Temporal and spatial scales matter: circannual habitat selection of bird communities in vineyards

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Abstract

Avian habitat selection studies in vineyards, a farmland habitat which is undergoing a rapid management revolution, are still rare. Yet, this agroecosystem is likely to be regionally important for birds. Vine cultivation is not only characterized by arid and warm climatic conditions, promoting species typical of southern biomes, but it can also extend over large areas. Intensively cultivated vineyards are mostly surrounded by few natural features; they also mostly offer a fairly mineral appearance, with little ground vegetation cover. Furthermore, amount and composition of the extant of ground vegetation cover may strongly vary throughout the annual cycle, influencing patterns of habitat selection by birds. As a result, bird communities in vineyards may change with respect to season. In this study, we aimed to model season-specific bird-habitat assocations to highlight the importance of semi-natural habitat features as well as vineyard ground vegetation cover upon avian communities. Habitat selection of birds is also known to differ between taxa and guilds and according to the spatial scale. Using mixed effects regression, we therefore modelled habitat selection patterns of birds in different months at two spatial scales. For the landscape scale analysis, birds were recorded along 1-km long transects (February 2014 – January 2015). For the field scale analysis, we compared the characteristics of visited and unvisited vineyard fields (parcels). Our results show that bird abundance in vineyards was double in winter compared to summer. Vineyards surrounded by a greater amount of hedges and small woods harboured higher numbers of birds, as well as greater species richness and diversity in all seasons. Regarding ground vegetation cover, birds showed a season-specific habitat selection pattern, notably a marked preference for ground vegetated parcels in winter and for intermediate vegetation cover in spring and summer. These season-specific habitat preferences can be directly related to bird species' life-history: more insectivorous, ground-foraging species occur during the breeding season whereas granivores predominate in winter. These results highlight the importance of investigating habitat selection all along the annual cycle in order to draw practical, season-specific management recommendations for the promotion of avian biodiversity in vineyards.

Keywords

Habitat selection, vineyards, farmland, bird diversity, finches, thrushes, spatial scale, season, annual cycle, landscape characteristics, ground vegetation, food abundance and accessibility

Introduction

To better understand the reasons for the dramatic decline in farmland biodiversity, which followed agriculture intensification and being able to design effective conservation actions, a wealth of evidence-based knowledge has been gathered during the last decades about wildlife in agroecosystems. It is nowadays widely recognized that habitat selection needs to be considered separately for different species, at multiple spatial and temporal scales (e.g. Orians & Wittenberger 1991; George & Zack 2001; Laiolo 2005; Vickery & Arlettaz 2012). However, a majority of studies have focussed on the breeding ecology of single species at a single spatial scale with its concomitant limitations for capturing the rapidly changing agroecosystems (e.g. Perkins *et al.* 2002; Arlt *et al.* 2008; Brambilla, Guidali & Negri 2008; Revaz, Schaub & Arlettaz 2008; Douglas, Vickery & Benton 2009; Mermod *et al.* 2009; Martinez *et al.* 2010; Weisshaupt *et al.* 2011; Ceresa *et al.* 2012; Tagmann-Ioset *et al.* 2012). Mainly due to agriculture management and seasonality, agroecosystems display temporally and spatially varying environmental conditions during the year (Benton, Vickery & Wilson 2003), which are likely to affect birds and underpin the importance of using an integrative approach where habitat selection is investigated for multiple taxa at different seasons.

To complete their life cycle, birds have to fulfil diverse resource requirements varying between and within seasons. Finding a suitable nesting place in close proximity to foraging locations to feed their chicks seems to be the challenge mostly faced by breeding pairs during reproduction (e.g. Eggers, Unell & Pärt 2011; Winqvist *et al.* 2011; Vickery & Arlettaz 2012). In winter, the main issue for farmland birds represents insufficient food provision threatening survival, especially late in the season when depletion of food supply causes a “hungry gap” (Henderson, Vickery & Carter 2004; Siriwardena, Calbrade & Vickery 2008; Buckingham *et al.* 2011; Baker *et al.* 2012). Not only inter-seasonal, but even intra-seasonal shifts in bird-habitat associations involving temporal changes in diet, food availability or habitat suitability have been demonstrated (e.g. Bairlein 1983; Franco *et al.* 2004; Brambilla & Rubolini 2009; Douglas, Vickery & Benton 2009; Gilroy *et al.* 2010; Eggers, Unell & Pärt 2011; Brambilla, Martino & Pedrini 2013; Herzon *et al.* 2014). As an illustration, Douglas, Vickery and Benton (2009) found that the use of field margins by yellowhammers *Emberiza citrinella* markedly declined during the breeding season, whilst use of cereal fields augmented. This shift was experimentally tested by the authors who could deduce that enhanced vegetation height in margins in late summer possibly impedes food accessibility.

Because different spatial scales are highlighting different crucial resource needs (relevant for one single or different species), heterogeneity of the agricultural matrix has to be investigated at multiple spatial scales (Robinson, Wilson & Crick 2001; Brambilla *et al.* 2009; Gabriel *et al.* 2010; Pickett & Siriwardena 2011; Guerrero *et al.* 2012; Cunningham *et al.* 2014). Increased habitat patchiness is known to offer a wider range of resources and support higher biodiversity (Benton, Vickery & Wilson 2003; Wretenberg, Pärt & Berg 2010; Vickery & Arlettaz 2012). **Landscape-scale heterogeneity** mainly affects birds over the proportions of different habitat types. Relative amounts of woodland, steppe, wetland and crop types strongly influence bird community composition and species richness (e.g. Verhulst, Báldi & Kleijn 2004; Winqvist *et al.* 2011). Semi-natural boundary habitats such as margins or hedges are also well recognised to be valuable for birds in case of adequate management (Perkins *et al.* 2002; Vickery, Feber & Fuller 2009; Vickery & Arlettaz 2012). For example, optimal territories of red-backed shrikes *Lanius collurio* seem to harbour around 15-35% hedge cover (Brambilla, Rubolini & Guidali 2007; Brambilla *et al.* 2010). In addition to compositional heterogeneity (number and proportions of different habitat types), spatial configuration of the habitat types should be taken into account when quantifying spatial heterogeneity in agricultural landscapes (Fahrig *et al.* 2011). Indeed, Pickett and Siriwardena (2011) showed that the spatial mixing of land uses best predicted bird abundance. **Within fields**, sward structure constitutes the key factor for foraging and breeding birds because it dictates food availability and accessibility of nesting sites for ground breeders. A botanically and structurally (height and cover) diverse sward harbours a higher food abundance and diversity (Vickery *et al.* 2001; Atkinson, Buckingham & Morris 2004) and makes seeds and invertebrates accessible to a broad range of bird species and foraging guilds (Vickery & Arlettaz 2012). Massive use of fertilizers has promoted uniformly higher and denser swards resulting in impeded foragers' mobility, prey inaccessibility, increased (actual or perceived) predation risk (Whittingham & Evans 2004; Wilson, Whittingham & Bradbury 2005) and even deleterious effects on population growth rates (Arlt *et al.* 2008). Larger areas of bare ground in agricultural fields have been associated to higher bird occupancy, especially in winter (e.g. Perkins *et al.* 2000; Moorcroft *et al.* 2002; Atkinson, Buckingham & Morris 2004; Buckingham, Peach & Fox 2006) and finer-grained habitat selection studies conducted in various farmland types during the breeding season also highlighted the importance of heterogeneous bare ground and vegetation cover combination for terrestrial invertebrate feeders, supporting the idea of a trade-off between food abundance and accessibility (Menz, Mosimann-Kampe & Arlettaz 2009; Schaub *et al.* 2010; Arlettaz *et al.* 2012). Creating undrilled patches in the middle of arable fields allows skylarks *Alauda arvensis* to breed longer during the season, probably because of enhanced food accessibility for foraging parents (Morris *et al.* 2004; Fischer, Jenny & Jenni 2009). In summary, scale-dependent habitat selection may differ between species and agricultural crops. Therefore, combining seasonal and spatial information will deliver a better understanding of the reality from a bird and management perspectives.

Vineyards of central Europe are known to vary in time and space especially owing to seasonality and the diverse management possibilities of vine plants and grapes. Vineyards can host many rare and specialized plant and animal species, especially when they are managed extensively and interspersed with natural elements such as hedgerows and surrounded by dry and warm natural habitat patches (Costello & Daane 1998; Sierro & Arlettaz 2003; Verhulst, Báldi & Kleijn 2004; Bruggisser, Schmidt-Entling & Bacher 2010; Gillespie & Wratten 2012; Nascimbene, Marini & Paoletti 2012; Trivellone *et al.* 2012; Kehinde & Samways 2014; Kosulic, Michalko & Hula 2014; Trivellone *et al.* 2014; Caprio *et al.* 2015; Cohen *et al.* 2015; Gaigher, Pryke & Samways 2015). Even though avian studies in this farmland habitat are still underrepresented, vineyards have been shown to be regionally important for birds because they cover large surfaces with very specific conditions like south-exposed slopes. There have been few attempts to date to study bird habitat selection in **vineyard agroecosystems** (Sierro & Arlettaz 2003; Verhulst, Báldi & Kleijn 2004; Laiolo 2005; Arlettaz *et al.* 2012; Duarte *et al.* 2014) and except Laiolo (2005) all other works paid exclusively attention to the breeding season. During reproduction, Duarte *et al.* (2014) could outline the outstanding role of soil conservation techniques for bird abundance, species richness and diversity. In line with these findings, the woodlark *Lullula arborea* also select patchy ground vegetation at the foraging patch scale (Arlettaz *et al.* 2012). Concerning habitat selection in winter, Laiolo (2005) was able to highlight the role played by vineyards in providing food for foraging birds and thus the stronger season-dependence of the effect of this system on birds compared to other land use types.

In this study, we focussed on vineyards facing continental climate (large variation in conditions between seasons) in south-western Switzerland in the canton of Valais. We wanted to investigate habitat selection of multiple bird species that use vineyards as breeding sites, as stop-over site during migration and as winter habitat, especially as feeding sites. We aimed to get overall and species-specific habitat selection curves at two spatial scales. At the landscape scale we wanted to find out which role do marginal (semi-)natural habitat patches play for birds within the agricultural matrix. At the field scale we wished to highlight the importance of ground vegetation structure and vineyard management for birds. Circannual variations in habitat selection patterns were assessed. With this information, we hoped to design future management recommendations of vineyards for specific times of the year, outside and within the production area. We carried out bird monitoring twice a month along transects from February 2014 to January 2015. Landscape structures were mapped and quantified within a 100m-buffer zone around each 1-km transect. At the field scale we compared vineyard characteristics of visited to unvisited parcels (vine crop units). Habitat selection patterns were assessed using mixed effects regression models and investigated for inter- and intra-seasonal variation in preferences by testing their interactions with circular month predictors.

Materials & methods

STUDY AREA & TRANSECTS

The study was carried out in the Rhone river valley in the Canton of Valais (SW Switzerland, 540-780 m a.s.l.). This inner alpine, west-east oriented valley is characterized by a continental climate with little rain, hot summers and cold winters. The south-exposed slopes are dominated by vineyards covering roughly 50 km^2 (Arlettaz *et al.* 2012) whereas intensive fruit tree plantations represent the main agricultural activity realized on the plain (Tagmann-Ioset *et al.* 2012). Most vineyards in the study area are farmed following the integrated production protocol involving a reduction in insecticide application. However, restriction in herbicide spraying is not mandatory in Valais. Consequently, about 95% of the vine plantations still exhibit a mineral appearance due to systematic herbicide application all over the ground (Arlettaz *et al.* 2012). This technique is employed to avoid competition for water between vine plants and ground vegetation (Tagmann-Ioset *et al.* 2012). Organic vineyards where vegetation is allowed to grow over the whole ground surface make scarcely 2% of the total area. Approximately 5% of the vine production surface where herbicides are typically sprayed in every second vine row offers a mosaic of ca. 50% vegetation cover interspersed with bare ground patches (Arlettaz *et al.* 2012).

From February 2014 to January 2015, 10 transects evenly distributed between Fully (46°08'43.0"N 7°07'30.5"E) and Leuk (46°19'03.5"N 7°37'59.7"E) were monitored (Sierro & Arlettaz 2003). For the geographic repartition of the ten study sites see Fig.S1 in Supporting Information (Swisstopo, http://map.geo.admin.ch). The retained vineyards aimed at representing varying habitat characteristics. For each transect, four categories of landscape structures were mapped in August 2014 (Table 1a & Fig.1c): grove area, natural grassy surfaces' area, number of isolated bushes and trees as well as number of buildings. Grove was defined as a surface densely covered with bushes and trees, like e.g. a hedge or a small patch of forest. Natural grassy surfaces included steppe surfaces and grassy vineyard margins. Buildings mainly constituted sheds in vineyards. Mapped habitat features were quantified into Quantum Geographic Information System version 2.6.1 (QGIS 2015) in a buffer zone of 100 metres on both sides of each transect. The importance of ground vegetation was assessed at a finer scale because of its intra-annual variation which cannot be captured by Normalized Difference Vegetation Index (NDVI) values from remote sensing aerial pictures. Landscape characteristics and exact coordinates of extremities of transects can be found in Table S1.

BIRD MONITORING

Data collection of bird observations was performed using the line transect sampling method (Fig. 1a; Buckland *et al.* 2001). For each of the ten selected vineyards, one footpath of 1.12 ± 0.10 km (mean ± SE) following the topographic contour lines (whenever possible) was visited twice a month in a randomized order from February 2014 to January 2015, except for April when only five transects could be monitored during the second sampling session. Transect monitoring only took place under weather conditions without precipitations and strong wind. During the breeding season (from April to mid July), survey only took place between sunrise and eleven o'clock (Schmid, Zbinden & Keller 2004). In autumn and winter, sampling was performed between one hour after dawn and one hour before dusk in order to avoid biases caused by birds travelling between feeding and roosting sites (Moorcroft *et al.* 2002). Bird counts, associated habitat variables and pseudo-absences (see later) were recorded using the application Biolovision v.0.21 (Biolovision SARL, Ardon) on a smartphone (Samsung Galaxy Note 3 SM-N9005, South Korea).

Monitoring at the landscape scale

The landscape scale comprised all birds (Fig.1a) and four landscape structure categories (Table 1a & Fig.1c) recorded within the area delimited by the 100-m buffer zone around transects, including flying birds. Observations of single birds or flocks of a given species were recorded as a single observation point for a species. Bird abundance data was pooled per species, survey and transect (sum).

Monitoring at the field scale

A parcel represents a vine surface managed in a uniform way which translates into homogeneous habitat characteristics within a field. A vine field usually displays a different ground vegetation structure as well as a different cultivation type (e.g. gobelets or wires) from the neighbouring parcels, making the identification of parcel delimitations obvious in the field. Whenever a bird was located in a specific vine parcel, meaning on the ground, on a vine plant or flushed from this parcel, we considered this observation as a presence parcel. If a bird flock was spread over more than one parcel, we recorded the number of parcels on which birds occurred (multiple presence parcels). As habitat selection modelling requires comparison between exploited (presence parcels) and available but unused (pseudo-absence parcels) resources, an equivalent number of random (by birds) non-visited parcels were generated. For each presence parcel, one parcel adjacent to the visited one was treated as a pseudo-absence (sort of paired design, Fig.1b). The selection of a pseudo-absence parcel among all adjacent parcels had to be ascertained to be non-visited by the same species at the same sampling time. For each observation at the parcel scale, vegetation structure and vineyard management variables were immediately quantified in presence and corresponding pseudo-absence parcels. Visually estimated ground vegetation structure variables were green cover, brown or yellow vegetation cover and mean vegetation height. Vineyard management variables included vineyard cultivation type (gobelets or wires), grape abundance and parcel area (Arlettaz *et al.* 2012 & Table 1).

Given that the quality of parcel characteristics might be conditional to adjacent semi-natural habitat features (Brotons *et al.* 2005), we additionally measured the distances of exact presence point locations and random points to closest landscape elements using GIS ESRI® ArcMap™ 10.2.2 (ESRI Inc., Redlands, CA, USA; Table 1b). More specifically, for each presence point we generated a random point in QGIS, which had to be located in a vine parcel within the 100-m buffer zone of the same transect as for the presence point. Each random point was allocated to one presence point in a way to minimize the sum of the distances between random and presence points. The mean and standard deviation of the distances between paired random and presence points were 46.44 ± 32.45 meters, with a range of 1.87-135.05 meters. Comparison of distances to landscape elements between presence and random points was preferred because pseudo-absences were located very close to presence parcels, making a potential effect of the landscape context very unlikely to be detected with the presence-pseudo-absence design.

STATISICAL ANALYSES

All statistical analyses were conducted in R version 3.1.3 (R Core Team 2015).

Landscape scale

Landscape scale analyses included the four categories of landscape characteristics and circular month variables (Pewsey, Neuhäuser & Ruxton 2013) in relation to bird abundances (survey transect counts of pooled, Fringillidae and *Turdus* species), species richness and Shannon diversity (Oksanen *et al.* 2015). Since sample sizes of single species were usually insufficient to model species-specific habitat selection separately, some species commonly visiting vineyards were pooled into the genus *Turdus* (thrushes, 4 species: song thrush *Turdus philomelos*, mistle thrush *Turdus viscivorus*, fieldfare *Turdus pilaris* and blackbird *Turdus merula*) and the family of Fringillidae (finches, 6 species: chaffinch *Fringilla coelebs*, linnet *Carduelis cannabina*, goldfinch *Carduelis carduelis*, greenfinch *Carduelis chloris*, citril finch *Serinus citrinella* and serin *Serinus serinus*). Species richness refers to the number of species (Spellerberg & Fedor 2003). Concerning landscape explanatory variables, proportions were arcsin-square root transformed and counts (densities) log transformed. Values were then standardized (mean = 0, standard deviation = 1) to improve convergence of the model fitting algorithms. In case of (continuous) explanatory variables showing a Spearman correlation coefficient $|r_s| > 0.7$, the biologically less meaningful variable was excluded from modelling. Because the number of potential models was large relative to our sample size due to various possible combinations of explanatory variables, the model selection procedure was conducted in two steps.

In the first step, overall habitat preferences (complete data set from the whole year) were investigated using Generalized Linear Mixed Models (GLMMs) from the 'lme4' R package (R package version 1.1-10, Bates *et al.* 2015) with 'transect' and 'observation level' set as random effects to account for repeated visits of the same transects and correct for overdispersion when necessary (Gillies *et al.* 2006; Bolker *et al.* 2009). Varying transect length was taken into account by means of the offset argument (Korner-Nievergelt *et al.* 2015). For abundance data, a hierarchical Poisson regression model (log link function) was applied. For species diversity, a Linear Mixed Model (LMM) was adopted. To generate the set of candidate models, all possible combinations of the four landscape variables (Table 1c) were fitted using the 'dredge' function of the 'MuMIn' R package (R package version 1.15.1., Bartoń 2015). Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002; Johnson & Omland 2004).

In a second step, each landscape variable figuring in the best model (with the lowest AICc) of overall habitat preferences was further investigated for seasonal variation in habitat selection patterns by testing their interactions with circular month variables (Douglas, Vickery & Benton 2009). For this purpose, a set of candidate models including all possible combinations (with and without interactions) of a habitat variable and cosinus and sinus of month angles in radians (hereafter "cosmonth" and "sinmonth") were fitted by means of the 'dredge' function and ranked according to AICc. A significant main effect of cosmonth can be interpreted as a difference in bird abundance between winter (positive estimate because cos("December") = 1, max. cosmonth value) and summer (negative estimate because cos("June") = -1, min. cosmonth value). Sinus depicts the spring (positive estimate) vs autumn (negative estimate) sensitivity. A significant interaction between a habitat variable and cos/sinmonth suggests a variation of bird affinity for that habitat variable across seasons. Model fit was checked using residual plots, autocorrelation values and indications for overdispersion.

Field scale

Field scale analyses included the vegetation structure, vineyard management, distances to landscape elements and circular month variables in relation to bird occurrence (presence = 1 vs. pseudo-absence = 0 for pooled, Fringillidae and *Turdus* species). All explanatory variables were standardized to facilitate model fitting and comparison of effect sizes and checked for collinearity (kept if Spearman $|r_s| < 0.7$). A three-step habitat selection modelling approach was adopted.

First, in order to minimize the number of explanatory variables in the second step we pre-selected habitat variables to be explored in overall habitat selection. Vineyard management variables and distances to landscape element categories showing a trend ($P \leq 0.1$) in univariate models were inserted in the second modelling steps. In parallel, linear and quadratic effects of vegetation structure variables were tested for the presence of an optimum in a single model, because of a likely trade-off between food abundance and availability (e.g. Schaub *et al.* 2010; Arlettaz *et al.* 2012). Quadratic terms were discarded when they met the following two criteria: their 95%-credible intervals did include zero and the effect size of the squared effect was smaller than the one of the linear effect. This procedure ensured that no squared effects potentially playing an important role in habitat selection were missed. Linear effects of vegetation structure variables were systematically included because of their particular interest in this study.

In the second step, overall habitat preferences were modelled by means of hierarchical logistic regression models (logit link function) with 'transect' and 'paired ID' as random effects. 'Paired ID' as random factor is meant for the presence parcel as well as its adjacent pseudo-absence parcel and its random point. Since both random effects systematically displayed a variance < 0.0001, they were dropped and we ended up with logistic regression models. The set of candidate models was created by combining all vegetation structure variables (linear and kept squared effects) and other variables showing a trend in univariate models in all possible combinations and ranked according to AICc.

Third, variables occurring in the most parsimonious model (lowest AICc) were investigated for seasonal habitat selection patterns as in landscape scale analyses.

Finally, at both spatial scales, we used model averaging over the set of competitive models ranked by AICc to estimate coefficients and 95% credible intervals for each habitat predictor. Ranked models were considered as competitive when ΔAICc ≤ 2 (Burnham & Anderson 2002). Fixed effects always present within the competitive models and/or whose model-averaged p-values were significant were considered to be likely to play a significant role in habitat selection by birds and were used to construct predicted preference curves. Prediction plots are based on model-averaged estimates and predictions are bounded with 95%-Bayesian credible intervals, calculated by bootstrapping using 10000 repeats ('arm' R package version 1.8-6., Gelman & Su 2015).

Results

In total, we recorded 8719 individuals from 4421 observations (excluding pseudo-absences) belonging to 66 species and two undetermined categories within the 100-m buffer of all transects. At the field scale, 886 individuals from 589 presence and pseudo-absence observations and 29 species were recorded. See Table S2 for species list.

SEASONAL BIRD ABUNDANCES

Cosmonth was present and significant in all competitive models for pooled species, finches and species richness whereas sinmonth significantly affected thrushes and finches' abundances. Shannon diversity did not differ across seasons (Table 2b). Predicted overall bird abundance (pooled species) was about two times higher in winter (December) compared to summer (June; Table 3b, Fig.2a). Thrushes occurred in about threefold larger numbers in spring compared to autumn, with maximal and minimal predicted densities in March and September, respectively (Table 2b, Fig.2b). Finches' density in vineyards significantly differed between all four seasons (Table 3b), peaking in November (ca. 8 individuals per 20 ha) and then decreasing until May (ca. 2 individuals per 20 ha; Fig.2c). Finally, species richness increased in winter (on average 9 species in December) compared to summer (7 species in June on average; Table 3b, Fig.2d).

LANDSCAPE SCALE HABITAT SELECTION

For pooled species' and thrushes' abundances, species richness and Shannon diversity, grove cover (hedges and woody patches) came out to be the only landscape variable occurring systematically in (nearly) all competitive models (Table 2a). Model-averaged estimates of grove cover remained all significant except for the pooled species' abundance (Table 3a) where the set of competitive models included the null model, so the results should be interpreted with caution (Table 2a). Predictions showed a positive effect of increased grove proportion in vineyards for overall bird abundance, thrushes' abundance, species richness and diversity, where overall number of individuals as well as species richness are predicted to double (thrushes' abundance might even triple) with an increase of grove cover from 0 to 11% (Fig.3). This selection pattern for vineyards harbouring larger areas of hedges and forest fragments remain consistent throughout the year (no significant interaction(s) between any of the two circular month predictors and grove cover; Tables 2b, 3b). Density of isolated bushes and trees, buildings and proportion of natural grassy surfaces did not have any significant effect on birds (Table 3a). Furthermore, we did not detect any preferences of finches for considered landscape variables (Table 2a).

FIELD SCALE HABITAT SELECTION

Overall bird selection (pooled species) for green cover significantly differed across all four seasons (Tables 2d, 3d). Monthly prediction plots displayed two clearly distinct selection patterns of green vine fields: in winter (November-March) occurrence probability firstly increased and reached a plateau at around 50% ground cover, with parcels covered by < ca. 15% green vegetation clearly being avoided (see blue graphs in Figs 5a-c, k-l). In contrast, during spring and until late summer (May-September) birds tended to select parcels with intermediate green vegetation cover with an optimum around 15-60%, peaking at ca. 40% (see red graphs in Fig.5e-i). In April and October the habitat selection curves reflect intermediate stages between the two seasonal extremes (Figs 5d, i). Brown cover selection by birds significantly changed between summer and winter (Table 2d, 3d). Birds seem to profit from enhanced brown vegetation cover in autumn and winter (September-February; Tables 2d, 3d, Fig.6 c-d) while the large credible intervals of plotted predictions curves between March and August remain too large to make clear interpretations (Fig. 6a-b).

As for pooled species at the field scale, thrushes visited preferentially parcels where green cover exceeded 50% in winter with a predicted occurrence probability reaching its maximum at 100% (November-March; Figs 7a, d). In summer (June-July), the opposite selection pattern was observed: occurrence probability of thrushes is predicted to diminish with increasing green cover, with parcels offering more than ca. 15% green cover clearly avoided (Fig.7b). Uncertainty was too high to make reliable predictions for the remaining months (April-May and August-October). Thrushes also tended to select vine parcels located closer to natural grassy surfaces (< 35m; Tables 2c, 3c) as depicted by predicted occurrence probability of thrushes decreasing with increasing distance to natural grassy surfaces (Fig.4a). This relationship remained constant throughout the year.

A clear preference of finches for parcels where green vegetation cover amounted to 40-80% could be demonstrated, with maximal occurrence probability at around 60% green cover (Table 2c, Fig.4b). Moreover, finches were more likely to use parcels offering enhanced brown vegetation cover (> ca. 10%; Table 2c, Fig.4c). Both habitat selection patterns were consistent over the whole year (Tables 2d, 3d). As an overview, vegetation structure variables (green and brown cover; see Table 1b) played a far more crucial role in explaining bird occurrence compared to vineyard management or distance to landscape variables, which did not have any significant effect on birds at the field scale (except for distance to natural grassy surfaces which was relevant for thrushes; Table 3c).

Discussion

Several key findings emerged from this study with respect to the potential value of vineyards for birds at different spatial scales and times of the year. Overall, bird abundance and species richness were higher in winter than in summer. Grove cover (hedges and woody patches) turned out to positively influence bird abundance, species richness and diversity at the landscape scale. At the field scale, vegetation cover was revealed to constitute a crucial habitat requirement for birds changing between seasons. Finally, habitat associations were shown to vary according to avian taxa (thrushes, finches), highlighting the need to delineate resource needs of different species and guilds. This work was therefore able to demonstrate the importance of vineyard characteristics for bird communities within and outside the production area and that habitat selection patterns in this dynamic agroecosystem do vary between seasons.

The observed effects of higher bird abundance and richness in winter could be explained by the following non-mutually exclusive arguments. First, south-exposed slopes devoted to viticulture constitute the first locations released from snow in winter, rending the ground accessible and making vine surfaces likely to play a crucial role for foraging overwintering birds in our study area. As noted by Laiolo (2005), woodland birds such as thrushes, chaffinches or great tits *Parus major* often leave their habitat to search for weed seeds on parcels or insects in the bark of vines. This attraction for vineyards and its accessible food resources might also hold for birds performing altitudinal migrations during winter such as the alpine chough *Pyrrhocorax graculus* and the citril finch *Serinus citrinella*. Secondly, in winter, many bird species aggregate into larger, intra- and interspecific flocks and become more mobile to look for suitable foraging patches (Perkins *et al.* 2000). Those gatherings of overwintering birds might partly explain the observed increased abundance and species richness in winter and strongly contrast to territorial birds during the breeding season.

Given the relatively low sample size of ten transects at the landscape scale, effect sizes of bird-habitat associations should be underestimated and considered as conservative estimates. Detected relationships are therefore thought to be very strong. Although our study sites only comprised grove proportions ranging from 0 to 11%, a positive effect of grove cover (hedges and woody patches) on overall bird abundance, thrush abundance, species richness and diversity could still be pointed out. Those habitat associations with respect to grove proportion were consistent throughout the year. Our results coincide with past findings, which emphasized the importance of hedges within the agricultural matrix by providing foraging, nesting, sheltering opportunities and song posts for the avifauna (Evans, Bradbury & Wilson 2003; Brambilla, Rubolini & Guidali 2007; Brambilla, Guidali & Negri 2008; Brambilla *et al.* 2009; Brambilla, Guidali & Negri 2009; Batáry, Matthiesen & Tscharntke 2010; Ceresa *et al.* 2012; Siriwardena, Cooke & Sutherland 2012). Planting hedges might promote some rare and/or specialist species such as the cirl bunting *Emberiza cirlus* (Brambilla, Guidali & Negri 2008), the rock bunting *Emberiza cia* (Brambilla, Guidali & Negri 2009) or the red-backed shrike (Brambilla, Rubolini & Guidali 2007; Brambilla *et al.* 2009; Ceresa *et al.* 2012) as well as some woodland species in case of small forest fragments. Nevertheless, tall structures such as groves might be detrimental to some open-land species such as the yellow wagtail *Motacilla flava* (Gilroy *et al.* 2010) and the woodlark, which need large open, “homogeneous” landscape patches (Fahrig *et al.* 2011) and might perceive hedges as unsuitable habitat, especially when they are very large or high. Hedgerow characteristics are known to affect birds in a species-specific way, (Macdonald & Johnson 1995; Hinsley & Bellamy 2000; Fuller *et al.* 2001; Henderson, Vickery & Carter 2004), which underpins the importance of quantifying hedge structure and composition in future studies. As an illustration of the need to assess habitat determinants of individual species, we couldn’t detect any habitat selection by finches at a larger scale, potentially linked to the great interspecific heterogeneity in ecological requirements within this family (Fringillidae). Unfortunately, habitat selection could not be modelled separately for single species due to insufficient data.

At the field scale, vegetation cover was revealed to be a crucial factor for birds’ habitat selection. An overall seasonal shift in field use by birds was observed with respect to green and brown vegetation cover. Parcels with a 100% green cover were visited more often in winter (November-March) whereas from spring to late summer (May-September) birds tended to select parcels with intermediate green vegetation cover with an optimum at 40%. For brown vegetation cover, avian occurrence probability increased in autumn and winter (September-February) for high values. The winter trend to select more vegetated parcels (100% green and/or brown) might be dictated by the lack of food supply for seed-eating birds occurring in large flocks during the cold season (Henderson, Vickery & Carter 2004; Siriwardena, Calbrade & Vickery 2008; Buckingham *et al.* 2011; Baker *et al.* 2012). Granivorous birds might directly pick the weed seeds on the plants and consequently do not require bare ground to enhance food accessibility. On the opposite more ground-foraging insectivores are present in spring and summer and parents (including granivores) usually need invertebrate prey rather than seeds to rear their chicks (Wilson *et al.* 1999). Since ground vegetation develops further during the breeding season, food accessibility rather than abundance might become the limiting factor during this period. This supports the hypothesis that occurrence probability is highest at intermediate vegetation cover (ca. 40%) because of the trade-off between food abundance and accessibility, in accordance with previous findings (Perkins *et al.* 2000; Moorcroft *et al.* 2002; Atkinson, Buckingham & Morris 2004; Morris *et al.* 2004; Buckingham, Peach & Fox 2006; Douglas, Vickery & Benton 2009; Menz, Mosimann-Kampe & Arlettaz 2009; Schaub *et al.* 2010; Eggers, Unell & Pärt 2011; Arlettaz *et al.* 2012).

Different vegetation structures are selected by birds according to their foraging strategy (Buckingham, Peach & Fox 2006). Thrushes are known to feed upon soil-dwelling invertebrates like earthworms and to complete their diet with berries additionally in winter (Tucker 1992). In our study, this taxonomic group was predicted to clearly avoid field displaying more than 15% cover in summer. This pattern might be explained by the fact that thrushes seem to require large areas of bare ground to access the earthworms and other invertebrates in the soil. However, contrary to past findings demonstrating the importance of bare ground patches in grasslands especially in winter for the same reason (Perkins *et al.* 2000; Buckingham, Peach & Fox 2006), our results suggested that thrushes are more likely to visit vine fields with 100% green cover in winter. This preference might be related to the enhanced invertebrate food abundance on green fields, a rare resource in intensive viticulture landscapes and potentially even more important in late winter when hedgerow fruits have been depleted. Moreover, thrushes tended to select parcels located nearer to natural grassy surfaces, possibly due to cover or further food sources.

Finally, optimal parcels for finches offered about 60% green and more than 10% brown cover. Five out of six species of finches, which occurred in vineyards in this study, constitute granivores foraging either directly on herbaceous plants or on the ground all over the year. As a consequence, preference for enhanced vegetation cover might reflect higher seed supply. As an exception, the chaffinch represents the only species feeding on invertebrates during the breeding season and only visited vineyards during winter when this bird is predominantly granivorous and ground-foraging (Perkins *et al.* 2000). The observed decrease of finches' occurrence probability towards 100% cover might mirror the chaffinch's ground-foraging behaviour, so that some bare ground might be necessary for this species to detect and access seeds. Since more than one third of the observations among finches belonged to the chaffinch, the overall pattern for finches' family is likely to be influenced by the requirements of this particular species.

Management recommendations

On the basis of the results, we recommend to plant and/or conserve hedges and woody patches outside of the production area between vine parcels to bolster avian biodiversity at the landscape scale. In spite of the very low amounts of forest fragments and hedgerows (mean ± SE = 5.21 ± 3.12% cover per transect), overall number of individuals as well as species richness were predicted to double (thrushes' abundance might even triple) with an increase of grove cover from 0 to 11%. In line with Ceresa *et al.* (2012) our results suggest that even only a low increase in grove cover will trigger a strong response of avian biodiversity. This conservation practice is likely to be most effective in intensively managed vineyards which are often situated in a homogenous landscape context (Tscharntke *et al.* 2005; Batáry, Matthiesen & Tscharntke 2010; Wretenberg, Pärt & Berg 2010; Tscharntke *et al.* 2012), but we argue that this measure should be implemented independent of surrounding landscape complexity. Biodiversity-related ecosystem services such as biocontrol are expected to occur mainly when hedgerows are added in agricultural landscapes with heterogeneous surroundings (Tscharntke *et al.* 2007; Winqvist *et al.* 2011). Consequently, hedgerow planting might be supported independently of the landscape context owing to diverse benefits for birds and landowners. Even though hedge quality was not quantified in this research, previous works have advocated botanically and structurally diverse hedges including mature trees combined with an adjacent grass/wildflower margin as a key means of enhancing avian biodiversity in agricultural landscapes (Parish, Lakhani & Sparks 1994; Macdonald & Johnson 1995; Parish, Lakhani & Sparks 1995; Hinsley & Bellamy 2000; Fuller *et al.* 2001; Birrer *et al.* 2007).

As mentioned above and since thrushes tended to select parcels closer to natural grassy surfaces at the field scale, structurally and floristically diverse, regularly (only partly) cut field margins should be created and ideally located just next to a high quality hedgerow. According to the gathered evidence-based knowledge, such a measure will benefit most birds by offering foraging locations near from cover as well as nesting opportunities (Perkins *et al.* 2002; Vickery, Carter & Fuller 2002; Vickery, Feber & Fuller 2009).

While previous recommendations focused on promoting landscape characteristics outside the production area, our results additionally demonstrate the importance of adapting the management within the cropped area. In spring and summer, ground vegetation should be allowed growing on every second row of a vine parcel while in winter, management guidelines should promote natural colonisation of weeds and ground vegetation on the whole field surface to combat the lack of food provision for overwintering birds. Duarte et al. (2014) demonstrated higher bird abundance, diversity and species richness in mechanically managed, vegetated vineyards compared to mineral and chemically managed viticulture surfaces, especially for insectivores. Consequently, we would argue that herbicide spraying should be restricted as much as possible because it is known to reduce plant species richness, consequently impact on invertebrates and finally decrease food resource value for birds (Boatman *et al.* 2004; McCracken & Tallowin 2004; Sanguankeo & León 2011; Nascimbene, Marini & Paoletti 2012) and ecosystem services provided by those taxa (Isbell *et al.* 2011). Mechanical clearing should therefore be preferentially adopted to manage ground vegetation on vine fields.

To increase the willingness of farmers to implement our findings, it is important to mention that not only flora and fauna are likely to benefit from environmentally-friendly agricultural practices. Vine growers might get advantages in “producing” biodiversity because high biodiversity levels might translate into better ecosystem functioning or service provision (Isbell *et al.* 2011; Vickery & Arlettaz

2012). Beyond their intrinsic value for multiple taxonomic groups (e.g. Merckx *et al.* 2012; M'Gonigle *et al.* 2015), hedges, field margins and ground cover between vine rows offer overwintering refuge for predatory arthropods of crop pests (Pfiffner & Luka 2000; Pywell *et al.* 2005). Moreover, when such boundary habitat elements are connected to surrounding natural habitat they may act as corridors for the circulation of important insects delivering pollination for the ground vegetation (Kremen *et al.* 2004; Morandin & Kremen 2013; Blaauw & Isaacs 2014) and pest control services improving vine plant growth (Nicholls, Parrella & Altieri 2001; Sanguankeo & León 2011; Morandin, Long & Kremen 2014). Increased bird abundance and diversity has even been shown to enhance biocontrol in vineyards (Jedlicka, Greenberg & Letourneau 2011) with potential increase in yield (Maas, Clough & Tscharntke 2013). Furthermore, established herbaceous cover on vine fields prevent soil erosion, enhance water retention and soil fertility (Gago, Cabaleiro & Garcia 2007; Tourte *et al.* 2008; Arlettaz *et al.* 2012; Duarte *et al.* 2014). As a conclusion, ameliorated ecosystem services might reduce the need for chemical control of weeds and diseases and slowly allow a development towards sustainable agriculture. Effectiveness of such services still needs to be investigated in more details in the case of viticulture.

Outlook

Further studies in this farmland habitat monitor the effectiveness of different management options of the proposed conservation measures in providing biodiversity benefits and associated ecosystem services, taking the landscape context into account. As highlighted by our failure in delineating habitat preferences of the heterogeneous finches' family at the landscape scale, future work should also focus on collecting more data to incorporate species-specific needs into conservation schemes. An organism's response depends on its perception of the environment and therefore is likely to be species specific (Wiens 1989). As previously discussed, not all species will universally profit from increased hedgerow occurrence or from similar hedge structure and composition. Species' identity matters (Atauri & de Lucio 2001) and habitat requirements of endangered, rare or indicator species such as the red-backed shrike should be assessed in priority (Brambilla *et al.* 2010). Although only compositional landscape heterogeneity was considered in our study, future work should also include configurational aspects (Fahrig *et al.* 2011).

As a conclusion, combining overall and species-specific approaches as well as applying a large variety of management targets should restore temporal and spatial multiscale farmland heterogeneity and ensure benefits for a wide range of plant and animal species, including birds. Land sparing and sharing should be applied as dual, complementary rather than mutualistic excluding measures within the countryside (Green *et al.* 2005). Given the area covered by agriculture and its permanent extension, it is nowadays inconceivable to save biodiversity uniquely by means of natural reserves. Human-dominated landscapes need to be incorporated into conservation programmes and will play a key role in sustaining biodiversity and ecosystem functioning.

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TABLES

Table 1. Explanatory variables recorded for habitat selection modelling. (a) Variables considered at the landscape scale. (b) Variables considered at the field scale. Vegetation structure and vineyard management variables were recorded both for presence and pseudo-absence parcels, whereas distance to landscape variables were compared between presence parcels and random points within the 100-m buffer zone around a transect.

Variable category	Variable	Variable type	Recording method	Definition
(a) Landscape scale				
Landscape	Grove cover	Continuous	QGIS	Proportion grove (% hedges and woodland patches) within the 100-m buffer zone around one transect.
	Natural grassy surfaces cover	Continuous	QGIS	Proportion grassy surfaces outside from vine parcels (% steppe and field margins) within the 100-m buffer zone around one transect.
	Isolated bushes & trees density	Continuous (discrete)	QGIS	Number of isolated bushes and trees within the 100-m buffer zone around one transect per km.
	Buildings density	Continuous (discrete)	QGIS	Number of buildings (mainly sheds) within the 100-m buffer zone around one transect per km.
(b) Field scale				
Vegetation structure	Green ground vegetation cover	Continuous	In the field	Visually estimated percentage of ground vegetation at the parcel scale (5%-precision, vines not considered).
	Yellow and brown ground vegetation cover	Continuous	In the field	Visually estimated percentage of ground vegetation at the parcel scale (5%-precision, vines not considered). Proxy for herbicide application and dry material.
	Ground vegetation height	Continuous	In the field	Visually estimated mean height of grass sward (cm).
Vineyard management	Vineyard cultivation type	Categorical	In the field	Distance between plant rows : short for gobelet (typically ca.100-110 cm spacing), large for wires (ca. 120-200 cm spacing, Arlettaz *et al.* 2012).
	Grape vine abundance	Continuous (discrete)	In the field	Counted number of grape bunches on five systematically selected vine plants on the parcel. Berries may attract frugivores.
	Parcel area	Continuous	QGIS	Area of the parcel (m^2).
Distance to landscape	Distance to nearest grove	Continuous	ArcGIS	Distance between a recorded bird observation or a random point and the border of the nearest grove in the same transect (m).
	Distance to nearest natural grassy surface	Continuous	ArcGIS	Distance between a recorded bird observation or a random point and the border of the nearest natural grassy surface in the same transect (m).
	Distance to nearest isolated bush or tree	Continuous	ArcGIS	Distance between a recorded bird observation or a random point and the nearest isolated bush or tree in the same transect (m).
	Distance to nearest building	Continuous	ArcGIS	Distance between a recorded bird observation or a random point and the nearest building border in the same transect (m).

Table 2. Outcome of the model selection procedures showing competitive models for (a) overall habitat selection at the landscape scale; (b) seasonal habitat selection at the landscape; (c) overall habitat selection at the field scale; (d) seasonal habitat selection at the field scale. At the landscape scale, Poisson GLMMs were fitted for abundance data, whereas Normal LMM was used for Shannon diversity. At the field scale, binomial GLM were applied to presence/pseudo-absence data. Explanatory variables are written in bold when significant ($P \leq 0.05$) and in italic when showing a trend ($P \leq 0.1$).

Response variable	**# Candidate models**	**Competitive models (ΔAICc ≤ 2)**	**Df**	**Deviance**	**ΔAICc**	**Weight**	**Sample size (# Obs./Transects)**
a) LANDSCAPE SCALE: OVERALL HABITAT SELECTION							
Pooled species' abundance	16	**G**	4	2128.53	0.00	0.248	235/10
		Intercept	3	2131.95	1.36	0.126	
		G + IBT	5	2128.31	1.87	0.097	
Thrushes' abundance	15	**G**	4	1385.35	0.00	0.274	235/10
		G + NGS	5	1384.39	1.13	0.156	
		G + IBT	5	1385.03	1.77	0.113	
Finches' abundance	16	**Intercept**	3	1566.33	0.00	0.194	235/10
		G	4	1565.79	1.53	0.090	
		NGS + IBT	5	1563.74	1.57	0.089	
		IBT	4	1565.88	1.62	0.086	
		NGS + IBT	4	1565.92	1.66	0.085	
		B	4	1566.01	1.75	0.081	
Species richness	16	**G**	3	1292.25	0.00	0.288	235/10
		G + IBT	4	1291.53	1.35	0.147	
		G + B	4	1291.98	1.80	0.117	
Shannon diversity	16	**G**	4	354.77	0.00	0.214	235/10
		G + IBT	5	353.59	0.92	0.135	
		G + IBT + B	6	351.57	1.00	0.130	
		G + B	5	354.14	1.47	0.103	

b) LANDSCAPE SCALE: SEASONAL HABITAT SELECTION							
Pooled species’ abundance	13	**G + cosmonth +** G:cosmonth	6	2101.35	0.00	0.197	235/10
		G + cosmonth	5	2103.65	0.18	0.180	
		G + cosmonth + sinmonth + G:cosmonth	7	2099.51	0.28	0.171	
		G + cosmonth + sinmonth	6	2101.78	0.43	0.159	
		cosmonth	4	2107.04	1.49	0.094	
		cosmonth + sinmonth	5	2105.18	1.72	0.084	
Thrushe’s abundance	13	**G + sinmonth**	5	1350.56	0.00	0.371	235/10
		G + sinmonth + G:sinmonth	6	1349.86	1.40	0.184	
		G + cosmonth **+ sinmonth**	6	1350.45	1.99	0.137	
Finches’ abundance	4	**cosmonth + sinmonth**	5	1536.03	0.00	0.963	235/10
Species richness	13	**G + cosmonth**	4	1277.96	0.00	0.287	235/10
		G + cosmonth + G:cosmonth	5	1276.15	0.27	0.250	
		G + cosmonth + sinmonth	5	1277.04	1.17	0.160	
		G + cosmonth + sinmonth + G:cosmonth	6	1275.25	1.48	0.137	
Shannon diversity	13	**G**	4	354.77	0.00	0.243	235/10
		G + cosmonth **+** *G:cosmonth*	6	351.43	0.85	0.159	
		G + sinmonth	5	353.92	1.24	0.131	
		G + cosmonth	5	354.51	1.84	0.097	
c) FIELD SCALE: OVERALL HABITAT SELECTION							
Pooled species’ occurrence	12	**green + green^2 + brown**	4	754.51	0.00	0.501	589
		green + green^2 + *brown* + vegheight	5	754.18	1.70	0.214	
		green + green^2	3	758.46	1.93	0.191	
Thrushes’ occurrence	16	**green + dist_NGS**	3	261.52	0.00	0.351	197
		green + vegheight + **dist_NGS**	4	260.61	1.18	0.195	
		green + brown + **dist_NGS**	4	261.41	1.98	0.131	
Finches’ occurrence	12	**green + green^2 + brown**	4	193.91	0.00	0.392	165
		green + green^2 + *brown* **+** vegheight	5	192.05	0.26	0.344	

d) FIELD SCALE: SEASONAL HABITAT SELECTION

Pooled species' occurrence	38	**green + green^2** + cosmonth + sinmonth + **green:cosmonth + green:sinmonth**	7	729.40	0.00	0.397	589
		green + green^2 + *cosmonth* + sinmonth + **green:cosmonth** + green^2:cosmonth + **green:sinmonth**	8	728.40	1.05	0.234	
		green + green^2 + cosmonth + sinmonth + **green:cosmonth + green:sinmonth** + green^2:sinmonth	8	728.77	1.43	0.195	
Pooled species' occurrence	13	**brown** + cosmonth + **brown:cosmonth**	4	801.29	0.00	0.382	589
		brown + cosmonth + sinmonth + **brown:cosmonth** + *brown:sinmonth*	6	798.09	0.88	0.246	
		brown + cosmonth + sinmonth + **brown:cosmonth**	5	800.90	1.65	0.168	
Thrushes' occurrence	13	**green** + cosmonth + sinmonth + **green:cosmonth + green:sinmonth**	6	234.21	0.00	0.893	197
Thrushes' occurrence	13	**dist_NGS**	2	267.29	0.00	0.373	197
		dist_NGS + cosmonth	3	267.12	1.90	0.144	
Finches' occcurrence	38	**green + green^2** + cosmonth + green:cosmonth + *green^2:cosmonth*	6	191.75	0.00	0.190	165
		green + green^2 + cosmonth + *green^2:cosmonth*	5	194.75	0.84	0.125	
		green + green^2	3	199.12	0.99	0.116	
		green + green^2 + cosmonth	4	197.71	1.67	0.082	
		green + green^2 + cosmonth + green:cosmonth	5	195.66	1.75	0.079	
Finches' occcurrence	13	**brown**	2	218.81	0.00	0.346	165
		brown + sinmonth	3	217.80	1.06	0.203	
		brown + cosmonth	3	218.70	1.97	0.130	

Table 3. Model-averaged parameter estimates, standard errors (SE) and P-values for variables occurring in the respective sets of competitive models for (a) overall habitat selection at the landscape scale; (b) seasonal habitat selection at the landscape; (c) overall habitat selection at the field scale; (d) seasonal habitat selection at the field scale. Model averaging was performed over the set of competitive models (ΔAICc ≤ 2; see Table 2). Significance: . $P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Explanatory variables	**Pooled species**			***Turdus* species (Thrushes)**			**Fringillidae species (Finches)**			**Species richness**			**Shannon diversity**		
	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value	Estimate	SE	P-value
a) LANDSCAPE SCALE: OVERALL HABITAT SELECTION															
Intercept	2.32	1.40	0.098 .	1.23	0.11	<0.001 ***	0.94	0.65	0.146	2.06	0.05	<0.001 ***	1.62	0.04	<0.001 ***
Grove cover	0.16	0.13	0.234	0.29	0.12	0.018 *	0.02	0.08	0.816	0.16	0.06	0.004 **	0.12	0.05	0.010 *
Natural grassy surface cover	-	-	-	-0.04	0.09	0.683	-0.06	0.14	0.683	-	-	-	-	-	-
Isolated bushes & trees density (per km)	-0.01	0.06	0.846	-0.01	0.06	0.817	0.06	0.14	0.687	-0.01	0.04	0.721	-0.03	0.05	0.519
Buildings density (per km)	-	-	-	-	-	-	-0.01	0.07	0.857	-0.01	0.03	0.829	-0.02	0.04	0.593
b) LANDSCAPE SCALE: SEASONAL HABITAT SELECTION															
Intercept	3.16	0.11	<0.001 ***	1.24	0.11	<0.001 ***	1.37	0.18	<0.001 ***	2.05	0.05	<0.001 ***	1.62	0.04	<0.001 ***
Grove cover	0.17	0.12	0.183	0.27	0.11	0.017 *	NA	NA	NA	0.16	0.05	0.004 **	0.11	0.04	0.014 *
Cosmonth	0.36	0.07	<0.001 ***	-0.01	0.05	0.896	0.61	0.12	<0.001 ***	0.12	0.03	<0.001 ***	0.01	0.03	0.763
Sinmonth	-0.05	0.07	0.509	0.63	0.10	<0.001 ***	-0.38	0.13	0.003 **	-0.01	0.03	0.65	-0.01	0.03	0.746
Grove x cosmonth	0.04	0.07	0.524	-	-	-	NA	NA	NA	0.02	0.03	0.515	0.02	0.04	0.628
Grove x sinmonth	-	-	-	-0.02	0.07	0.729	NA	NA	NA	-	-	-	-	-	-
c) FIELD SCALE: OVERALL HABITAT SELECTION															
Intercept	0.03	0.09	0.696	0.06	0.15	0.703	0.04	0.18	0.812						
Green cover	0.55	0.09	<0.001 ***	0.38	0.16	0.021 *	0.68	0.19	<0.001 ***						
Green cover^2	-0.31	0.09	<0.001 ***	NA	NA	NA	-0.47	0.19	0.012*						

Brown cover	0.14	0.11	0.196	-0.01	0.07	0.891	0.43	0.21	0.048 *
Vegetation height	0.01	0.05	0.804	-0.04	0.11	0.692	0.13	0.20	0.520
Distance to natural grassy surface	NA	NA	NA	-0.35	0.15	0.022 *	NA	NA	NA
d) FIELD SCALE: SEASONAL HABITAT SELECTION									
Intercept	0.10	0.09	0.317	0.27	0.23	0.232	0.00	0.19	0.990
Green cover	0.64	0.11	<0.001 ***	0.84	0.33	0.012 *	0.81	0.21	<0.001 ***
Green cover^2	-0.33	0.10	0.001 **	NA	NA	NA	-0.59	0.19	0.002 **
Cosmonth	0.23	0.14	0.099 .	0.47	0.33	0.156	0.32	0.30	0.294
Sinmonth	0.05	0.13	0.721	0.28	0.24	0.250	-	-	-
Green x cosmonth	0.73	0.19	<0.001 ***	1.75	0.49	<0.001 ***	0.26	0.40	0.509
Green x sinmonth	0.41	0.13	0.002 **	0.87	0.32	0.007 **	-	-	-
Green^2 x cosmonth	0.05	0.12	0.687	NA	NA	NA	0.30	0.38	0.419
Green^2 x sinmonth	0.02	0.08	0.753	NA	NA	NA	-	-	-
Intercept	0.06	0.09	0.515				0.05	0.16	0.761
Brown cover	0.35	0.12	0.006 **				0.63	0.24	0.008 **
Cosmonth	0.02	0.12	0.843				-0.01	0.11	0.891
Sinmonth	-0.06	0.11	0.587				-0.07	0.18	0.676
Brown x cosmonth	0.38	0.15	0.010 **				-	-	-
Brown x sinmonth	-0.08	0.16	0.589				-	-	-
Intercept				0.06	0.15	0.710			
Distance to natural grassy surface				-0.35	0.15	0.020 *			
Cosmonth				0.03	0.13	0.841			
Sinmonth				-	-	-			
Distance to natural grassy surface x cosmonth				-	-	-			
Distance to natural grassy surface x sinmonth				-	-	-			

FIGURE LEGENDS

Fig.1 Study design: satellite picture of the transect in Miège with QGIS layers. (a) Landscape scale: design and recorded observations (white points); (b) field scale: presence-pseudo-absence design and recorded observations (stars); (c) mapping of four landscape elements categories.

Fig.2 Model-averaged predictions of bird seasonal abundance from Poisson regression models for seasonal habitat selection at the **landscape scale**. (a) pooled species; (b) *Turdus* spec. (thrushes); (c) Fringillidae (finches); (d) species richness. Relationships presented here showed a significant (model-averaged) effect of cosmonth and/or sinmonth in habitat selection modelling (see Table 3). Shown are model-averaged bird density predictions (per 20 ha) with 95%-Bayesian credible intervals.

Fig.3 Relationships between grove cover and predicted model-averaged bird density (per 20 ha) from Poisson regression models for overall habitat selection at the **landscape scale**. (a) pooled species; (b) *Turdus* spec. (thrushes); (c) species richness; (d) Shannon diversity. Those habitat preferences remained constant throughout the year. 95%-Bayesian credible intervals are delimited by the grey area.

Fig.4 Predicted probability of occurrence of (a) *Turdus* spec. (thrushes) with respect to distance to the nearest natural grassy surface; Fringillidae (finches) in relation to (b) green and (c) brown vegetation covers. Those **finer-scaled** habitat selection patterns consistent throughout the year. 95%-Bayesian credible intervals are drawn in grey. Occurrence probability was allowed to vary with the habitat variable under consideration, while other explanatory variables present in the average model were held constant at their mean values. Occurrence probabilities higher than 0.5 indicates selection or preference whereas values lower than 0.5 should be interpreted as avoidance.

Fig. 5 Predicted probability of occurrence of **pooled species** with respect to **green vegetation cover** from (a) January to (l) December. Selection of green cover by birds significantly varied between seasons (months) at the **field scale**. 95%- Bayesian credible intervals are depicted by coloured areas. Different colours stand for different selection patterns. Occurrence probabilities higher than 0.5 indicates selection or preference whereas values lower than 0.5 should be interpreted as avoidance.

Fig. 6 Predicted probability of occurrence of **pooled species** with respect to **brown vegetation cover** in (a) March; (b) June; (c) September; (d) December. Selection of brown cover by birds significantly varied between seasons (months) at the **field scale**. Predictions are only shown for four months to avoid overloading with graphs and because those months correspond to the extreme values of cosmonth (cos(Jun) = -1, cos(Dec) = 1) and sinmonth (sin(Mar) = 1, sin(Sep) = -1) which therefore reflect the greatest changes in habitat selection between months. 95%-Bayesian credible intervals are depicted by coloured areas. Different colours stand for different selection patterns. Occurrence probabilities higher than 0.5 indicates selection or preference whereas values lower than 0.5 should be interpreted as avoidance.

Fig. 7 Predicted probability of occurrence of *Turdus* spec. (**thrushes**) with respect to **green vegetation cover** in (a) March; (b) June; (c) September; (d) December. Selection of green cover by thrushes significantly varied between seasons (months) at the **field scale**. Predictions are only shown for four months to avoid overloading with graphs and because those months correspond to the extreme values of cosmonth (cos(Jun) = -1, cos(Dec) = 1) and sinmonth (sin(Mar) = 1, sin(Sep) = -1) which therefore reflect the greatest changes in habitat selection between months. 95%-Bayesian credible intervals are depicted by coloured areas. Different colours stand for different selection patterns. Occurrence probabilities higher than 0.5 indicates selection or preference whereas values lower than 0.5 should be interpreted as avoidance.

FIGURES

Fig.1

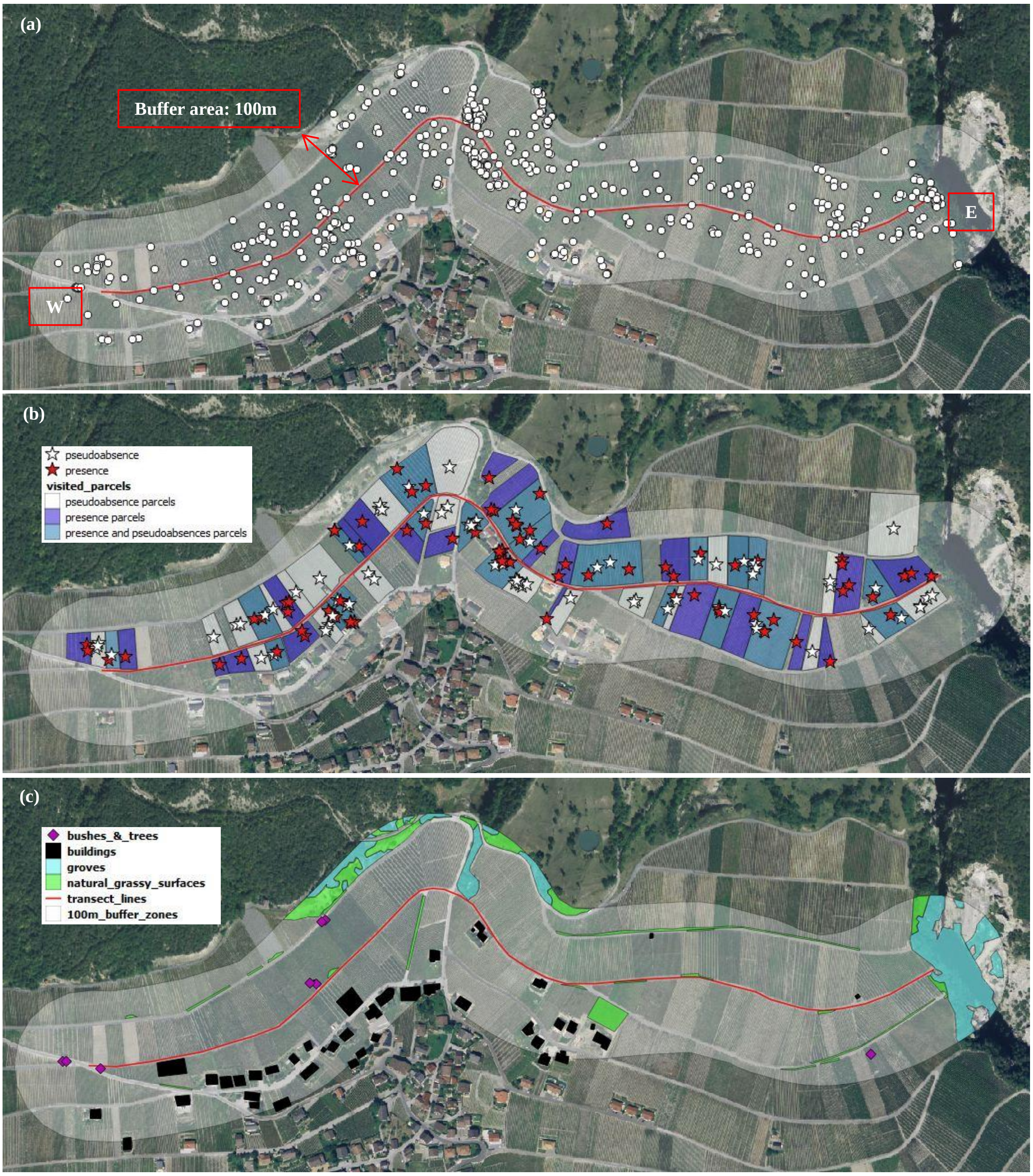


Fig.2

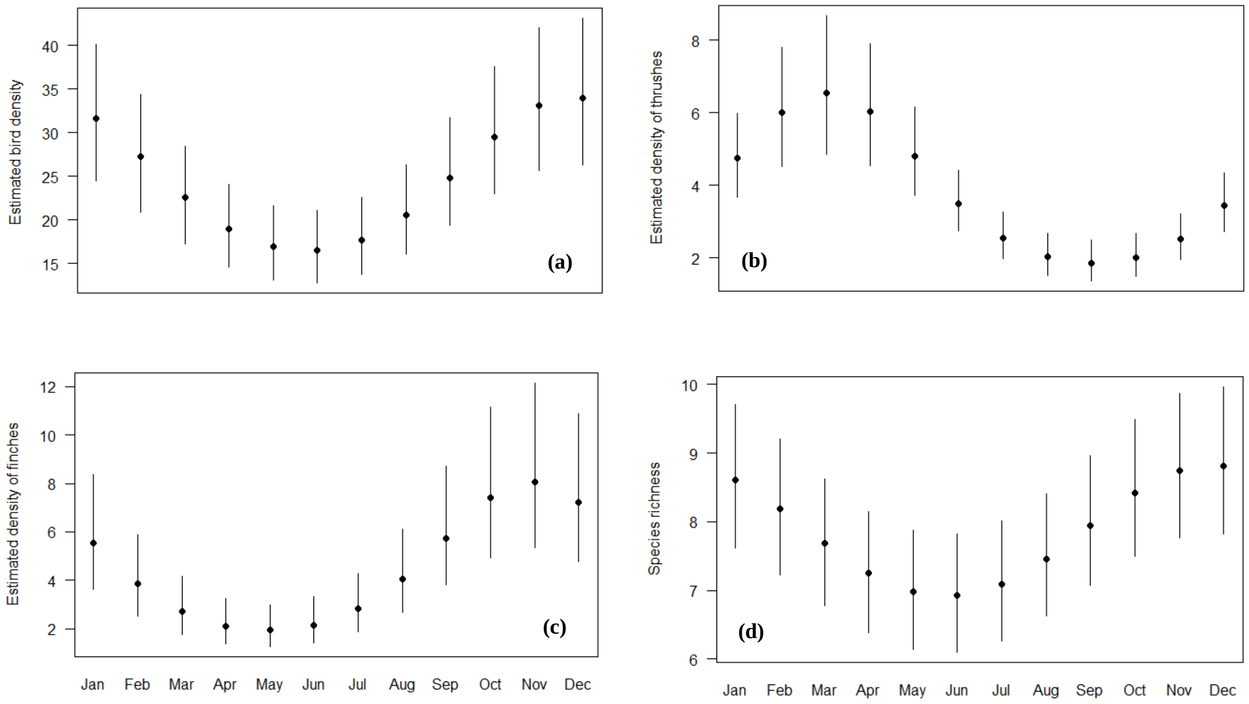

Estimated bird density
40
35
30
25
20
15
(a)
Estimated density of thrushes
8
6
4
2
(b)
Estimated density of finches
12
10
8
6
4
2
(c)
Species richness
10
9
8
7
6
(d)
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

Fig.3

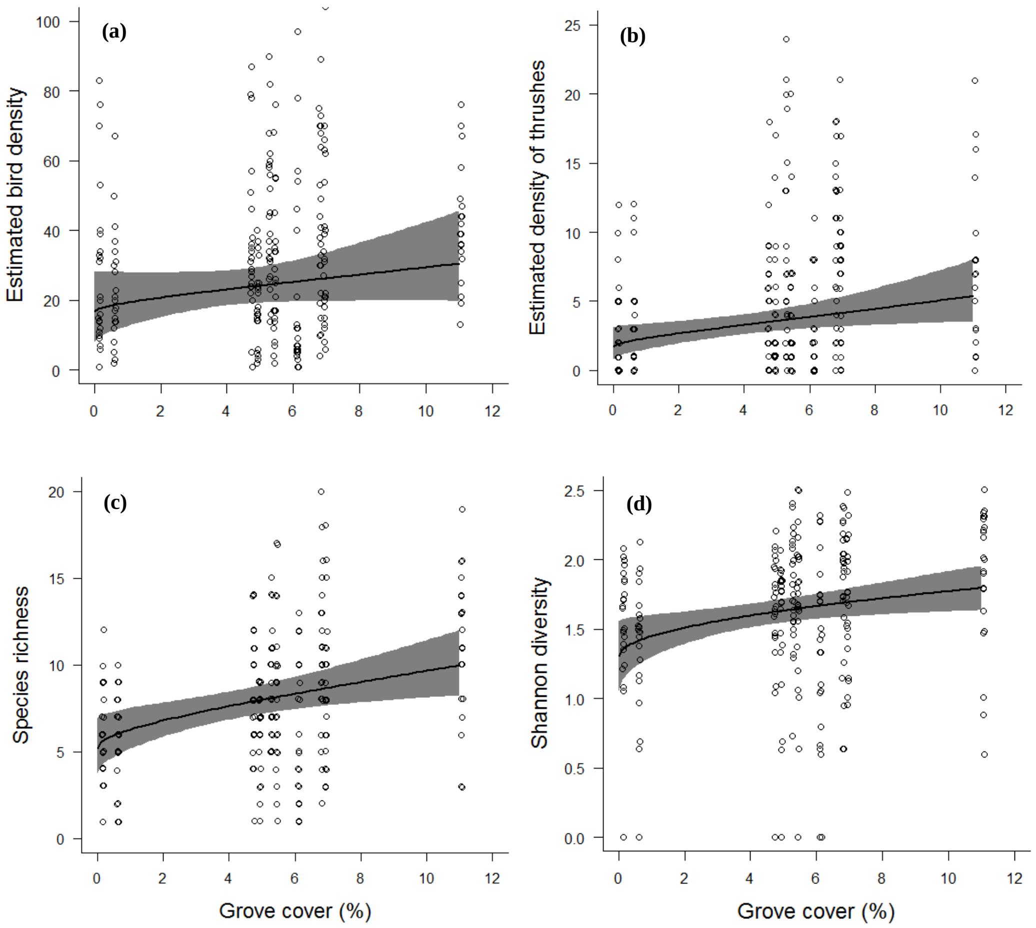

(a)
Estimated bird density
0
20
40
60
80
100
(b)
Estimated density of thrushes
0
5
10
15
20
25
(c)
Species richness
0
5
10
15
20
(d)
Shannon diversity
0.0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
12
Grove cover (%)
Grove cover (%)

Fig.4

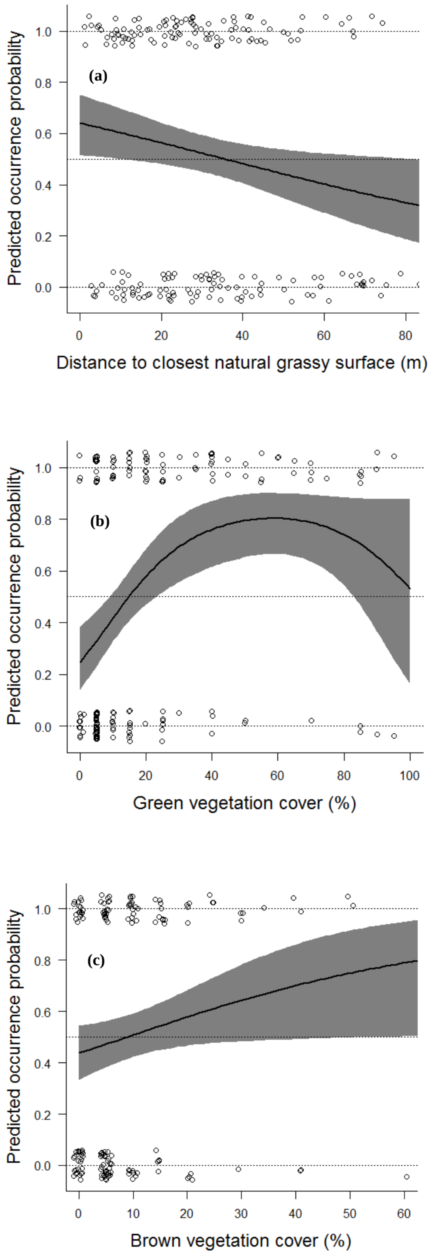

(a)
Predicted occurrence probability
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Distance to closest natural grassy surface (m)
(b)
Predicted occurrence probability
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
Green vegetation cover (%)
(c)
Predicted occurrence probability
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
60
Brown vegetation cover (%)

Fig.5

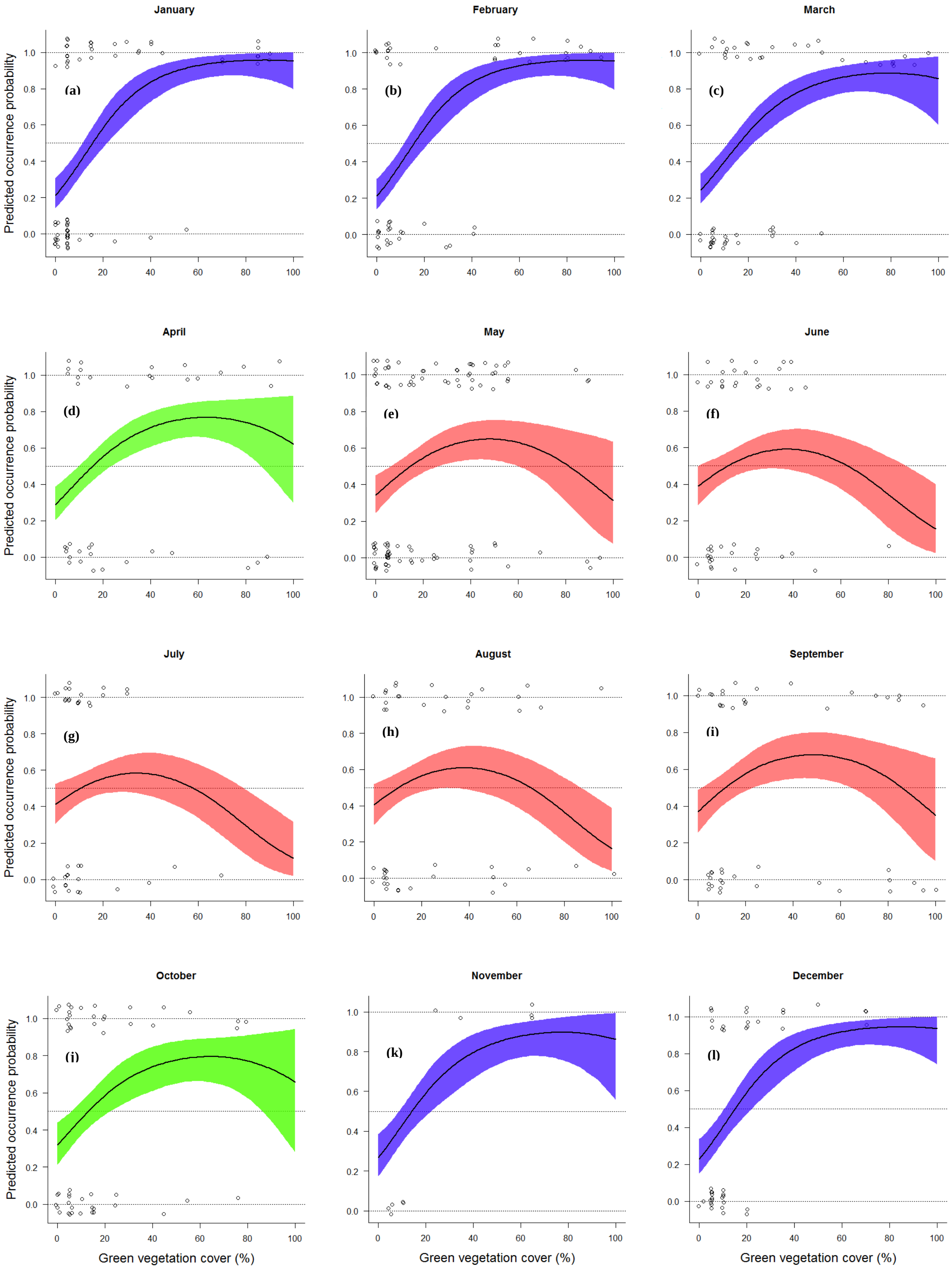

January
February
March
April
May
June
July
August
September
October
November
December
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
Predicted occurrence probability
Green vegetation cover (%)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100

Fig.6

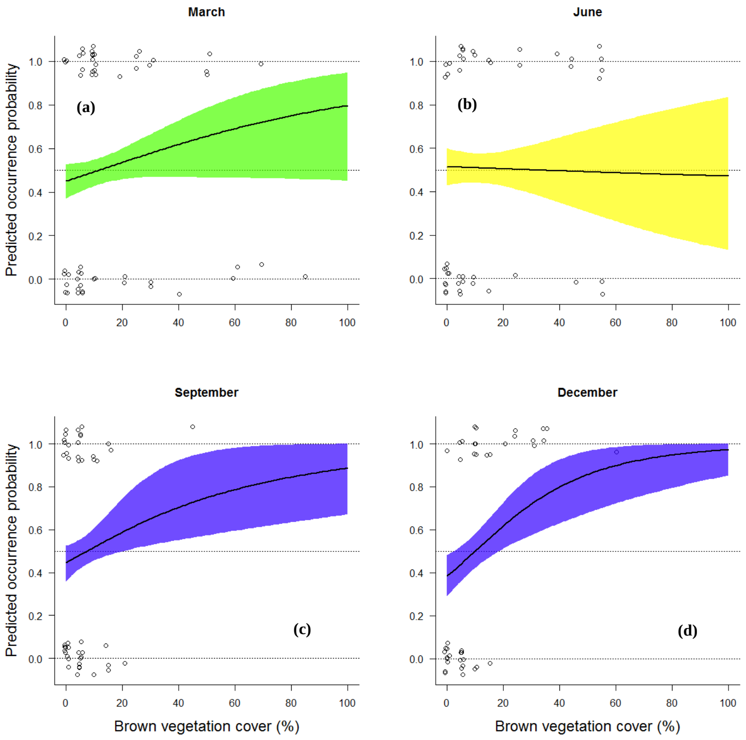
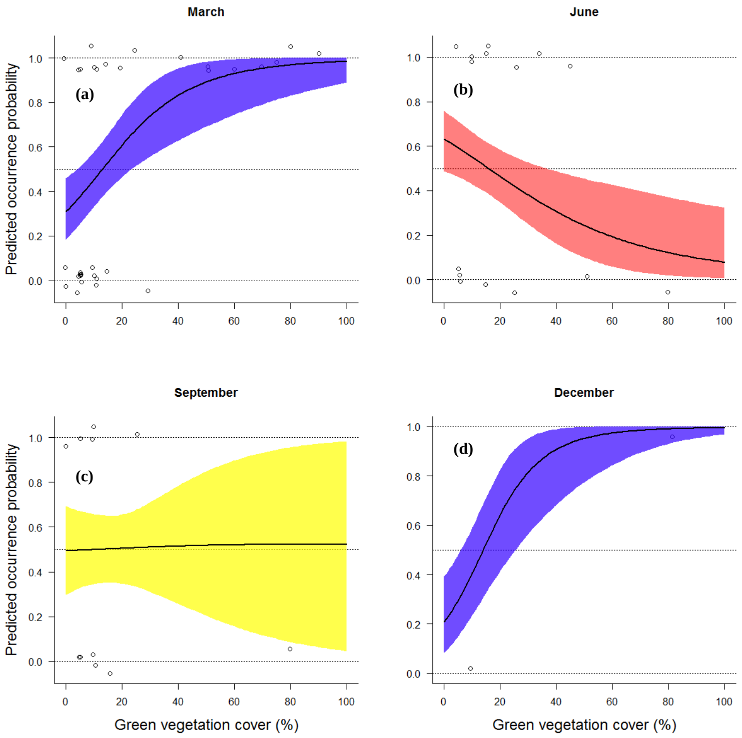

March
June
September
December
(a)
(b)
(c)
(d)
Predicted occurrence probability
Brown vegetation cover (%)
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100

Fig.7


March
June
September
December
(a)
(b)
(c)
(d)
Predicted occurrence probability
Predicted occurrence probability
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
Green vegetation cover (%)
Green vegetation cover (%)

Supporting Information

Table S1. Transect characteristics

Table S2. Species list

Fig. S1. Geographic repartition and sampling randomization of study sites

Supporting Information

Table S1. Transect characteristics

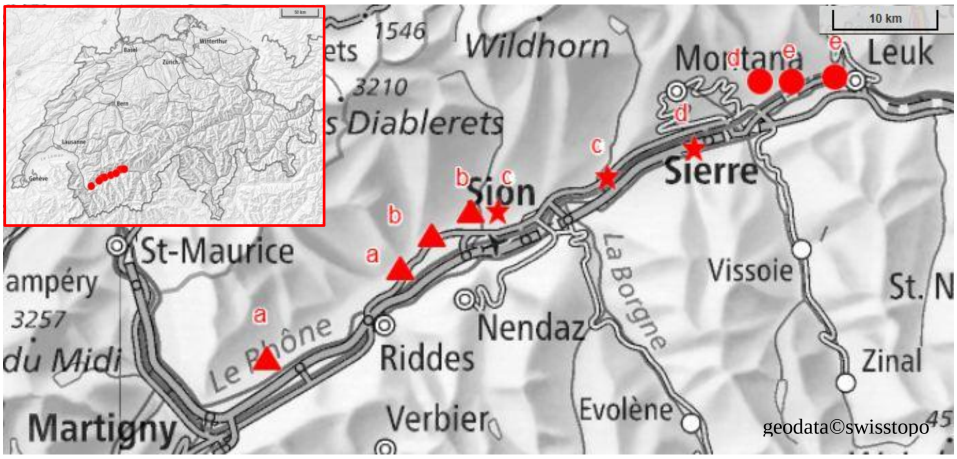
Commune (locality)	**Altitude (m)**	**Transect line length (km)**	**Natural grassy surfaces area (m2)**	**Grove area (m2)**	**Nr. of Buildings**	**Nr. of Isolated Bushes & Trees**	**East coord. (WGS84)**	**West coord. (WGS84)**
Fully (Châtaignier)	560	1.11	18510.80	15170.41	19	31	46°09'05.2"N 7°07'33.5"E	46°08'46.7"N 7°06'59.3"E
Chamoson (Gru)	540	1.21	13099.68	407.18	6	14	46°12'21.9"N 7°14'21.6"E	46°11'50.2"N 7°14'15.3"E
Vétroz (Péteille)	600	1.10	13518.74	11830.83	52	38	46°13'36.5"N 7°16'21.6"E	46°13'15.9"N 7°15'42.0"E
Conthey (Sensine)	660	1.17	5739.81	1637.03	27	30	46°14'26.7"N 7°18'15.5"E	46°14'00.3"N 7°17'41.5"E
Savièse (La Soie)	690	0.99	15607.69	11141.88	8	44	46°14'27.8"N 7°19'46.0"E	46°14'14.1"N 7°19'06.4"E
St-Léonard (La Brunière)	610	0.95	13475.23	12034.75	25	35	46°15'32.8"N 7°25'32.5"E	46°15'30.5"N 7°24'49.5"E
Chermignon (Ollon)	560	1.05	7496.66	16735.82	25	44	46°16'39.3"N 7°29'45.2"E	46°16'24.4"N 7°29'02.0"E
Miège (Rotse)	780	1.27	9864.65	15019.69	42	8	46°18'56.0"N 7°33'25.7"E	46°18'51.9"N 7°32'33.2"E
Salquenen (Hell)	650	1.12	8312.61	16986.84	9	23	46°18'53.3"N 7°35'01.7"E	46°19'04.4"N 7°34'19.0"E
Varen (Dude)	700	1.21	52901.93	29425.22	2	91	46°19'06.4"N 7°37'15.2"E	46°18'56.4"N 7°36'28.4"E
Transect mean ± SE	635 ± 75.46	1.12 ± 0.10	15852.78 ± 13594.33	13038.97 ± 8177.62	22 ± 16	36 ± 23		

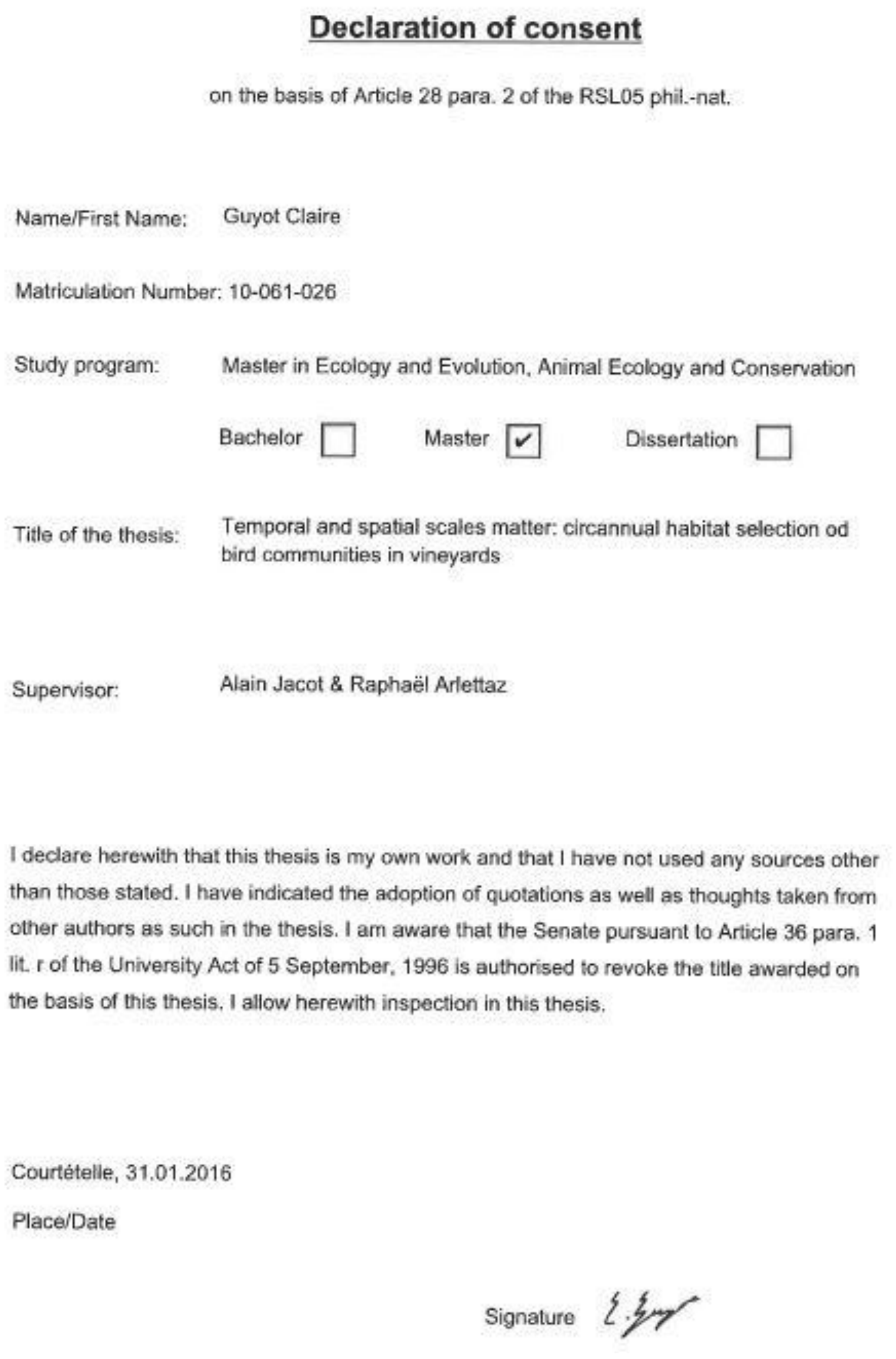
Table S2. Species list

Species - English name	**Species - Latin name**	**Species recorded at the field scale**	**Total number of individuals at the landscape scale**	**Total number of recorded observations**
Common Buzzard	*Buteo buteo*		17	16
European Honey Buzzard	*Pernis apivorus*		2	1
European Sparrowhawk	*Accipiter nisus*		9	9
Common Kestrel	*Falco tinnunculus*		20	20
Common Wood Pigeon	*Columba palumbus*		34	15
Hoopoe	*Upupa epops*	x	15	11
Black Woodpecker	*Dryocopus martius*		1	1
European Green Woodpecker	*Picus viridis*		4	3
Great Spotted Woodpecker	*Dendrocopos major*	x	12	12
Lesser Spotted Woodpecker	*Dendrocopos minor*		2	2
Eurasian Wryneck	*Jynx torquilla*		2	2
Woodlark	*Lullula arborea*	x	103	71
Eurasian Crag Martin	*Ptyonoprogne rupestris*		5	3
Common House Martin	*Delichon urbicum*		46	6
Meadow Pipit	*Anthus pratensis*	x	24	4
Tree Pipit	*Anthus trivialis*	x	4	3
White Wagtail	*Motacilla alba*	x	43	33
Grey Wagtail	*Motacilla cinerea*	x	16	15
Dunnock	*Prunella modularis*		3	3
European Robin	*Erithacus rubecula*	x	231	228
Common Nightingale	*Luscinia megarhynchos*		1	1
Common Redstart	*Phoenicurus phoenicurus*		3	3
Black Redstart	*Phoenicurus ochruros*	x	526	419
Northern Wheatear	*Oenanthe oenanthe*	x	9	7
Black-eared Wheaear	*Oenanthe hispanica*		1	1
Whinchat	*Saxicola rubetra*	x	3	3
Song Thrush	*Turdus philomelos*	x	6	6
Mistle Thrush	*Turdus viscivorus*	x	239	90
Fielfare	*Turdus pilaris*	x	232	27
Common Blackbird	*Turdus merula*	x	1215	897
Blue Rock Thrush	*Monticola solitarius*		4	3
Garden Warbler	*Sylvia borin*		2	2
Eurasian Blackcap	*Sylvia atricapilla*		89	74
Common Whitethroat	*Sylvia communis*		2	1
Lesser Whitethroat	*Sylvia curruca*		3	3
Western Bonelli's Warbler	*Phylloscopus bonelli*		2	2
Common Chiffchaff	*Phylloscopus collybita*		4	4
Goldcrest	*Regulus regulus*		1	1
Winter Wren	*Troglodytes troglodytes*		23	21
European Pied Flycatcher	*Ficedula hypoleuca*		1	1
Great Tit	*Parus major*	x	433	280
Coal Tit	*Periparus ater*		1	1

Blue Tit	*Cyanistes caeruleus*		85	69
European Crested Tit	*Lophophanes cristatus*		2	2
Marsh Tit	*Poecile palustris*		14	9
Long-tailed Bushtit	*Aegithalos caudatus*		19	3
Eurasian Nuthatch	*Sitta europaea*		4	3
Red-backed Shrike	*Lanius collurio*		15	10
Eurasian Magpie	*Pica pica*	x	57	40
Eurasian Jay	*Garrulus glandarius*	x	301	208
Spotted Nutcracker	*Nucifraga caryocatactes*		4	2
Alpine Chough	*Pyrrhocorax graculus*	-	141	9
Carrion Crow	*Corvus corone*		147	44
Northern Raven	*Corvus corax*		59	26
Common Starling	*Sturnus vulgaris*	x	145	10
House Sparrow	*Passer domesticus*	x	147	61
Eurasian Tree Sparrow	*Passer montanus*	x	273	94
Common Chaffinch	*Fringilla coelebs*	x	869	270
Common Linnet	*Carduelis cannabina*	x	546	155
European Golldfinch	*Carduelis carduelis*	x	196	86
European Greenfinch	*Carduelis chloris*	x	384	143
Citril Finch	*Serinus citrinella*	x	73	9
European Serin	*Serinus serinus*	x	402	203
Eurasian Bullfinch	*Pyrrhula pyrrhula*		1	1
Cirl Bunting	*Emberiza cirlus*	x	38	34
Rock Bunting	*Emberiza cia*	x	493	300
Undetermined passerines	-		909	323
Undetermined raptors	-		2	2

Fig. S1. Geographic repartition and sampling randomization of study sites. The three shape-coded vs. five letter-coded regional zones regroup transects for random selection of visit order during the breeding and the non-breeding seasons, respectively. Source: Swisstopo (http://www.map.geo.admin.ch).





Declaration of consent

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

Name/First Name: Guyot Claire

Matriculation Number: 10-061-026

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

Bachelor ☐ Master ☑ Dissertation ☐

Title of the thesis: Temporal and spatial scales matter: circannual habitat selection od bird communities in vineyards

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.

Courtételle, 31.01.2016

Place/Date

Signature