

**Semi-natural habitat versus ground vegetation in vineyards : disentangling birds' habitat preferences at a landscape scale**

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**Semi-natural habitat versus ground vegetation in vineyards : disentangling birds' habitat preferences at a landscape scale.**

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**Abstract**

Agricultural expansion and intensification happen at the expense of natural habitat and its biodiversity. These processes imply multiple changes on a landscape scale, ranging from habitat homogenization to loss in natural structures. These alterations on a landscape scale are known to impact habitat preferences of birds. In particular, landscape composition and configuration are known to be of crucial importance for decision making during winter, migration and for territory settlement. Yet, the relative importance of these factors remain mostly unknown, often owing to the correlation between their gradients. Here, we selected a series of spatially distributed transects in intensively managed vineyards across a dual gradient of two important and statistically independent habitat variables, grove cover (bushes & hedges) and ground vegetation cover in vineyard fields. Ground vegetation cover in vineyard fields reflects a biodiversity-friendly management compared to the surface-wide application of herbicides, the latter resulting in monotonous fields with extensive bare ground. We investigated their separate and interdependent effects on bird abundance, species richness and diversity throughout the annual cycle. Our results demonstrated the utmost importance of grove cover within vineyard areas at landscape scale, independently of the amount of vineyard ground vegetation cover. This effect was detectable in all three seasons, winter, spring and summer. In contrast, ground vegetation cover at landscape scale was shown to be less important for overall bird communities, with only a few strictly ground-foraging granivorous species driven by that sole factor, independently from the amount of grove cover. We conclude that conservation actions at landscape scale should primarily focus on the preservation and implementation of grove networks within vineyard landscapes and in a more opportunistic way on the enhancement of ground vegetation in the production surface of vineyards.

**Keywords**

Vineyard, landscape scale, production surface, birds, habitat selection, habitat preferences, grove, ground vegetation

## Introduction

Agricultural intensification started with the Green Revolution in the mid-20<sup>th</sup> century, leading to dramatic changes in agricultural landscapes and its concomitant negative effects on biodiversity (Gardner 1996; Pingali 2012). Multiple factors were altered during this intensification processes. Farmland numbers and habitat complexity decreased simultaneously, leading to a global homogenisation of the agricultural ecosystems (McGarigal & Cushman 2002; Vickery & Arlettaz 2012; Viers *et al.* 2013; Pretty & Bharucha 2014). Heterogeneity being one of the keys for high levels of biodiversity (Wilcove, McLellan & Dobson 1986; Newmark 1991; Gaston 2000; Vickery *et al.* 2001; Benton, Vickery & Wilson 2003), this intensification resulted in a strong loss of animals and plants (Krebs *et al.* 1999; Boatman *et al.* 2004; Schmitt, Augenstein & Finger 2008; Knaus *et al.* 2011). The decrease of farmland biodiversity following this fragmentation and loss of habitat has been widely established and studied, touching many different taxas (Newmark 1991; Fischer & Lindenmayer 2007; Bruggisser, Schmidt-Entling & Bacher 2010; Korfanta *et al.* 2012; Tagman-Ioset *et al.* 2012; Trivellone *et al.* 2012; Bornand *et al.* 2016). But the relative importance of different factors on biodiversity is often unclear, resulting in a gap of such knowledge in management recommendations (Mortelliti *et al.* 2010).

Often, biodiversity decline is multifactorial, as animals need to fulfil several requirements throughout the year. Birds need to find breeding, wintering, foraging and sheltering sites, which are different from each other in location and relevance for their survival and are impacted by various factors (habitat loss and fragmentation). Within foraging patterns, it has been shown that different habitats are required by species like Wryneck *Jynx torquilla*, Hoopoe *Upupa epops* and Woodlark *Lulula arborea*, highlighting the complexity of the system ('kitchen – dining room configuration'; Keller *et al.* 2010b; Arlettaz *et al.* 2012; Vickery & Arlettaz 2012). It has been shown that use of fertilizers induces a densification of the herbaceous stratum and hence the creation of a uniform thick lawn, reducing food accessibility and predator detection (Whittingham & Evans 2004). This idea of accessibility / detection trade-off has been confirmed by a recent study (Schaub *et al.* 2010). The focus of the vast majority of researches are single species habitat selection patterns (Perkins *et al.* 2002;

Brambilla & Rubolini 2009; Menz, Mosimann & Arlettaz 2009; Brambilla *et al.* 2010; Martinez *et al.* 2010; Arlettaz *et al.* 2012; Balmford, Green & Phalan 2012) or the detection of the multiple causes of the decline (Laiolo 2005; Vickery & Arlettaz 2012; Guyot *et al.* 2017) but only rarely the disentangling of the relative effects of several factors at different spatial scales. This indicates the need of trying to quantify independently the importance of these single factors, using designs to disentangle their effects and interactions, as they often require different conservation strategies (Smith *et al.* 2009; Mortelliti *et al.* 2010). Appropriate designs with two statistically independent gradients are hard to obtain in natural settings as environmental variables often show some degrees of correlation (McGarigal & Cushman 2002; Fahrig 2003; Koper, Schmiegelow & Merrill 2007; Smith *et al.* 2009). In the context of conservation management recommendations, combining several factors can be counter-productive as their effect magnitude might vary according to the taxa and spatial scale used (Fahrig 2003). Bird habitat selection analysis is indeed scale-dependant and it is hence additionally advisable to encompass different spatial scales during the research (Robinson, Wilson & Crick 2001; Gabriel *et al.* 2010; Assandri *et al.* 2016; Guyot *et al.* 2017).

Studies disentangling relative effects of two statistically uncorrelated factors using appropriate designs are existing, but still rare (Smith *et al.* 2009; Mortelliti *et al.* 2010). For example, Marini *et al.* (2010) linked orthopteran diversity to two uncorrelated gradients and were able to demonstrate that habitat loss (in hectares) was the main driver of species extinction, irrespective of habitat diversity. Using similar statistically independent gradients, Mortelliti *et al.* (2010) strategically selected 30 landscapes and demonstrated that the abundance of several forest-dwelling birds was mostly driven by habitat loss, while structural connectivity played a weaker role. Those findings are in line with those of Honkanen *et al.* (2009), who disentangled effects of multiple factors on birds in 104 protected forest areas in Finland. Species richness was mostly influenced by the amount of forest rather than habitat heterogeneity. However, Devictor, Julliard & Jiguet (2008) found that the more specialised a forest-dwelling bird species is, the more sensitive its response was to landscape fragmentation, highlighting the necessity to consider species-specific habitat selection patterns. In the United Kingdom, winter habitat quality played the most important role in determining the location of breeding Yellowhammer, a fast-declining songbird (Whittingam *et al.* 2005), when compared to 9 other bird predictors, but was

dependant on the scale used. Those researches highlight the importance of habitat selection analysis at different seasons and spatial scales.

While most of the research focus on woodland (forest-dwelling species) or cereals (where crop rotation occurs), permanent crop (such as vineyard and orchard) are less studied and have not been spared by the increase in pesticide and herbicide use and hence biodiversity decline (Altieri & Nicholls 2002; Birrer *et al.* 2007; Keller *et al.* 2010b; Arlettaz *et al.* 2012). Vineyard settings make it an ideal model system trying to disentangle different habitat selection patterns on a landscape scale, as its environmental variables (such as semi-natural habitat amount or ground vegetation inside the production surface) can easily be considered and managed separately (Smith *et al.* 2009), while evidence-based management recommendations are still lacking. Vineyards surrounded by semi-natural habitat (hedges, bushes, natural grasslands) have the potential to host locally rare species (not only birds but also arthropods, insects, plants) owing to their xeric conditions (Costello & Daane 1998; Sierro *et al.* 2001; Sierro & Arlettaz 2003; Košulič, Michalko & Hula 2014; Bornand *et al.* 2016; Irvin, Bistline-East & Hoddle 2016). Additionally, viticulture is spreading in the temperate region outside the Mediterranean basin, at the expense of natural habitat (Sierro & Arlettaz 2003; Jedlicka *et al.* 2014). Previous studies in vineyards of Valais (Guyot *et al.* 2017) and northern Italy (Assandri *et al.* 2016) measured landscape- and fine-scale habitat preferences of birds, but the relative effects of vineyard ground vegetation and semi-natural habitat amount remained elusive. However, this approach was necessary to understand on which scales birds show preferences. What is hence still lacking is a comprehensive study disentangling the relative importance of ground vegetation characteristics and semi-natural habitat on habitat preferences of birds. It is yet unclear what should be targeted for conservation, as both gradients have never been studied independently. Knowing that a large proportion of south-exposed slopes in Valais are shaped by vineyard, it is of primary importance to disentangle the relationship between this intensively cultivated agroecosystem and avifauna

In this study, we aimed to disentangle the relative effects of two statistically independent environmental variables, ground vegetation inside the vineyard (=inside the production surface) and semi-natural habitat like grove (=outside the production surface) on bird abundance, richness and diversity in the vineyard of Valais (south-western Switzerland) at a landscape-scale. Additionally, we

took a special care about birds specialised on open habitats (and especially vineyard), occurring in higher density in this agro-ecosystem than anywhere else in this part of Switzerland, for whom a sound vineyard management is likely to produce significant effects. By mean of a quasi-experimental study design, we monitored birds over 40 400-meters long line-transects, selected along two gradients: from a low to a high vineyard ground vegetation, and from a low to a high amount of semi-natural habitat surrounding the vineyard, but not along both gradients. This study was hence designed to allow the disentangling of both environmental variables independently, at a landscape scale. This allowed an extensive coverage of our study area in winter, spring and summer, to encompass a bird diversity as large as possible, including winter visitors, spring migrants and summer breeders. We used linear mixed-effect regression to link bird and environmental predictors and tested all possible combinations of effects and interactions. With those results, we aimed to design effective conservation recommendations to preserve and enhance bird communities in this intensively managed agro-ecosystem.

## **Materials and methods**

### *Study area*

In Switzerland, more than 11480 ha of arable land are dedicated to vineyards, of which a third occur in Valais, south-western Switzerland (Arlettaz *et al.* 2012). This inner-alpine valley is characterized by a semi-continental climate with low precipitations throughout the year, hot summers and cold winters. The study area consists of intensively managed vineyards located along the south-exposed slope of the Rhône valley in the Canton of Valais, between Fully (46°07'57.7"N 7°05'54.5"E) and Leuk (46°18'55.4"N 7°38'52.8"E; 474 – 881 m a.s.l.). Vineyards are one of the most pesticide-consuming agro-ecosystem in Switzerland (Aubertot *et al.* 2005), while there is an ongoing trend towards more biodiversity-friendly management. First, vine fields are mostly cultivated following the integrate production protocol, leading to a decrease of the use of pesticides over the past decades. However, farmers following the integrate production protocol are not obliged to reduce their herbicide use, one of the main reasons of the very mineral appearance of vineyards with bare ground covering most of all fields (Arlettaz *et al.* 2012). Secondly, due to the steep topography of the Rhône valley, a high

proportion of vineyard fields are organized as successive terraces, interspersed with a variable amount of semi-natural habitats (bushes, trees, grasslands; Arlettaz *et al.* 2012).

### *Transect selection*

This study aims at disentangling the separate and interdependent effects of vineyard ground vegetation cover and semi-natural habitat (groves, natural grasslands and isolated trees) on avian biodiversity. Based on visual inspection of high-resolution aerial photographs (WorldView-2, Swisstopo), we selected a series of study sites (N=40) across a dual gradient of ground vegetation cover (5-54%) and semi-natural habitats (0-30%), covering a wide range of landscape compositions. Both variables, ground vegetation cover and semi-natural habitat, were not correlated among transects ( $r_s = 0.05$ ;  $p = 0.55$ ; Appendix 1). Each transect had to be at a minimal distance of 200m from the nearest other transect.

Around each transect, we delineated a buffer of 100m in which we quantified the ground vegetation cover of all vineyard fields and all semi-natural habitats ('sel\_MO\_Biens\_fonds\_MN03.shp', Departement für Volkswirtschaft, Energie und Raumentwicklung & Dienststelle der Grundbuchämter und der Geomatik Kanton Wallis 2014) using GIS software (Quantum GIS Development Team, 2016). To estimate the amount of ground vegetation cover, we used the Normalized Difference Vegetation Index (NDVI) of satellite pictures (15.04.16; WorldView-2, Swisstopo). This measure is known to correlate with chlorophyll activity where values range from -1 to +1, with negative values associated with a lack of vegetation (Pettorelli *et al.* 2005; Acevedo-Opazo *et al.* 2008). This technique consists in estimating the proportion of vegetated areas, thanks to the red/near-infrared reflectance ratio [ $NDVI = (NIR - RED) / (NIR + RED)$ ], where NIR is the amount of near-infrared light and RED the amount of red light. In addition to remote sensing data, we quantified the amount of green and brown vegetation cover (%), type of dominant green vegetation (annual or perennial), vegetation height (visually estimated), vine grapes (number of grapes counted within 5 seconds from a random point) and cultivation type (in Valais, only 2 cultivation types: gobelet and row; Arlettaz *et al.* 2012) (Table 1) for each field. Mapping vineyard fields was performed twice and included recording all vineyard characteristics at a field scale: It was first done before the winter (21-25.11.16) and secondly during the spring monitoring sessions, after first herbicide

application (24-28.04.17) to account for differential cover of ground vegetation between winter and spring and summer. Area-weighted mean vineyard ground vegetation per transect was then calculated on QGIS for winter (using the winter mapping session) and spring and summer (using the spring mapping session). The quantity of semi-natural habitats was first assessed, using satellite pictures (WorldView-2, Swisstopo) and secondly corrected by mapping in the field at the beginning of the study in november (Table 1).

### *Bird surveys*

We applied the well-established line transect method (Bibby *et al.* 2000; Guyot *et al.* 2017) using multiple short transects (N=40;  $411.9 \pm 22.5$ m) that covered well the study area in respect to ground vegetation cover and natural structures (Assandri *et al.* 2016). To minimize any bias in respect to sampling effort, each transect was surveyed for 30-45 minutes. The surveys were performed by two observers of similar knowledge, Gabriel Marcacci (GM) and Julien Mazenauer (JM), where both observers surveyed across all landscape compositions (in respect to the gradients of ground vegetation cover and natural structures). Any bird seen within the predefined buffer zone, including birds in fields, in natural structures and birds flying over the fields was considered for the analysis, if it showed interest for the vineyard (sightings of migrating birds were not taken into account). All birds seen and heard within the transect buffer were recorded on a paper map and latter digitized on the website [www.ornitho.ch](http://www.ornitho.ch) (Swiss Ornithological Institute, Sempach). All surveys took place during the first five hours after dawn under favourable weather conditions (low wind, no precipitation; Schmid, Zbinden & Keller 2004). Indeed, bird activity is at its highest during the first hours of the morning and declines steeply at midday (Guyot *et al.* 2017). Additionally, a similar amount of transect-types was surveyed each morning. Each transect was surveyed twice by the same observer within a short time window (48 hours) and at different times in the morning. Birds were recorded during three different sessions (winter: 28.11.16 - 19.01.17; spring: 15.03. - 01.06.17; summer: 02.06. - 01.08.17), allowing to test the differential or consistent seasonal effects of landscape composition on bird abundance, richness and diversity. Each transect was surveyed twice in winter and summer and four times (twice during the

first half and twice during the second half of the session) in spring, to allow a wider detection of migratory birds.

### *Habitat selection analyses*

All analysis were performed on R version 3.4.3 (R Core Team 2017). Habitat preferences were investigated using Generalized Linear Mixed Models (GLMMs) from the 'lme4' R-package (Bates *et al.* 2015) with 'transect' as random effect to account for repeated visits per transect. We used a poisson model with a log-link function for abundance data and species richness, while a gaussian error structure was assumed for species diversity (Bolker *et al.* 2008; Bates *et al.* 2015). Covariates included all habitat variables (Table 1), time of day when the survey started and the date of the survey. To account for collinearity among explanatory variables, we excluded the biologically less meaningful variable when the Spearman correlation coefficient  $|r_s|$  exceeded 0.7. Explanatory landscape variables such as grove cover or number of trees (see Table 1), were arcsin-square root transformed and standardized (mean=0, standard deviation=1) to improve model fit. An 'observation level' random factor was added to correct for overdispersion when necessary (R package 'blmeco', function 'dispersion\_glmer'; Korner-Nievergelt *et al.* 2015). Bird abundance, species richness and Shannon diversity index were calculated using the 'VEGAN' package on R (Dixon 2003; Oksanen *et al.* 2015). In a first step, univariate models were performed using all explanatory variables as well as 2<sup>nd</sup> order polynomials in relation to bird characteristics (Bates *et al.* 2015). When non-significant ( $P > 0.05$ ), time, date and their polynomials were excluded from models. Polynomials of landscape variables and interactions were also dropped when non-significant (under the same criterion as above) to keep the model simple. The observer never had a significant effect on bird counts and was hence systematically excluded for model selection. In a second step, best-model selection (based on the lowest Akaike's Information Criterion) was performed by using the R package 'MuMIn', function 'dredge' (Bartoń 2013). Model averaging was then applied over the set of competitive models (with  $\Delta AIC \leq 2$ ; Burnham & Anderson 2002) to estimate coefficients and 95% credible intervals for each environmental variable contained in best models. The fit of each competitive model included in model averaging was checked by analysing residual's normality, normal distribution of the random factor and temporal

autocorrelation. All variables having a significant effect ( $p$ -value $<0.05$ ) on bird predictors, those present in all competitive models and those being relevant for this study (semi-natural habitat and vineyard ground vegetation cover) were then plotted by using model-averages with 95%-Bayesian credible intervals (R package ‘arm’; Gelman & Su 2015; Korner-Nievergelt *et al.* 2015).

Analyses were performed on different taxonomic levels: all species together, for the families Turdidae and Fringillidae and for several bird species. The abundances of Blackbird *Turdus merula*, Mistle Thrush *Turdus viscivorus*, Song Thrush *Turdus philomelos*, Fieldfare *Turdus pilaris* and Redwing *Turdus iliacus* were pooled together in the Turdidae family, as well as the abundances of Chaffinch *Fringilla coelebs*, Brambling *Fringilla montanus*, Common Linnet *Carduelis cannabina*, European Goldfinch *Carduelis carduelis*, European Greenfinch *Carduelis chloris*, Eurasian Siskin *Carduelis spinus*, Citril Finch *Serinus citrinella*, European Serin *Serinus serinus* in the Fringillidae family, as sample size of single species were often too low for modellisation. Turdidae and Fringillidae were then used as response variables and modelled using poisson regression. Species-specific habitat preferences were analysed separately for open-habitat specialists (European Serin *Serinus serinus*, Common Linnet *Carduelis cannabina*, Woodlark *Lullula arborea*, Cirl Bunting *Emberiza cirlus* and Rock Bunting *Emberiza cia*; Posse *et al.* 2011), as their sample sizes were often sufficient for modellisation and their habitat requirements may differ significantly from other species. Poisson regression was used when sample sizes of single species were high enough and binomial regression to obtain occurrence probabilities for too low sample sizes.

## Results

All seasons together, 7397 observations of 11'152 individuals belonging to 86 bird species were recorded (Table S1). 3220, 1642 and 1535 sightings belonging to 4390, 2358 and 4404 individuals were taken in spring, summer and winter, respectively. Mean species richness per transect was of  $9.9\pm 0.27$  in spring,  $10.1\pm 0.41$  in summer and  $9.1\pm 0.48$  in winter. Mean bird abundance per transect was of  $27.4\pm 1.04$  in spring,  $29.4\pm 1.56$  in summer and  $55\pm 4.69$  in winter. Mean Shannon diversity index per transect was of  $1.96\pm 0.02$  in spring,  $1.92\pm 0.04$  in winter and  $1.65\pm 0.06$  in winter. Mean Fringillidae abundance per transect was  $5.1\pm 0.33$ ,  $4.7\pm 0.5$  and  $23.9\pm 3.3$  in spring, summer and winter

respectively. Mean Turdidae abundance per transect was  $7.0 \pm 0.3$ ,  $9.7 \pm 0.7$  and  $8.2 \pm 1.06$  in spring, summer and winter respectively.

#### *Habitat selection in spring – pooled species*

Bird abundance, species richness and bird diversity (Shannon index) were all three significantly affected by environmental variables related to vineyard management. They were best explained by grove (bushes and hedges) cover (Table 2a & 4a), while ground vegetation cover only significantly affected bird diversity (Figure 3). The effects of grove cover on bird abundance, richness and diversity were independent of ground vegetation cover (all interactions non-significant). While the date of monitoring was only significantly linked to abundance, the time when the survey started was never significant. Species richness is predicted to double and bird abundance to triple in vineyard landscapes varying from a grove cover of 0 to 30% (Figure 2).

Turdidae abundance was best explained by grove cover (hedges and bushes), but ground vegetation cover often appeared in competitive models, despite being non-significant (Table 2a & 4a). Turdidae abundance is predicted to double from a grove cover of the vineyard landscapes of 0 to 30% (Fig. 4). Fringillidae abundance was unrelated to any measured landscape variables (Table 4a).

#### *Habitat selection in summer – pooled species*

Like in spring, bird richness, abundance and diversity (Shannon index) were best explained by grove cover. Ground vegetation cover positively affected bird abundance (it appeared in most of competitive models) while it was less important for species richness (Table 2b & 4b; Figure 3). Natural grassland cover seemed to be an important feature for species richness as it appeared in one competitive model, but the effect was non-significant (Table 2b). Again, the effects of grove cover on bird abundance richness and diversity were independent of ground vegetation cover (all interactions non-significant). As in spring, species richness is predicted to double and bird abundance to triple in vineyard landscapes varying from grove cover of 0 to 30% (Fig. 2).

Turdidae and Fringillidae abundance were best explained by grove cover (Table 2b & 4b). Fringillidae abundance was negatively influenced by grove cover (trend absent in spring but reversed during

winter; Fig. 5). Vineyard ground vegetation cover appeared in competitive models for Turdidae and Fringillidae but all links were non-significant. Turdidae abundance is predicted to double from a grove cover of 0 to 30% (Fig. 4).

#### *Habitat selection in winter – pooled species*

Bird richness, abundance and diversity in winter were best explained by grove cover. Vineyard ground vegetation cover appeared in competitive models for all bird predictors but had marginal effects only (non-significant effects; Table 2c & 4c; Figure 3). Natural grassland cover never appeared in any of the competitive models. Again, the effects of grove cover on bird abundance richness and diversity were independent of ground vegetation cover (all interactions non-significant). Bird richness and abundance are both predicted to quadruple in vineyard landscape varying in grove cover from 0 to 30%, a stronger effect than in spring or summer (Fig. 2).

Fringillidae and Turdidae abundance were best explained by grove cover, like in spring and summer. But ground vegetation inside the vineyard did play a positive significant role on Fringillidae abundance, unlike spring and summer (Table 2c & 4c). Turdidae abundance is predicted to sixfold in a vineyard landscape varying from 0 to 30% of grove cover (Fig. 4). Fringillidae abundance is predicted to quintuple in vineyards varying in ground vegetation cover from 0 to 50%, and triple in vineyard landscapes varying in grove cover from 0 to 30% (Fig. 5).

#### *Species-specific habitat selection of open-habitat species*

Five open-habitat species (European Serin, Common Linnet, Woodlark, Cirl Bunting, Rock Bunting; Posse *et al.* 2011) were modelled individually. Woodlark and European Serin, two short-distance migrants, were only modelled in spring and summer since sample sizes were too low in winter. Timing of the monitoring and date hardly ever affected species' abundance (exceptions for time: Rock Bunting in summer and Common Linnet in winter; exceptions for date: European Serin and Common Linnet in spring). Grove cover seemed to affect all open-habitat specialists, as it occurred in nearly all the competitive models for all species. Ground vegetation cover occurred in fewer competitive models and its effects seemed to be more species- and season-specific.

European Serin abundance in spring and summer was best explained by ground vegetation cover on a landscape scale (Table 3 & 5; Fig. 6). Competitive models for both seasons also contained grove cover, but it was never a significant feature for this species. European Serin abundance is predicted to triple in spring and summer in vineyard landscapes with a ground vegetation cover varying from 0 to 50% (Fig. 6).

Common Linnet abundance in spring and summer was best explained by grove cover (significant link in spring; Table 3 & 5), while ground vegetation cover also appeared in most of competitive models, without being significant. In winter, its occurrence probability was best explained by ground vegetation cover and natural grassland cover (significant effects), while grove cover also appeared in competitive models (non-significant effects).

Woodlark occurrence probability in spring and summer was best explained by ground vegetation and grove cover, but no significant effects of any habitat predictor were found (Table 3 & 5).

Cirl Bunting occurrence probability in spring, summer and winter was best explained by grove cover (significant effect only in spring), while ground vegetation cover appeared in most of the best models, without being significant (Table 3 & 5; Fig. 7).

Rock Bunting occurrence probability was best explained by grove cover in spring, summer and winter, while ground vegetation cover seemed to be important in spring only, as it did not appear in competitive models for other seasons (Table 3 & 5; Fig. 8).

## **Discussion**

Our study shows that using appropriate designs trying to disentangle the habitat preferences of birds along the annual cycle along dual habitat variable axes, in our case semi-natural habitat outside and ground vegetation inside the production surface, is a promising technique to design effective management recommendations. Using this approach, previous knowledge about existing patterns is necessary to quantify the relative importance of both factors (grove cover: Guyot *et al.* 2017; ground vegetation; Arlettaz *et al.* 2012 and Guyot *et al.* 2017). Habitat preferences of birds were mainly driven by grove (bushes and hedges) cover, irrespective of the ground vegetation inside the vineyard. While several studies showed that the importance of a habitat variable depends on a second landscape

trait, we never detected any significant interactions among habitat variables, indicating that grove and ground vegetation cover act in an additive and non-synergistic way throughout the year. Grove surrounding the vineyard (outside the production area) hence played the most important role in explaining bird richness, abundance and diversity in vineyards in all seasons. Nevertheless, vineyard ground vegetation cover at a landscape scale seems to be important showing season- and species-specific effects. In contrast, natural grasslands surrounding the vineyard (relict of the former steppe habitat covering the south-exposed slopes of Valais) seems to play only a marginal role for birds, partly due to lower inter-transect variation.

This study demonstrates the utmost importance of grove structures throughout the seasons with most pronounced effects in spring, even for open-habitat specialists. Those findings are in line with previous studies (Brambilla, Rubolini & Guidali 2007; Brambilla, Guidali & Negri 2008; Brambilla *et al.* 2009; Assandri *et al.* 2016; Guyot *et al.* 2017), and additionally demonstrate the relative importance of this habitat variable in relation to ground vegetation cover. Grove structures as measured in our study vary in structure and plant species composition and are likely to fulfil several purposes for multiple bird species during their life cycle, ranging from nesting habitat in spring (Brambilla *et al.* 2010; Guyot *et al.* 2017), acting as refuges against predators and as feeding sites throughout the year. While most detected species reflect grove-dwelling generalists (e.g. blackbird, chaffinch), we also found rare ,open-habitat and red-listed species such as Cirl and Rock Buntings (Keller *et al.* 2010a; Keller *et al.* 2010b; Posse *et al.* 2011). Both species rely on grove structures and its importance was highest in spring and summer (Brambilla, Guidali & Negri 2008; Fig. 7 & 8). Focussing outside the production area by planting hedges and bushes would hence be an efficient way to promote not only a high bird richness and abundance, but also rare species inhabiting the vineyard. Red-backed Shrike is another red-listed species encountered during this study (but in sample size insufficient for statistical analysis), which could potentially be promoted by increasing the amount of groves (Brambilla *et al.* 2010). We were not able to study the relationship between the quality of the hedges and birds, but it is likely to play a significant role on richness, abundance and diversity (Parish, Lakhani & Sparks 1994; Macdonald & Johnson 1995; Parish, Lakhani & Sparks 1995; Hinsley & Bellamy 2000; Fuller *et al.* 2001). A higher grove cover could also lead to an efficient biocontrol by

natural predators of pests, like spiders (Tschardt *et al.* 2007; Winqvist *et al.* 2011). Excessive hedge-planting might however have a negative effect for some open-habitat species like the Woodlark (Gilroy *et al.* 2010) which rely on large open spaces to feed and breed. The negative significant link in summer between Fringillidae abundance and grove cover is explained by the large proportion of birds being Common Linnet and European Serin, two Fringillidae of open-habitats showing preferences for vineyard ground vegetation (Posse *et al.* 2011). When modelled individually both showed a negative trend linked to grove cover but a positive link to vineyard ground vegetation.

Vineyard ground vegetation cover on a landscape scale seemed to be less important than grove cover. These results contrast with previous findings in the same study area, indicating that ground vegetation cover on a local, field-scale is highly important for breeding (Buehler *et al.* 2017) and feeding birds (Guyot *et al.* 2017, Arlettaz *et al.* 2012). This preference for ground vegetation on a fine-scale was not automatically translated on a higher scale as highlighted in our study. As it is widely acknowledged that the importance of habitat variables is scale-dependant (Robinson, Wilson & Crick 2001; Gabriel *et al.* 2010; Assandri *et al.* 2016; Guyot *et al.* 2017), results of studies focussing on a single scale must be interpreted cautiously. On a local scale, an increased layer of vegetation positively affects the abundance of arthropods, known to be a key prey for most bird species, even granivorous, during reproduction (Morris *et al.* 2001; Boatman *et al.* 2004). For open-habitat specialist, such as the European Serin, vineyard ground vegetation cover seemed highly important also on a landscape-scale. Serins, as well as Fringillidae, rely on extensive seeding fields, especially so to bridge the ‘hungry gap’ in winter (Henderson, Vickery & Carter 2004; Siriwardena, Calbrade & Vickery 2008; Fry & Slater 2011). For other species (e.g., woodlark) we failed to find any relationships which could partly be due to reduced sample sizes. Ground vegetation inside the production area should hence be improved and enhanced in a more opportunistic way than grove cover, as its importance on a local, field scale has been demonstrated by several authors (Arlettaz *et al.* 2012; Guyot *et al.* 2017)

### *Management recommendations*

This study highlights that hedges and bushes (called ‘grove’) are of the highest importance, not only for common species but also for rare and threatened ones like the Cirl Bunting and open-habitat

specialists like Rock Bunting. Based on these results, we recommend focussing on the conservation and plantation of hedges and bushes, leading to a network of groves within vineyard landscapes. This strategy should be applied irrespective of the existing amount of grove cover, since bird abundance, richness and diversity did not reach a plateau at highest grove cover values in our study (Ceresa *et al.* 2012; Guyot *et al.* 2017). Within the production area, our results indicate the positive effects of ground vegetation cover for several species. An increased ground vegetation cover on a landscape scale is predicted to produce moderate effects on birds (effect much lower than for grove cover), yet some open-habitat species like European Serin strongly rely on a high ground vegetation cover throughout the year. While the effect is weaker on a landscape scale, previous studies indicate the importance on a local foraging scale for birds. With these combined results we strongly suggest increasing the amount of vegetated field in a more opportunistic manner, without focussing on the spatial arrangement and configuration of vegetated fields. Applying these measures inside and outside the production area is likely to promote avian communities, leading to biodiversity-rich viticultural landscapes.

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## Tables

**Table 1.** Environmental variables recorded for the habitat selection analysis.

Variable	Type	Method	Definition
<b>a) SEMI-NATURAL HABITAT – LANDSCAPE-SCALE</b>			
Grove cover	Continuous	QGIS + Field	Proportion of grove (bushes, hedges, forest) inside the 100m buffer. First calculated on QGIS, then checked in field
Natural grassland cover	Continuous	QGIS + Field	Proportion of natural grassland and steppe inside the 100m buffer. First calculated on QGIS, then checked in field
Isolated trees	Continuous	QGIS + Field	Proportion of isolated bushes and trees inside the 100m buffer. First calculated on QGIS, then checked in field
Tracks	Continuous	QGIS + Field	Proportion of tracks and roads inside the 100m buffer. First calculated on QGIS, then checked in field
<b>b) VINEYARD CHARACTERISTICS – FIELD-SCALE</b>			
Green ground vegetation cover	Continuous	QGIS + Field	First, estimation on QGIS using NDVI. Then, visual estimation (%) in field of the green ground vegetation (=living vegetation) inside the field (in 10% steps)
Brown ground vegetation cover	Continuous	Field	Visual estimation (%) of the brown ground vegetation (=dry vegetation) inside the field (in 10% steps)
Annual or perennial vegetation	Categorical	Field	Visual determination of dominant ground vegetation type (annual or perennial). As herbicide spraying is allowed in Valais (Arlettaz <i>et al.</i> 2012), it is assumed that a dominance of perennial ground vegetation cover represents a vine field not treated with herbicide. Perennial vegetation is mainly dominated by Poaceae in vineyard, annual by Solanum nigrum.
Vegetation height	Continuous	Field	Mean vegetation height estimation
Vine grape	Continuous (discrete)	Field	Number of grapes per field counted during 5 seconds at a randomly determined point
Cultivation type	Categorical	Field	Two cultivation types: gobelet or wire

**Table 2.** Competitive models obtained from the modelling selection showed for each response variable with degrees of freedom of the model (Df), Deviance,  $\Delta$  Akaike Information Criterion ( $\Delta$ AICc) and the weight of each competitive model, for a) in spring, b) in summer and c) in winter. To model species richness and abundance, GLMMs were used. For Shannon diversity index, LMMs. Explanatory variables are written in bold when significant ( $P \leq 0.05$ ).

Response variable	# Candidate models	Competitive models ( $\Delta$ AICc $\leq$ 2)	Df	Deviance	$\Delta$ AIC	Weight
<b>a) HABITAT SELECTION IN SPRING: POOLED SPECIES</b>						
Species richness	16	<b>G + GV</b>	4	83.44	0	0.273
		<b>G</b>	3	81.29	0.84	0.179
		<b>G + GV + Time</b>	5	84.16	1.26	0.145
		<b>G + GV + NG</b>	5	84.16	1.47	0.131
Bird abundance	24	<b>G+ Date + Date<sup>2</sup></b>	5	217.42	0	0.419
		<b>G + GV + Date + Date<sup>2</sup></b>	6	218.31	1.7	0.179
Shannon diversity index	8	<b>G + GV</b>	5	35.31	0	0.533
		<b>G + GV + NG</b>	6	34.44	1.28	0.281
Turdidae	8	<b>G</b>	3	156.92	0	0.516
		<b>G + GV</b>	4	156.92	1.78	0.211
		<b>G + NG</b>	4	157.02	1.95	0.194
Fringillidae	16	Date	3	240.62	0	0.288
		GV + Date	4	240.51	0.38	0.238
		NG + Date	4	240.72	1.82	0.116
<b>b) HABITAT SELECTION IN SUMMER : POOLED SPECIES</b>						
Species richness	128	<b>G + Time</b>	4	72.31	0	0.38
		<b>G + GV + Time</b>	5	71.25	1.22	0.206
		<b>G + NG + Time</b>	5	71.93	1.9	0.147
Bird abundance	16	<b>G + GV + Time</b>	5	123.88	0	0.276
		<b>G + Time</b>	4	123.43	0.05	0.27
Shannon diversity index	8	<b>G</b>	4	61.99	0	0.564

Turdidae	8	<b>G</b>	3	90.92	0	0.482
		<b>G + GV</b>	4	91.15	1.53	0.225
Fringillidae	8	<b>G</b>	3	98.76	0	0.403
		<b>G + NG</b>	4	99.83	0.36	0.337
<b>c) HABITAT SELECTION IN WINTER: POOLED SPECIES</b>						
Species richness	24	<b>G + GV + Date + Date<sup>2</sup></b>	6	44.14	0	0.452
		<b>G + Date + Date<sup>2</sup></b>	5	42.34	1.01	0.274
Bird abundance	16	<b>G + Date</b>	5	9.86	0	0.227
		<b>G + GV + Date</b>	6	9.95	0.15	0.211
		<b>G</b>	4	9.48	0.26	0.199
		<b>G + GV</b>	5	9.47	1.34	0.116
Shannon diversity index	24	<b>G + Date + Date<sup>2</sup></b>	6	58.89	0	0.424
		<b>G + GV + Date + Date<sup>2</sup></b>	7	57.24	0.75	0.291
Turdidae	8	<b>G</b>	4	29.04	0	0.433
		<b>G + GV</b>	5	29.12	0.99	0.264
		<b>G + NG</b>	5	28.96	1.83	0.173
Fringillidae	72	<b>G + GV</b>	5	17.81	0	0.132
		<b>G + GV + NG</b>	6	17.81	0.47	0.104
		<b>G + GV + Time</b>	6	17.74	1.81	0.053
		<b>G + GV + Date</b>	6	17.97	1.88	0.051

**Table 3.** Competitive models obtained from the modelling selection showed for each open-habitat specialist with degrees of freedom of the model (Df), Deviance,  $\Delta$  Akaike Information Criterion ( $\Delta$ AICc) and the weight of each competitive model, for a) in spring, b) in summer and c) in winter. Explanatory variables are written in bold when significant ( $P \leq 0.05$ ).

Response variable	# Candidate models	Competitive models ( $\Delta$ AICc $\leq 2$ )	Df	Deviance	$\Delta$ AICc	Weight
<b>a) HABITAT SELECTION IN SPRING: OPEN-HABITAT SPECIES</b>						
European Serin	48	G + G <sup>2</sup> + <b>GV</b> + Time + <b>Date</b>	7	149.12	0	0.318
		<b>GV</b> + Time + <b>Date</b>	5	147.05	1.96	0.119
Common Linnet	36	G + <b>G<sup>2</sup></b> + Date + <b>Date<sup>2</sup></b>	6	206.25	0	0.472
		G + <b>G<sup>2</sup></b> + NG + Date + <b>Date<sup>2</sup></b>	7	205.55	1.7	0.201
Woodlark	8	G	3	120.6	0	0.213
		G + NG	4	120.38	0.46	0.169
		NG	3	119.97	0.52	0.165
		G + GV	4	121.09	0.55	0.162
		G + GV + NG	5	120.92	1.06	0.125
		GV + NG	4	120.32	1.44	0.104
Cirl Bunting	48	<b>G</b> + GV + <b>Date</b>	5	104.15	0	0.301
		<b>G</b> + <b>Date</b>	4	103.39	0.37	0.25
		<b>G</b> + GV + NG + <b>Date</b>	6	104.82	0.68	0.214
		<b>G</b> + NG + <b>Date</b>	5	103.86	1.06	0.177
Rock Bunting	8	<b>G</b> + GV + NG	5	91.38	0	0.37
		<b>G</b> + NG	4	89.7	0.41	0.302
		<b>G</b> + GV	4	90.04	1.6	0.166
		<b>G</b>	3	89.09	1.66	0.161
<b>b) HABITAT SELECTION IN SUMMER: OPEN-HABITAT SPECIES</b>						
European Serin	16	G + GV + Time	5	58.18	0	0.185
		G + GV	4	59.68	0.32	0.157

		G	3	59.7	1.35	0.094
		GV	3	60.66	1.71	0.079
Common Linnet	8	G	3	96.39	0	0.267
		G + NG	4	97.71	0.17	0.245
		G + GV	4	96.73	0.49	0.209
		G + GV + NG	5	97.83	0.89	0.171
Woodlark	8	G + GV + NG	5	50.82	0	0.223
		GV + NG	4	51.54	0.17	0.205
		NG	3	51.82	0.36	0.187
		G + NG	4	51.58	0.67	0.159
		GV + NG	4	50.12	1.24	0.12
		G	3	51.11	1.91	0.086
Cirl Bunting	8	G	3	29.95	0	0.257
		G + GV	4	30.15	0.09	0.246
		G + NG	4	30.28	0.55	0.196
		G + GV + NG	5	30.51	0.76	0.176
Rock Bunting	16	<b>G + Time</b>	4	22.17	0	0.433
		<b>G + NG + Time</b>	5	22.45	1.25	0.231

**c) HABITAT SELECTION IN WINTER: OPEN-HABITAT SPECIES**

Common Linnet	12	GV + GV <sup>2</sup> + NG	5	63.24	0	0.642
		G + GV + GV <sup>2</sup> + NG	6	63.4	1.87	0.253
Cirl Bunting	8	G	3	35.59	0	0.309
Rock Bunting	8	<b>G</b>	4	33.02	0	0.412

**Table 4.** Model-averaged estimates, standard error, P-values for environmental variables occurring in competitive models ( $\Delta AICc \leq 2$ ) of Pooled species' richness, abundance, diversity and Fringilidae and Turdidae abundance, with a) in spring, b) in summer and c) in winter. Significance:  $P < 0.1$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ .

Explanatory variables	Species richness			Abundance			Shannon diversity index			Turdidae			Fringillidae		
	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
<b>a) HABITAT SELECTION IN SPRING</b>															
Intercept	2.26	0.03	<0.001***	3.21	0.05	<0.001***	1.96	0.02	<0.001***	1.82	0.06	<0.001***	1.42	0.11	<0.001***
Grove cover	0.23	0.03	<0.001***	0.33	0.05	<0.001***	0.23	0.03	<0.001***	0.34	0.07	<0.001***	-	-	-
Grove cover^2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ground vegetation	0.04	0.03	0.24	0.01	0.03	0.7	0.06	0.02	0.02*	-0.008	0.03	0.8	0.05	0.1	0.58
Natural grassland	0.004	0.01	0.78	-	-	-	0.01	0.02	0.66	0.006	0.03	0.8	-0.01	0.05	0.83
Date	-	-	-	-0.12	0.2	0.55	-	-	-	-	-	-	-	-	-
Date^2	-	-	-	-0.51	0.18	0.006**	-	-	-	-	-	-	-	-	-
Time	0.07	0.01	0.27	-	-	-	-	-	-	-	-	-	-	-	-
<b>b) HABITAT SELECTION IN SUMMER</b>															
Intercept	2.29	0.035	<0.001***	3.3	0.05	<0.001***	1.92	0.03	<0.001***	2.14	0.081	<0.001***	1.32	0.11	<0.001***
Grove	0.17	0.322	<0.001***	0.15	0.05	0.007**	0.15	0.04	<0.001***	0.24	0.08	0.003**	-0.4	0.12	0.001**
Ground vegetation	0.01	0.025	0.6834	0.04	0.06	0.45	-	-	-	0.02	0.05	0.7	-	-	-
Natural grassland	-0.004	0.02	0.8124	-	-	-	-	-	-	-	-	-	0.07	0.11	0.51
Time	0.73	0.036	0.0252*	1.28	0.52	0.014*	-	-	-	-	-	-	-	-	-
<b>c) HABITAT SELECTION IN WINTER</b>															
Intercept	2.11	0.05	<0.001***	3.68	0.1	<0.001***	1.65	0.04	<0.001***	1.4	0.17	<0.001***	2.41	0.17	<0.001***
Grove	0.39	0.05	<0.001***	0.52	0.1	<0.001***	0.35	0.04	<0.001***	0.83	0.17	<0.001***	0.42	0.19	0.02*
Ground vegetation	0.05	0.05	0.96	0.06	0.1	0.61	0.02	0.04	0.562	-0.05	0.12	0.65	0.42	0.17	0.01*
Natural grassland	-	-	-	-	-	-	-	-	-	0.02	0.09	0.8	-0.08	0.17	0.61
Date	0.85	0.44	0.058	0.94	1.07	0.87	0.42	0.4	0.293	-	-	-	0.16	0.73	0.82
Date^2	1.45	0.44	0.0015**	-	-	-	1.79	0.38	<0.001***	-	-	-	-	-	-
Time	-	-	-	-	-	-	-	-	-	-	-	-	0.17	0.74	0.81

**Table 5.** Model-averaged estimates, standard error, P-values for environmental variables occurring in competitive models ( $\Delta AICc \leq 2$ ) of open-habitat specialists (European Serin, Common Linnet, Woodlark, Cirl Bunting and Rock Bunting, with a) in spring, b) in summer and c) in winter. Sample size of European Serin and Woodlark was too low in winter to model their habitat selection during this season. Significance: .  $P < 0.1$ , \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

Explanatory variables	European Serin			Common Linnet			Woodlark			Cirl Bunting			Rock Bunting		
	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
<b>a) HABITAT SELECTION IN SPRING</b>															
Intercept	0.079	0.26	0.76	0.97	0.247	<0.01***	-0.07	0.37	0.846	-1.08	0.44	0.015*	-0.45	0.36	0.22
Grove cover	0.16	0.16	0.33	-0.05	0.207	0.8	-0.55	0.5	0.27	1.41	0.52	0.006**	2.08	0.56	<0.01***
Grove cover <sup>2</sup>	-0.27	0.2	0.19	-0.62	0.201	<0.01**	-	-	-	-	-	-	-	-	-
Ground vegetation	0.54	0.15	<0.001***	-	-	-	0.18	0.32	0.57	0.34	0.43	0.42	-0.31	0.56	0.43
Natural grassland	-	-	-	-0.04	0.136	0.74	-0.41	0.48	0.39	-0.23	0.41	0.56	0.56	0.53	0.3
Date	2.97	0.95	0.002**	1.31	0.711	0.06	-	-	-	8.81	3.23	0.006**	-	-	-
Date <sup>2</sup>	-	-	-	-2.05	0.6	<0.01***	-	-	-	-	-	-	-	-	-
<b>b) HABITAT SELECTION IN SUMMER</b>															
Intercept	0.18	0.18	0.32	-0.009	0.43	0.98	-0.77	0.17	<0.001***	-0.9	0.86	0.3	-0.22	0.52	0.66
Grove	-0.28	0.17	0.06	-0.51	0.61	0.4	-0.09	0.17	0.58	1.99	1.22	0.11	4.07	1.51	0.008**
Ground vegetation	0.31	0.17	0.07	0.4	0.51	0.4	0.04	0.1	0.69	0.5	0.76	0.51	-	-	-
Natural grassland	-	-	-	-0.84	0.66	0.98	-0.34	0.25	0.18	-0.47	0.86	0.58	0.26	0.61	0.66
Time	0.86	1.46	0.55	-	-	-	-	-	-	-	-	-	-16.98	8.15	0.04*
<b>c) HABITAT SELECTION IN WINTER</b>															
Intercept	-	-	-	-2.09	0.63	0.001**	-	-	-	-2.59	1.17	0.02*	1.29	0.18	<0.001***
Grove	-	-	-	-0.27	0.4	0.49	-	-	-	1.04	0.64	0.1	0.39	0.18	0.03*
Ground vegetation	-	-	-	0.59	0.36	0.1	-	-	-	-	-	-	-	-	-
Ground vegetation <sup>2</sup>	-	-	-	0.76	0.28	0.008**	-	-	-	-	-	-	-	-	-
Natural grassland	-	-	-	-1.19	0.53	0.02*	-	-	-	-	-	-	-	-	-

## Figure legends

**Figure 1:** Aerial picture of a transect with semi-natural habitat, vineyard fields and transect.

**Figure 2:** Pooled species model-averaged predictions in relation to grove cover. Species richness in spring (a), in summer (b) and in winter (c); bird abundance in spring (d), in summer (e) and in winter (f); Shannon diversity index in spring (a), summer (b) and winter (c). All relationships presented are significant with 95% confidence ( $P < 0.01$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in dark-grey ( $p < 0.01$ ).*

**Figure 3:** Pooled species model-averaged predictions in relation to ground vegetation inside the vineyard in spring, summer and winter. Vineyard ground vegetation was calculated as the area-weighted mean ground vegetation in the vineyard of the transect. Species richness in spring (a), in summer (b) and in winter (c); bird abundance in spring (d), in summer (e) and in winter (f); Shannon diversity index in spring (a), summer (b) and winter (c). Relationships presented are not significant except on Fig. 2g ( $P < 0.05$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in light-grey (non-significant) and grey ( $p < 0.05$ ).*

**Figure 4:** Turdidae's (Thrushs) model-averaged predictions in relation to grove cover in spring (a), summer (b) and winter (c). All relationships presented are significant with 95% confidence ( $P < 0.01$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in dark-grey ( $p < 0.01$ ).*

**Figure 5:** Fringillidae (finches) model-averaged predictions in relation to grove cover in summer (a), grove cover in winter (b) and ground vegetation inside the vineyard in winter (c). Spring predictions

are not shown due to the lack of significance. All relationships presented are significant with 95% confidence ( $P < 0.01$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in grey ( $p < 0.05$ ) and dark-grey ( $p < 0.01$ ).*

**Figure 6:** European Serin model-averaged predictions in relation to ground vegetation cover in spring (a) and in summer (b). Those predictions are significant with 95% confidence ( $P < 0.01$ ). Predictions in winter are not shown due to the lack of sightings of this species. *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in light-grey (non-significant) and dark-grey ( $p < 0.01$ ).*

**Figure 7 :** Cirl Bunting model-averaged occurrence probabilities in relation to grove cover in spring (a), summer (b) and winter (c). Those predictions (a and b) are significant with 95% confidence ( $P < 0.01$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in light-grey (non-significant) and dark-grey ( $p < 0.01$ ).*

**Figure 8 :** Rock Bunting model-averaged occurrence probabilities in relation to grove cover in spring (a), summer (b) and winter (c). Those predictions are significant with 95% confidence ( $P < 0.01$ ). *Model-averaged estimates are shown with a 95%-Bayesian credible interval. Confidence intervals are coloured in grey ( $p < 0.05$ ) and dark-grey ( $p < 0.01$ ).*

**FIGURES**

**Fig. 1**

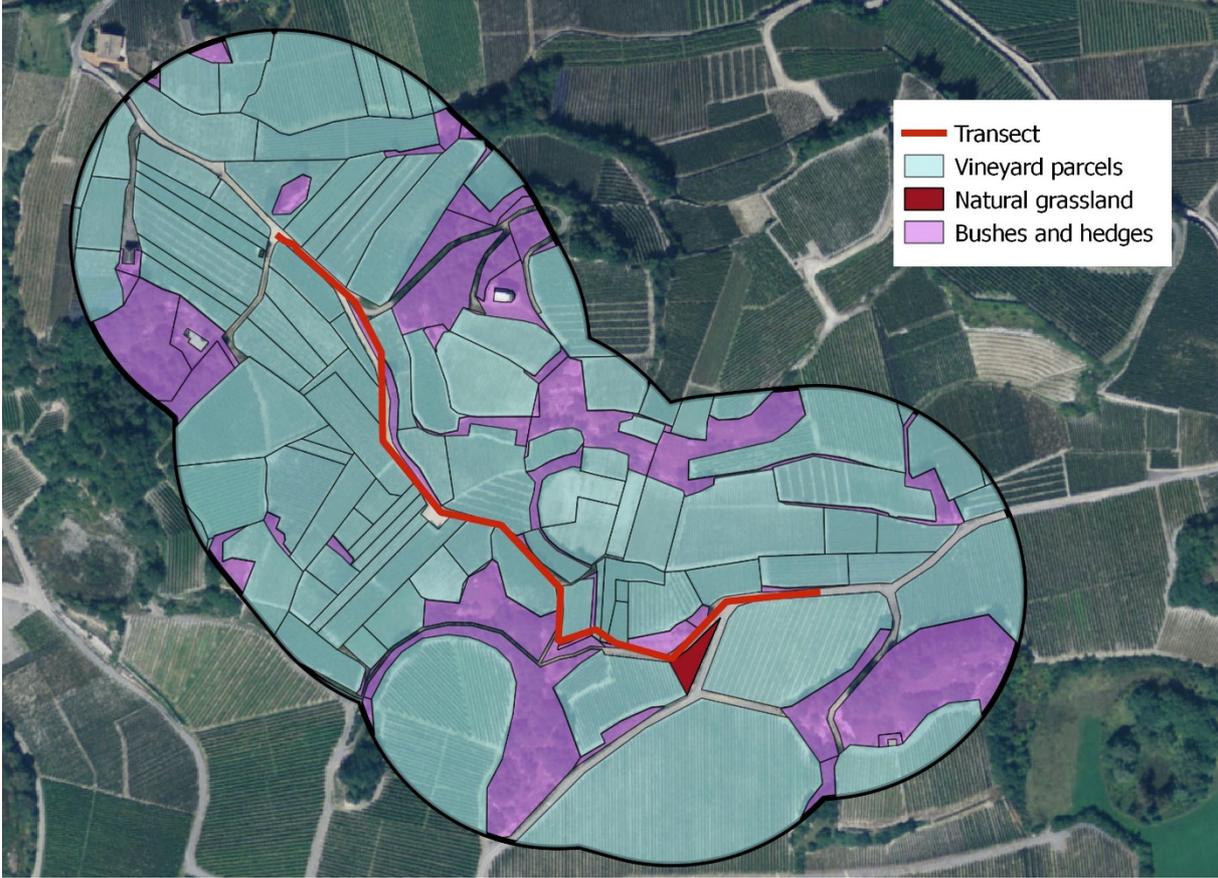


Fig. 2

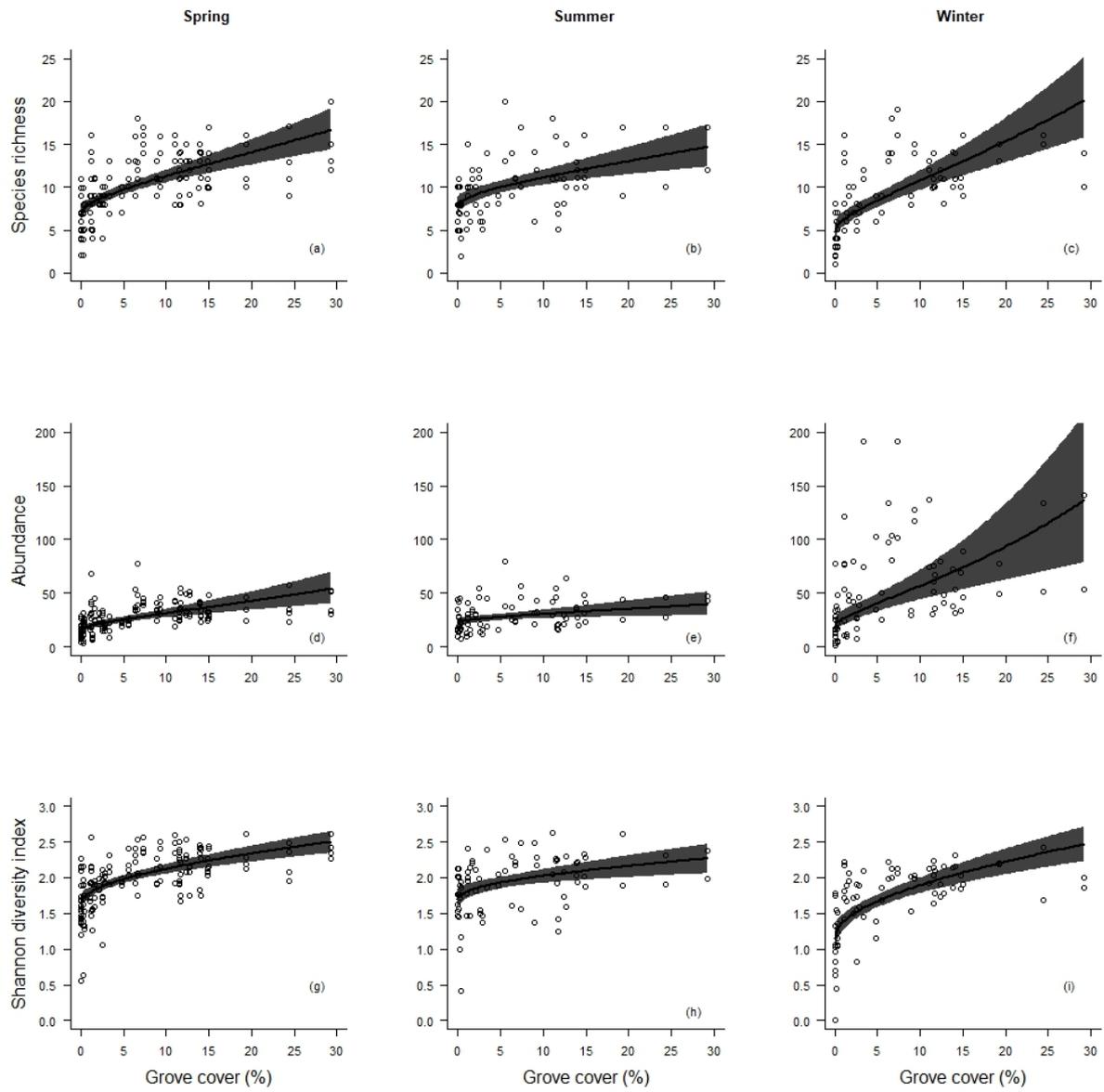


Fig. 3

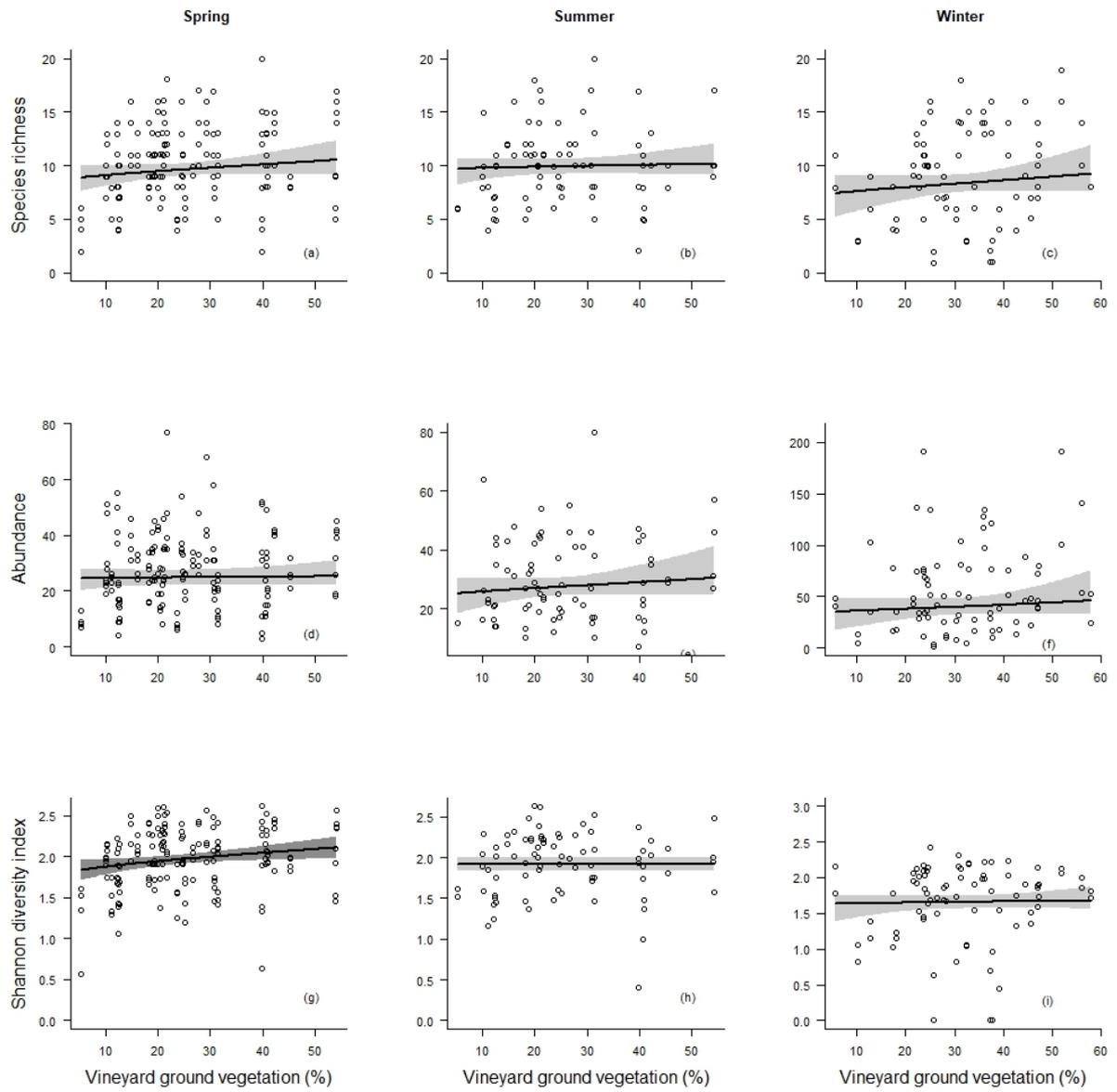


Fig. 4

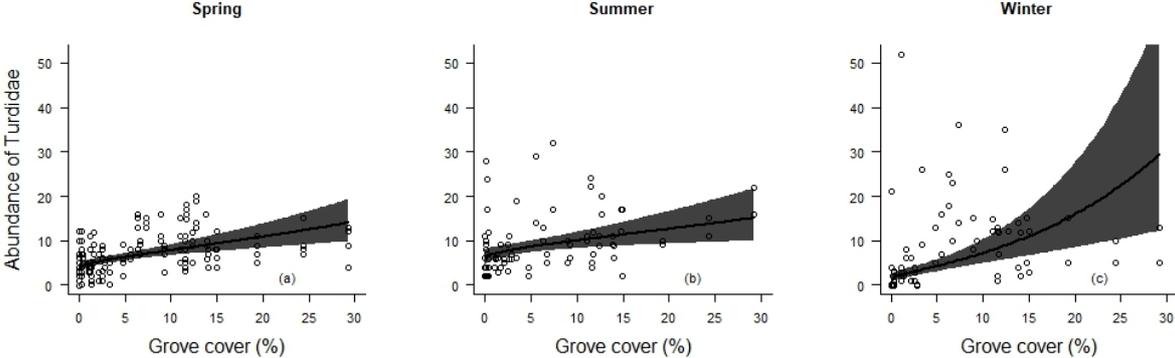


Fig. 5

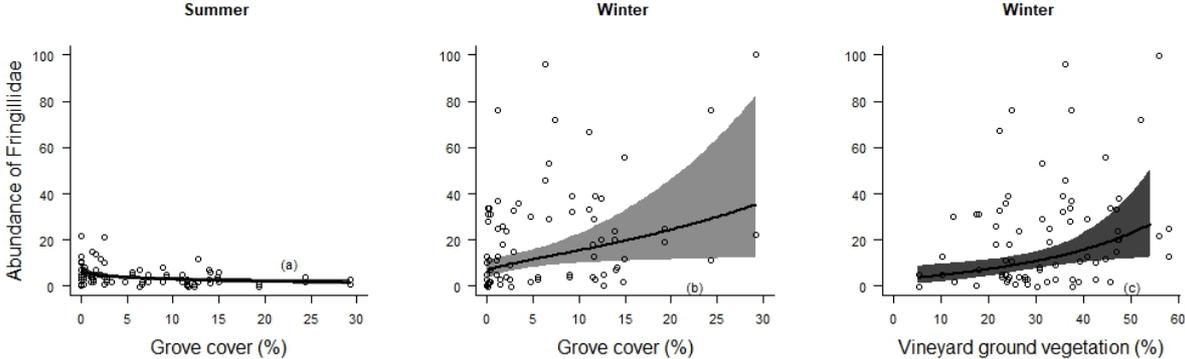


Fig. 6

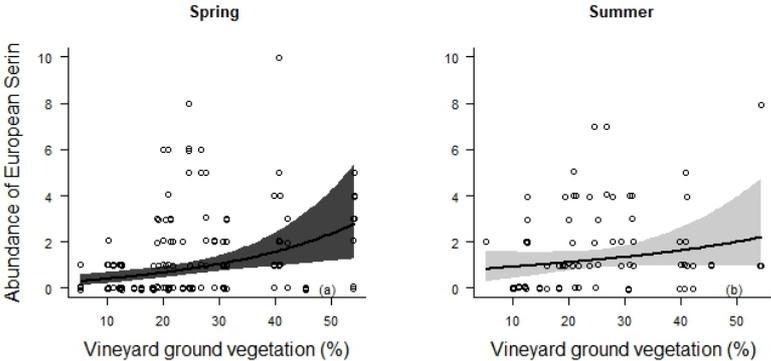


Fig. 7

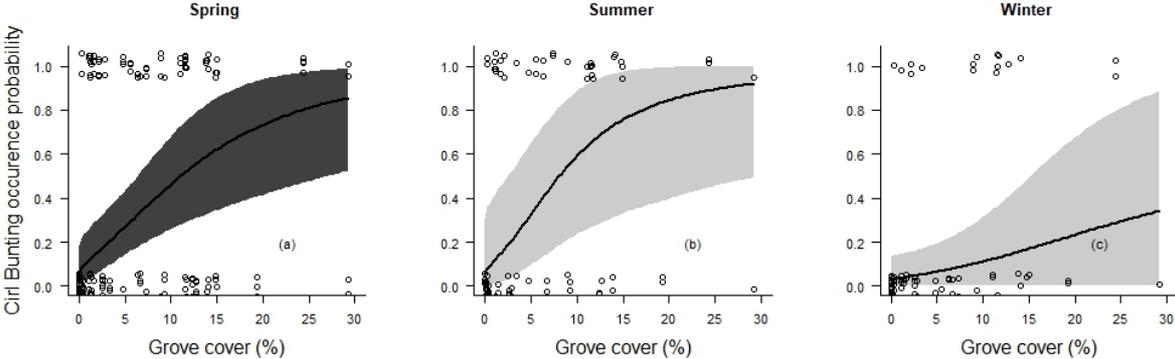
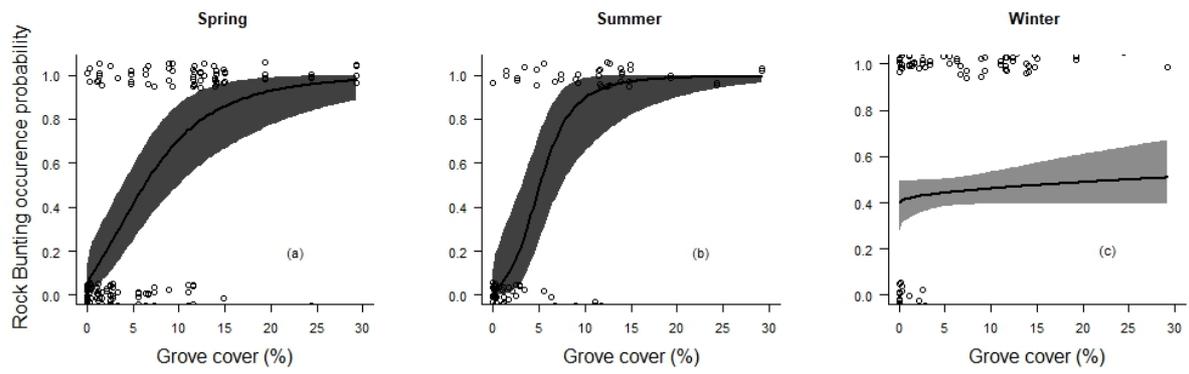
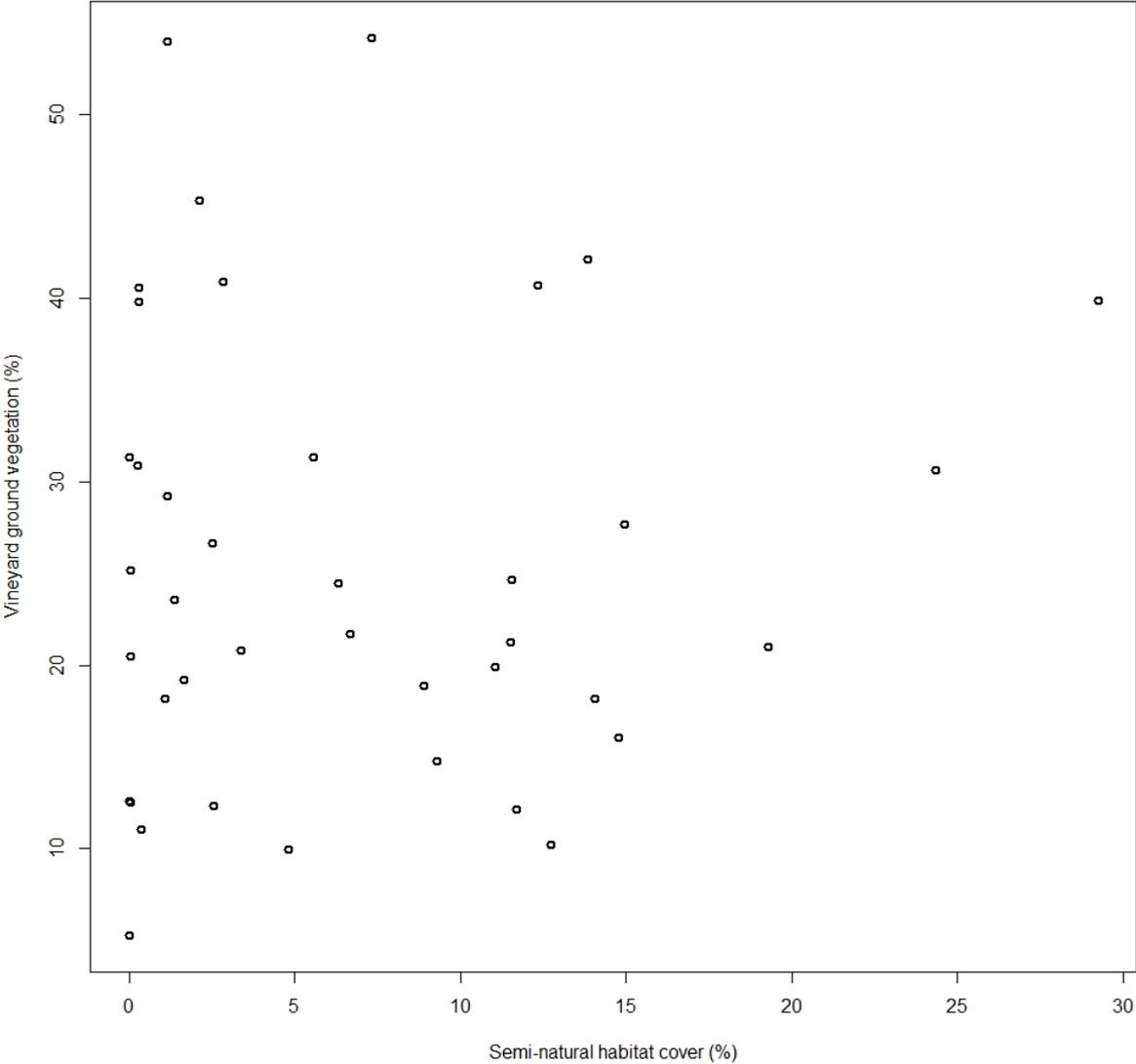


Fig. 8



**SUPPORTING MATERIAL**

**Appendix 1:** Repartition of all the 40 transects according to vineyard ground vegetation and semi-natural habitat amount, in percentages.



**Table S1** Species list (N=86) and number of sightings per species

English name	Scientific name	Number of sightings
Alpine Accentor	<i>Prunella collaris</i>	1
Black Redstart	<i>Phoenicurus ochrorus</i>	382
Blue Tit	<i>Parus caeruleus</i>	57
Brambling	<i>Fringilla montifringilla</i>	8
Carrion Crow	<i>Corvus corone corone</i>	60
Cirl Bunting	<i>Emberiza cirlus</i>	172
Citril Finch	<i>Serinus citrinella</i>	3
Coal Tit	<i>Parus ater</i>	14
Common Chaffinch	<i>Fringilla coelebs</i>	354
Common Chiffchaff	<i>Phylloscopus collybita</i>	18
Common Cuckoo	<i>Cuculus canorus</i>	2
Common Firecrest	<i>Regulus ignicapilla</i>	3
Common Grasshopper-warbler	<i>Locustella naevia</i>	2
Common Hoopoe	<i>Upupa epops</i>	17
Common Kestrel	<i>Falco tinnunculus</i>	6
Common Linnet	<i>Carduelis cannabina</i>	321
Common Nightingale	<i>Luscinia megarhynchos</i>	12
Common Raven	<i>Corvus corax</i>	19
Common Redstart	<i>Phoenicurus phoenicurus</i>	39
Common Reed-warbler	<i>Acrocephalus scirpaceus</i>	1
Common Starling	<i>Sturnus vulgaris</i>	21
Common Woodpigeon	<i>Columba palumbus</i>	27
Crested Tit	<i>Lophophanes cristatus</i>	2
Dunnock	<i>Prunella modulatis</i>	73
Eurasian Blackbird	<i>Turdus merula</i>	1388
Eurasian Blackcap	<i>Sylvia atricapilla</i>	385
Eurasian Buzzard	<i>Buteo buteo</i>	16
Eurasian Green Woodpecker	<i>Picus viridis</i>	17
Eurasian Jay	<i>Garrulus glandarius</i>	183
Eurasian Magpie	<i>Pica pica</i>	48
Eurasian Nuthatch	<i>Sitta europaea</i>	3
Eurasian Siskin	<i>Carduelis spinus</i>	2
Eurasian Skylark	<i>Alauda arvensis</i>	1
Eurasian Sparrowhawk	<i>Accipiter nisus</i>	10
Eurasian Tree Sparrow	<i>Passer montanus</i>	65
Eurasian Wren	<i>Troglodytes troglodytes</i>	47
Eurasian Wryneck	<i>Jynx torquilla</i>	7

European Bee-eater	<i>Merops apiaster</i>	1
European Goldfinch	<i>Carduelis carduelis</i>	197
European Greenfinch	<i>Chloris chloris</i>	183
European Nightjar	<i>Caprimulgus europaeus</i>	1
European Robin	<i>Erithacus rubecula</i>	265
European Serin	<i>Serinus serinus</i>	293
European Turtle-dove	<i>Streptopelia turtur</i>	1
Fieldfare	<i>Turdus pilaris</i>	13
Garden Warbler	<i>Sylvia borin</i>	6
Goldcrest	<i>Regulus regulus</i>	2
Great Spotted Woodpecker	<i>Dendrocopos major</i>	22
Great Tit	<i>Parus major</i>	427
Grey Wagtail	<i>Motacilla cinerea</i>	30
Hawfinch	<i>Coccothraustes coccothraustes</i>	1
House Sparrow	<i>Passer domesticus</i>	89
Lesser Spotted Woodpecker	<i>Dendrocopos minor</i>	1
Lesser Whitethroat	<i>Sylvia curruca</i>	7
Long-tailed Tit	<i>Aegithalos caudatus</i>	10
Marsh Tit	<i>Poecile palustris</i>	7
Meadow Pipit	<i>Anthus pratensis</i>	9
Melodious Warbler	<i>Hippolais polyglotta</i>	1
Mistle Thrush	<i>Turdus viscivorus</i>	143
Northern Wheatear	<i>Oenanthe oenanthe</i>	19
Ortolan Bunting	<i>Emberiza hortulana</i>	1
Pied Flycatcher	<i>Ficedula hypoleuca</i>	4
Red-backed Shrike	<i>Lanius collurio</i>	32
Red-footed Falcon	<i>Falco vespertinus</i>	1
Redpoll	<i>Acanthis flammea</i>	1
Redwing	<i>Turdus iliacus</i>	9
Reed Bunting	<i>Emberiza schoeniclus</i>	7
Rock Bunting	<i>Emberiza cia</i>	392
Rock Dove	<i>Columba livia domestica</i>	4
Rock Partridge	<i>Alectoris graeca</i>	3
Rook	<i>Corvus frugilegus</i>	1
Rufous-tailed Rock-thrush	<i>Monticola saxatilis</i>	1
Song Thrush	<i>Turdus philomelos</i>	58
Spotted Flycatcher	<i>Muscicapa striata</i>	1
Tawny Pipit	<i>Anthus campestris</i>	1
Tree Pipit	<i>Anthus trivialis</i>	6
Water Pipit	<i>Anthus spinoletta</i>	15

Western Bonelli's Warbler	<i>Phylloscopus bonelli</i>	86
Western Yellow Wagtail	<i>Motacilla flava</i>	2
Whinchat	<i>Saxicola rubetra</i>	4
White Wagtail	<i>Motacilla alba</i>	46
White-throated Dipper	<i>Cinclus cinclus</i>	1
Willow Warbler	<i>Phylloscopus trochilus</i>	7
Woodlark	<i>Lullula arborea</i>	186
Yellow-billed Cough	<i>Pyrrhocorax graculus</i>	1
Yellowhammer	<i>Emberiza citrinella</i>	13

**Table S2** : Transect characteristics

Municipality	Transect length	Altitude	Latitude (WGS84)	Longitude (WGS84)	Semi-natural habitat cover		Natural	Area-weighted mean
					(%)	Grove cover (%)	grassland cover (%)	vineyard ground vegetation (%)
Ardon	401	475.7836	46.20382268	7.273317535	7.54	0.00	7.54	12.57
Ayent	404	651.4914	46.25270275	7.395564022	2.07	2.13	0.14	45.33
Ayent	417	761.4673	46.25645359	7.395615035	1.53	1.08	0.26	18.16
Chamoson	429	495.8425	46.20325448	7.249558288	0.05	0.05	0.00	20.52
Chamoson	415	510.3675	46.18841314	7.231383069	0.31	0.24	0.07	30.88
Chamoson	428	554.4964	46.19800428	7.235155761	0.04	0.05	0.00	25.16
Conthey	409	669.8527	46.23197534	7.279137738	19.73	14.79	3.47	16.08
Conthey	400	732.5726	46.23497398	7.287995059	3.05	2.56	0.49	12.37
Fully	411	501.6570	46.14948021	7.128823428	20.95	14.07	5.18	18.18
Fully	399	503.0435	46.13347061	7.101301467	0.48	0.00	0.48	31.37
Fully	412	520.1096	46.14521382	7.118002691	2.26	1.37	0.89	23.57
Fully	405	743.1093	46.14965114	7.117115984	25.27	9.30	10.22	14.75
Grimisuat	446	639.1957	46.25000045	7.387482026	1.27	1.16	0.05	29.24
Lens	379	596.7017	46.27086701	7.466722833	22.38	6.69	0.04	21.70
Lens	400	682.5423	46.26471882	7.446306162	5.63	4.79	0.00	9.94
Leuk	403	637.3750	46.31593198	7.628504469	13.58	11.05	1.48	19.93
Leuk	433	836.6844	46.31580182	7.646832739	37.20	24.36	1.74	30.66
Leytron	392	492.2381	46.18480504	7.217638423	0.01	0.01	0.00	5.27
Leytron	404	538.4351	46.19065402	7.220186309	1.25	1.17	0.13	54.00

Leytron	399	596.2520	46.18565967	7.197736193	0.79	0.36	0.43	11.03
Miège	395	689.0179	46.30829087	7.552652556	0.30	0.30	0.00	39.81
Miège	405	699.2427	46.31267528	7.554276401	0.04	0.04	0.00	12.52
Montana	421	731.3858	46.28148022	7.495488665	14.70	11.70	3.03	12.11
Randogne	474	596.8608	46.28574198	7.510659162	3.34	2.52	0.83	26.65
Randogne	396	622.6336	46.29018194	7.514965523	3.62	2.83	0.74	40.93
Saillon	397	518.4043	46.181319	7.196234599	1.82	1.65	0.17	19.23
Saillon	413	549.9624	46.1750372	7.186093589	18.07	11.56	3.44	24.69
Saillon	409	670.6133	46.1741455	7.177497419	19.84	13.85	5.99	42.15
Salgesch	403	580.9775	46.30676766	7.57197466	19.55	19.30	0.25	20.99
Salgesch	402	593.9734	46.31226226	7.583136126	24.36	12.35	10.84	40.70
Salgesch	391	654.4065	46.31722581	7.573197134	5.54	5.55	0.00	31.34
St. Léonard	411	589.3861	46.25792717	7.41767407	11.40	8.91	0.98	18.90
St.Léonard	409	610.4017	46.25869232	7.428706992	21.19	12.71	3.91	10.19
St.Léonard	401	675.4653	46.26177464	7.419579263	10.49	7.34	3.15	54.22
Varen	455	667.3843	46.31350591	7.593209502	21.32	14.96	6.35	27.67
Varen	435	680.9885	46.31565096	7.600791251	3.06	3.36	0.00	20.80
Varen	488	702.9198	46.31796084	7.616628723	13.06	11.51	0.46	21.24
Varen	398	740.1481	46.31641469	7.588053806	7.65	6.32	0.43	24.50
Varen	370	783.9589	46.31805945	7.599638911	31.39	29.24	0.37	39.88
Venthône	417	754.3359	46.29910195	7.518396704	0.65	0.28	0.37	40.59

### Declaration of consent

on the basis of Article 28 para. 2 of the RSL05 phil.-nat.

Name/First Name: Mazenauer Julien

Matriculation Number: 10-509-032

Study program: Master in Ecology and Evolution, Animal Ecology and Conservation

Bachelor  Master  Dissertation

Title of the thesis: Semi-natural habitat versus ground vegetation in vineyards:  
disentangling bird's habitat preferences at a landscape scale

Supervisor: Alain Jacot & Raphaël Arlettaz

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 para. 1 lit. r of the University Act of 5 September, 1996 is authorised to revoke the title awarded on the basis of this thesis. I allow herewith inspection in this thesis.

Neuchâtel, 21.08.18

Place/Date

Signature

