard (*Tetrax tetrax*) males in Central Spain: the role of arthropod availability. *Ecological Research*, **23**, 615-622.

- Trivellone, V., Pollini-Paltrinieri, L., Jermini, M. & Moretti, M. (2012). Management pressure drives leafhopper communities in vineyards in Southern Switzerland. *Insect Conservation and Diversity*, **5**, 75-85.
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J. & Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, **151**, 53-59.
- Vandermeer, J. & Perfecto, I. (2005). The future of farming and conservation. *Science*, **308**, 1257-1257.
- Venables, W.N. & Ripley, B.D. (2002). Modern applied statistics with S. Fourth Edition. Springer, New York.
- Vickery, J. & Arlettaz, R. (2012). The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. In: *Birds and Habitat: Relationships in Changing Landscapes* (ed. R.J. Fuller), pp. 177-204. Cambridge University Press, Cambridge.
- Viers, J.H., Williams, J.N., Nicholas, K.A., Barbosa, O., Kotzé, I., Spence, L., Webb, L.B., Merenlender, A. & Reynolds, M. (2013). Vinecology: pairing wine with nature. *Conservation Letters*, **6**, 287-299.
- Wolpert, J.A., Phillips, P.A., Striegler, R.K., McKenry, M.V. & Foott, J.H. (1993). Berber orchardgrass tested as cover crop in commercial vineyard. *California Agriculture*, **47**, 23-25.
- Yanahan, A.D. & Taylor, S.J. (2014). Vegetative communities as indicators of ground beetle (Coleoptera: Carabidae) diversity. *Biodiversity and Conservation*, **23**, 1591-1609.

TABLE 1 The best glmer models with a delta AIC <2, describing arthropod abundance (models 30, 26, 32) and arthropod richness (models 18, 10, 22, 20). For each model all included variables, degrees of freedom, the difference of the AIC between that and the best model (ΔAIC) and the Akaike weight are given.

Model No.	Variables	df	ΔAIC	Akaike weight
Arthropod abundance				
30	Arthropod biomass + parcel slope + ground vegetation + (ground vegetation) ²	6	0.00	0.40
26	Arthropod biomass + ground vegetation + (ground vegetation) ²	5	0.94	0.25
32	Arthropod biomass + parcel size + parcel slope + ground vegetation + (ground vegetation) ²	7	1.37	0.20
Arthropod richness				
18	Arthropod biomass + (ground vegetation) ²	4	0.00	0.17
10	Arthropod biomass + ground vegetation	4	0.42	0.137
22	Arthropod biomass + parcel slope + (ground vegetation) ²	5	1.85	0.067
20	Arthropod biomass + parcel size +(ground vegetation) ²	5	1.95	0.063

TABLE 2 Estimated coefficients \pm standard errors, degrees of freedom, *t* and *p* values for the abundance and richness of the five different arthropod orders with ground vegetation as explanatory variable. Model 3 only shows the results for abundance, as dipterans were only classified to order level.

No.	Variable	Estimate \pm SE	df	t value	p value
1	Beetles				
	Abundance	0.009 \pm 0.003	123	3.028	0.003
	Richness	0.009 \pm 0.002	123	5.67	< 0.0001
2	Spiders				
	Abundance	0.008 \pm 0.003	123	3.12	< 0.0001
	Richness	0.005 \pm 0.002	123	2.84	0.0053
3	Dipterans				
	Abundance	0.13 \pm 0.003	123	3.75	< 0.0001
4	Hymenoptera				
	Abundance	0.020 \pm 0.004	123	4.85	< 0.0001
	Richness	0.012 \pm 0.004	123	3.26	0.0014
5	Heteropterans				
	Abundance	0.03 \pm 0.007	123	4.40	< 0.0001
	Richness	0.026 \pm 0.006	123	4.44	< 0.0001

TABLE 3 Estimated coefficients \pm standard errors, degrees of freedom, *t* and *p* values for the abundance of the six different beetle species (families are given in brackets) in relation to ground vegetation and the number of plant species. Model 4 shows additionally the interaction of both variables.

No.	Variable	Estimate \pm SE	df	t value	p value
1	<i>O.sabulosum</i> (Tenebrionidae)				
	Vegetation	0.009 \pm 0.004	109	2.54	0.013
	Nr.plants	0.01 \pm 0.05	101	0.21	0.84
2	<i>A.aenea</i> (Carabidae)				
	Vegetation	0.04 \pm 0.008	109	5.04	< 0.0001
	Nr.plants	0.21 \pm 0.09	101	2.43	0.017
3	<i>N.brevicollis</i> (Carabidae)				
	Vegetation	0.01 \pm 0.004	109	2.95	0.004
	Nr.plants	0.10 \pm 0.05	101	2.26	0.03
4	<i>B.crepitans</i> (Carabidae)				
	Vegetation	0.002 \pm 0.005	109	0.37	0.72
	Nr.plants	0.18 \pm 0.06	101	3.13	0.002
	Veg * nr.plants	-0.004 \pm 0.002	100	-2.22	0.03
5	<i>S.obscura</i> (Silphidae)				
	Vegetation	0.03 \pm 0.007	109	3.81	0.0002
	Nr.plants	-0.15 \pm 0.07	101	-2.05	0.04
6	<i>R.germanus</i> (Scarabaeidae)				
	Vegetation	0.009 \pm 0.007	109	1.21	0.23
	Nr.plants	0.07 \pm 0.102	101	0.63	0.53

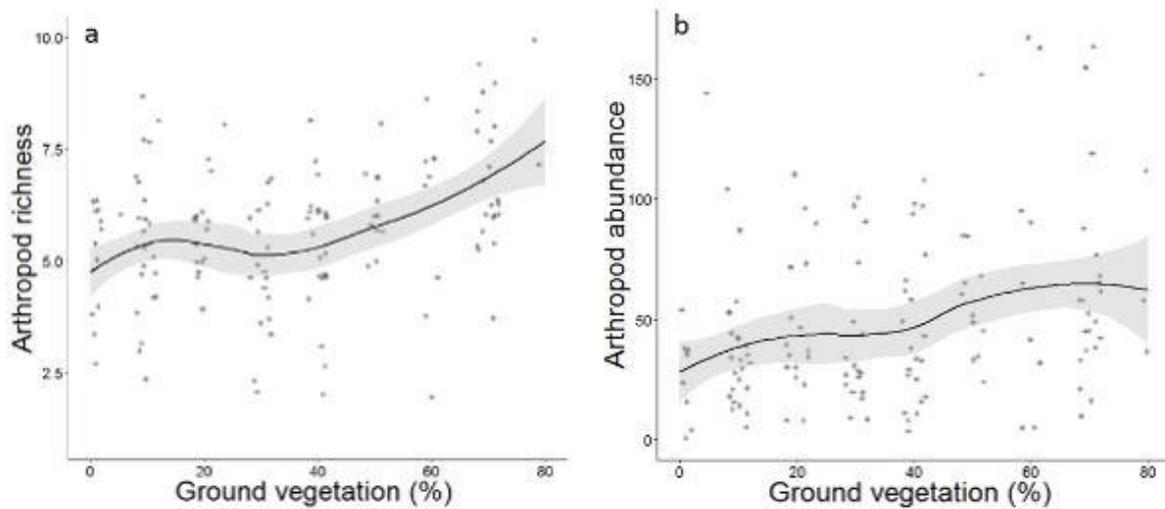


FIGURE 1 Regressions with quadratic fit of ground vegetation and 95% confidence intervals of **a)** arthropod richness (as number of arthropod orders per trap) and **b)** arthropod abundance.

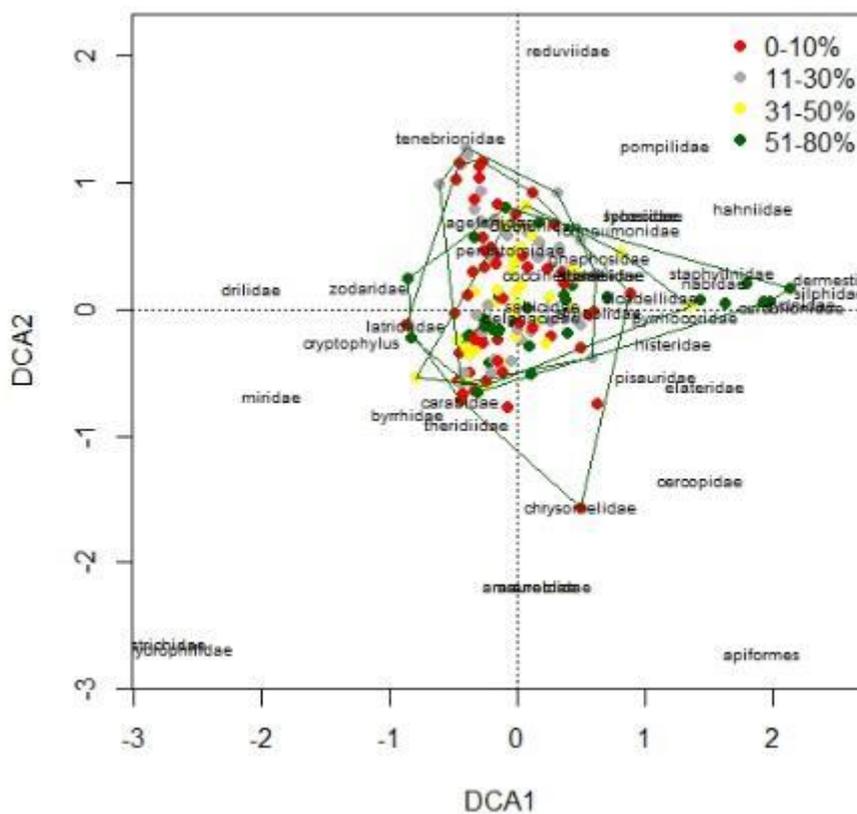


FIGURE 2 Detrended correspondence analysis (DCA) of all arthropod families against the four different vegetation classes, indicated in red (0-10%), grey (11-30%), yellow (31-50%) and green (51-80%) and showing the difference in community composition of vegetation class 4 (green points) to the classes 1 (red points) and 2 (grey points).

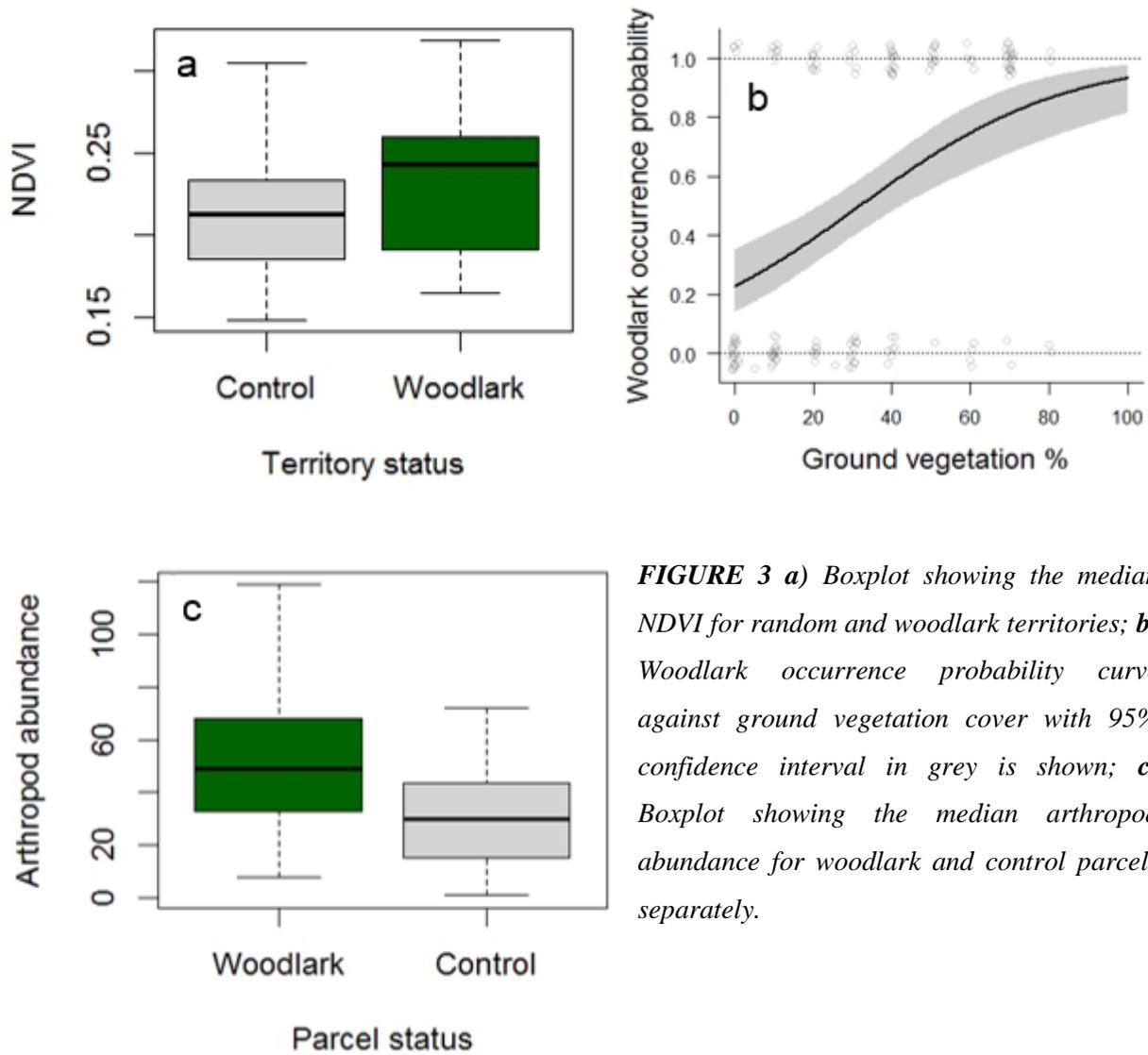


FIGURE 3 a) Boxplot showing the median NDVI for random and woodlark territories; b) Woodlark occurrence probability curve against ground vegetation cover with 95% confidence interval in grey is shown; c) Boxplot showing the median arthropod abundance for woodlark and control parcels separately.

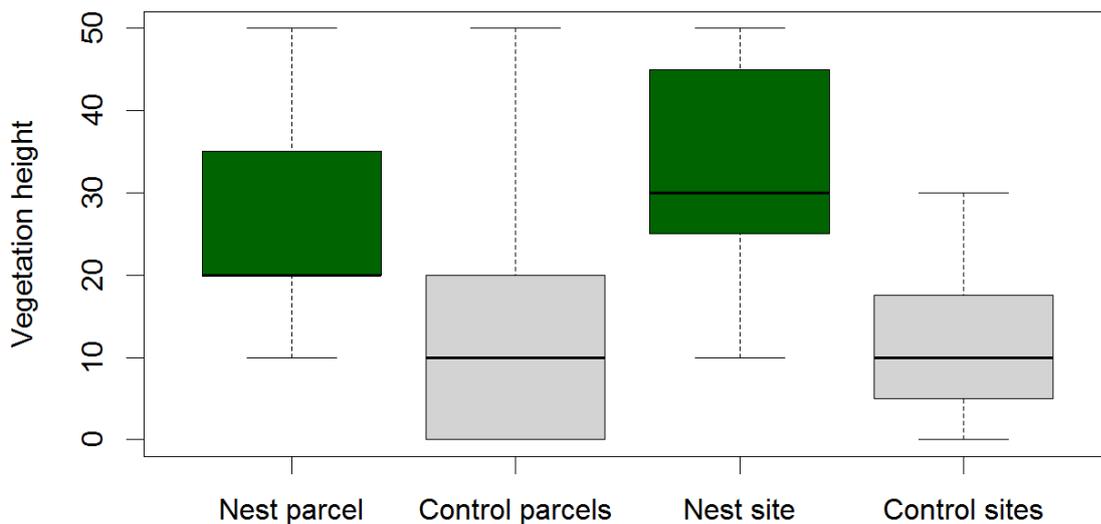


FIGURE 4 Boxplot showing the median ground vegetation height on a parcel scale (woodlark nest parcels against the surrounding control parcels), and on a square meter scale (1 m^2 around the nest against four random 1 m^2 sites within the nest parcels).

SUPPORTING MATERIAL

TABLE A1 Table showing the details of all captured woodlarks (Woodlark: bird ID; Capture date: the date on which the bird was captured; Days running: number of days the radio-transmitter battery was running; Locations: Number of locations we obtained during radio-tracking; Site: S/V = Salgesch/Varen; Ch = Chamoson; Comments: if known, the gender and the date on which we found the nests, are given).

Woodlark	Capture Date	Days running	Locations	Site	Comments
1	10.03.2013	40	62	S/V	
2	10.03.2013	38	59	S/V	
3	12.03.2013	35	53	Ch	
4	12.03.2013	38	60	Ch	
5	20.03.2013	41	59	Ch	
6	22.03.2013	29	59	Ch	female, nest 21.04.13
7	03.04.2013	34	63	S/V	
8	05.04.2013	18	23	Praveriaz	transmitter lost 22.04.13
9	09.04.2013	35	43	Ch	female, nest 18.04.13
10	10.04.2013	36	52	Ch	male, nest 26.04.13
11	14.04.2013	26	35	Loc	female, nests 25.04.13 & 09.05.13
12	16.04.2013	33	56	S/V	nest 18.05.13
13	17.04.2013	32	56	Ch	nest 29.04.13

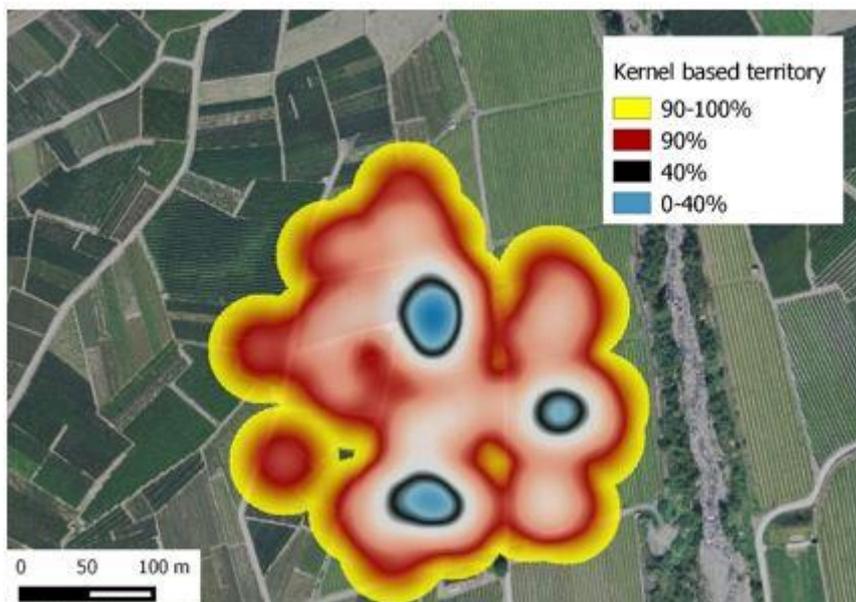


FIGURE A1 Exemplary kernel density based woodlark territory, calculated with the plugin “heatmap” in QGIS. Different colours show the density isopleths (darkred: 90% isopleth indicates territory borders; black: 40% isopleth shows core area borders). (copyright@swisstopo.ch)

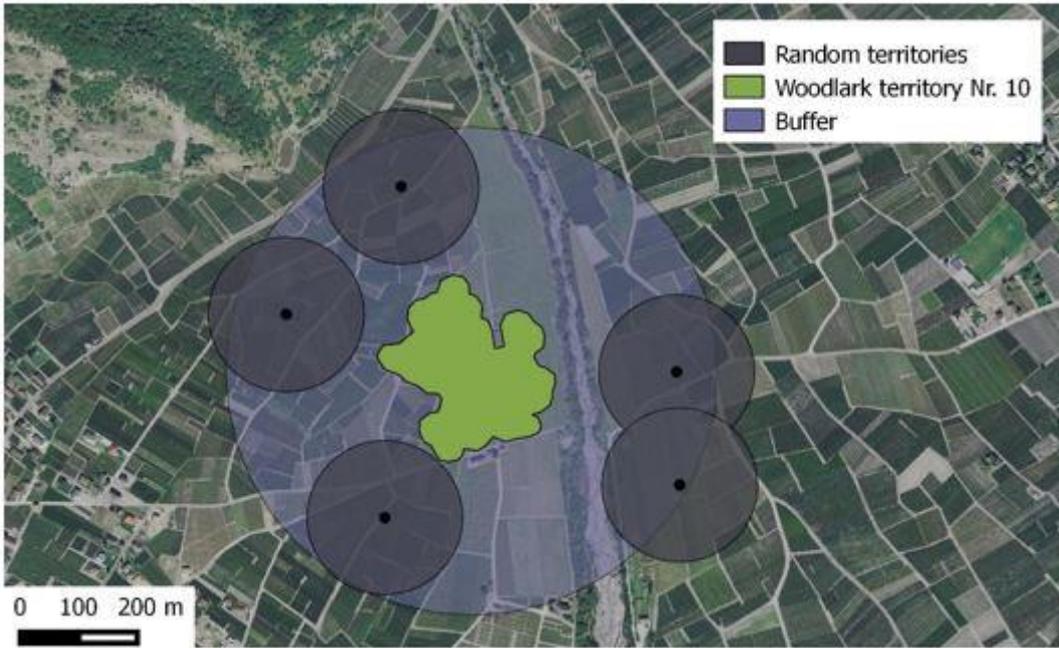


FIGURE A2 Territory scale: Example of a woodlark territory (green), its buffer (lightgrey) and the five dummy territories (darkgrey), created based on the five randomly chosen points (black dots). (copyright@swisstopo.ch)



FIGURE A3 Parcel scale: In lightgreen all woodlark parcels are shown, i.e. all parcels which were visited during radio-tracking - while in grey all control parcels, i.e. all parcels within the territory which were not visited during radio-tracking, are shown. Radio-tracking locations are represented as white dots. (copyright@swisstopo.ch)

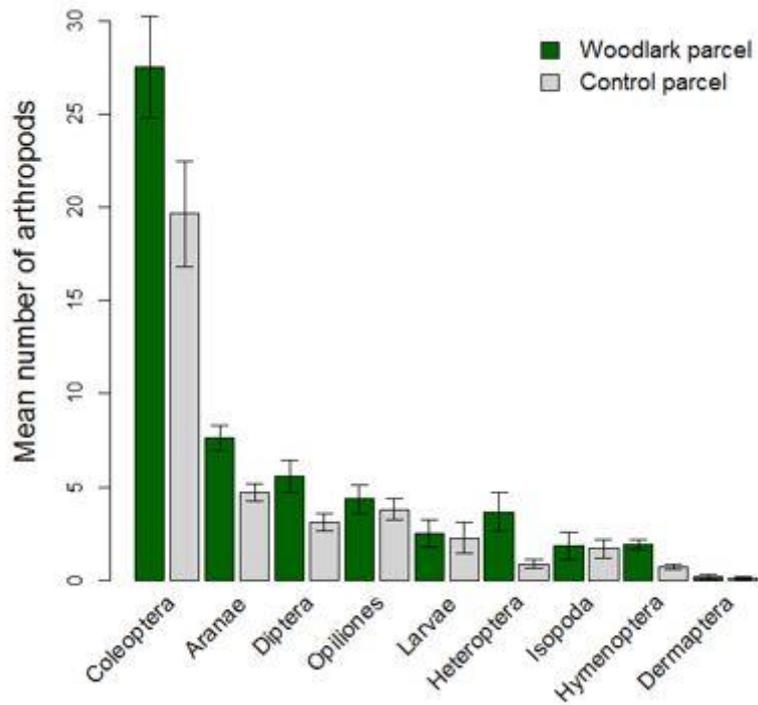


FIGURE A4 Barplot showing the mean number of arthropods per pitfall trap for the nine most abundant orders and for both parcel types separately. (Green: woodlark parcels; grey: control parcels).

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname: Bosco Laura

Matrikelnummer: 07.640.840

Studiengang: Master in Ecology and Evolution

Bachelor Master Dissertation

Titel der Arbeit: The effects of ground vegetation cover on the habitat use of the woodlark Lullula arborea and its prey

LeiterIn der Arbeit: Prof. Dr. R. Arlettaz, Dr. A. Jacot

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetzes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist. Ich gewähre hiermit Einsicht in diese Arbeit.

Bern, 15.08.2014

Ort/Datum


.....

Unterschrift