



Landscape heterogeneity and management practices drive habitat preferences of wintering and breeding birds in intensively-managed fruit-tree plantations



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ABSTRACT

Intensively-managed fruit-tree plantations consisting of low-stem trees have progressively replaced traditional high- and mid-stem orchards in Europe during the intensification of agriculture in the second part of the 20th century. Such perennial agricultural systems often form dense, homogeneous landscapes interspersed with open fields, urban areas and semi-natural structures. This observational study investigated the patterns driving landscape- and field-scale habitat preferences of bird communities in landscape units with varying fractions of intensively-managed fruit-tree plantations. At landscape scale, habitat homogeneity, notably a large proportion of fruit-tree plantations, had negative effects on both overall bird species richness and on the abundance of insectivorous birds. A higher proportion of semi-natural features, such as natural woody structures (hedgerows, isolated trees and forest patches) and marshes, positively affected overall bird species richness and abundance as well as insectivorous bird abundance. At field scale, we detected general, trait- and species-specific preferences for older trees during both winter and spring. In winter, leftover fruit is a crucial resource driving field selection by the avifauna. In spring, bird preferences for low and sparse ground vegetation were best explained by increased food accessibility for terrestrially foraging birds. Overall landscape heterogeneity as well as in situ management practices both matter to enhance bird habitat in fruit-tree plantations. Increasing the proportion of diverse semi-natural structures would promote wintering and breeding bird diversity and abundance. At field scale, conditions for birds can be improved by preserving older fruit-tree plantations and by maintaining patches of bare ground and short vegetation in the plantation inter-tree rows. However, given the current high-intensity management in most fruit-tree plantations in our study area, promoting natural features within the wider landscape matrix might represent a more cost-effective solution to enhance bird biodiversity in this agro-ecosystem.

1. Introduction

In Western Europe, agro-ecosystems are dramatically affected by land use intensification processes, leading to an impoverishment of farmland biodiversity (Matson et al., 1997; Butler et al., 2007), which is mainly due to the loss of semi-natural habitats and an increase in habitat homogeneity (Benton et al., 2003; Tschamntke et al., 2005; Fahrig et al., 2011). Bird communities are particularly affected, with massive declines in the populations of many farmland species (Tucker and Heath, 1994; Chamberlain et al., 2000; Donald et al., 2001; Inger et al., 2014; Gamero et al., 2017). Among agricultural habitats that

underwent a severe alteration, high-stem orchards were especially heavily impacted (Herzog, 1998). Fruit production changed radically with the development of industrial fruit-tree cultures consisting of intensively-managed plantations of low-stem fruit trees (Werth, 1980).

Traditional orchards harbour high biodiversity through the combination of extensively-managed grasslands under the trees and perennial deciduous trees, thereby supplying variegated structures and resources for foraging and breeding birds (Herzog, 1998; Simon et al., 2010). In particular, old fruit trees with hollow trunks and branches offer breeding sites and perches for birds while supporting arthropods (Bailey et al., 2010; Vickery and Arlettaz, 2012; Gruebler et al., 2013)

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whereas the associated grasslands, as far as they are managed extensively, provide invertebrate prey (Horak et al., 2013; Brambilla et al., 2015). Not surprisingly, these were prime habitats for insectivorous and cavity-nesting birds that are nowadays threatened throughout Europe, if not locally extinct, e.g. Woodchat Shrike *Lanius senator* in Switzerland (Keller et al., 2010; Knaus et al., 2011). Furthermore, the high degree of fragmentation and isolation of traditional orchards in modern farmland impacts birds and other organisms surviving in such habitat islands (Bailey et al., 2010).

Intensively-managed, low-stem fruit-tree plantations are a very simplified habitat compared to traditional high-stem orchards. In conventional agriculture, vegetation is regularly cut between tree rows and typically treated with herbicides beneath the trees. In addition, fruit-tree plantations are systematically sprayed with insecticides and fungicides, decreasing arthropod abundance (Suckling et al., 1999; Brown and Schmitt, 2001; Simon et al., 2007) and reducing the reproductive success of nesting birds (Fluetsch and Sparling, 1994; Bishop et al., 2000). Actually, an absence of synthetic chemical treatment explains the positive effects of organic orchard management for birds (Genghini et al., 2006; Bouvier et al., 2011; MacLeod et al., 2012). However, treatments with copper, sulphur and natural insecticides in vineyards have been shown to affect non-targeted invertebrate prey (Eijsackers et al., 2005; Nash et al., 2010) and are more frequent than in conventional plantations, resulting in additional disturbance for breeding birds (Assandri et al., 2017c). In intensive perennial cultures such as vineyards and fruit-tree plantations, targeted conservation measures can mitigate the negative footprint of management intensification and landscape homogenization on bird communities (Arlettaz et al., 2012; Brambilla et al., 2015; Assandri et al., 2016). Although commercial fruit-tree cultures are very homogenous and intensively managed, they provide vertical structural woody elements that can potentially benefit a broad range of species typical of forest edges and open woodland, supporting them in the otherwise widely open cultivated landscape (Wiacek and Polak, 2008; Myczko et al., 2013; Brambilla et al., 2015). They even harbour endangered species such as Eurasian Hoopoe *Upupa epops* and Wryneck *Jynx torquilla* as long as nesting sites, i.e. nest boxes, are available (Mermod et al., 2009; Schaub et al., 2010; Weisshaupt et al., 2011). Promoting birds might even be advantageous for fruit producers as passerines like Great Tits *Parus major* play an active role in pest control in orchards by reducing caterpillar damages (Mols and Visser, 2002; Mols et al., 2005). Yet, the potential ecological function of farmland birds is only known for a handful of species. Investigating the basic ecological requirements and functions of more bird species inhabiting fruit-tree plantations is a prerequisite for the development of evidence-based conservation strategies (Arlettaz et al., 2010b).

Habitat selection is driven by various spatio-temporal environmental factors. Studies carried out at both landscape scale (accounting for the natural habitat in the matrix and the cultivated fields surrounding fruit-tree plantations) and field scale (micro-habitat within fruit-tree cultures) are necessary to disentangle those species-specific ecological requirements that are relevant for conservation (Vickery and Arlettaz, 2012; Gonthier et al., 2014). On a landscape level, breeding site availability, semi-natural structures and habitat heterogeneity are key for enhancing bird diversity as established for both vineyards (Assandri et al., 2016; Guyot et al., 2017) and intensively-managed fruit-tree plantations (Brambilla et al., 2015; Assandri et al., 2018). At field scale, the pattern of habitat selection of ground-feeding insectivorous birds often depends on foraging opportunities that are dictated by food availability, i.e. food abundance mediated by the structure of the ground vegetation that rules prey accessibility (Vickery and Arlettaz, 2012). Yet, if knowledge about species-specific ecological preferences is essential to promote targeted species-friendly farming practices, information about variation in seasonal patterns is key to embrace the bird community of fruit-tree plantations as a whole during an entire year cycle. For instance, previous studies have shown that bare ground patches are crucial for ground-feeding insectivorous birds

such as Hoopoe (Tagmann-Ioset et al., 2012) and Wryneck (Schaub et al., 2010; Weisshaupt et al., 2011) as they increase prey accessibility. The age of fruit trees (Wiacek and Polak, 2008), tree height (Brambilla et al., 2015) and tree density (Myczko et al., 2013) also influence field-scale habitat selection in both traditional or intensively-cultivated orchards. Furthermore, seasonality influences temporal bird assemblages and habitat use in perennial cultures like vineyards (Assandri et al., 2016; Guyot et al., 2017). Similar patterns are expected in fruit-tree plantations, but there is a deficit of year-round information about the bird community in that type of ecosystem. Crossing the information accrued from different species is especially relevant as habitat responses can be highly specific, potentially leading to mutually exclusive conservation measures (Besnard and Secondi, 2014; Assandri et al., 2019). For instance, an increased proportion of hedgerows might be beneficial for structured-land species like Red-backed Shrike *Lanius collurio* (Brambilla et al., 2007; Ceresa et al., 2012), but detrimental for open-land species such as Skylark *Alauda arvensis* (Hinsley and Bellamy, 2000), both being of conservation concern in farmland.

We conducted an observational study in a landscape dominated by intensively cultivated fruit-tree plantations in order to determine species-habitat relationships of the entire bird community. By accounting for fine-scaled variation in management practices, landscape configuration and composition and their seasonal effects, our study aims at providing detailed recommendations for bird-friendly management of intensively-managed, modern fruit-tree plantations.

2. Material and methods

2.1. Study area

The study area is situated along the Rhone Valley between Sierre (46°16'39.7"N 7°31'43.5"E) and Martigny (46°07'15.5"N 7°03'26.2"E) in southwestern Switzerland. Study sites are distributed over a 40 km stretch of the valley at an elevation of 455–520 m above the sea level. The climate of this intra-alpine valley is typically continental, with a mean temperature of -0.1 °C in January and 18.1 °C in June, and a total annual rainfall of 600 mm for the city of Sion (MeteoSwiss, 2020a, b). On south-exposed slopes, vineyards are the dominant cultures, while on north-facing slopes at low elevation apricot plantations prevail, interspersed by forests, hay meadows and pastures. The valley bottom landscape is dominated by intensive agriculture and a dense network of infrastructures, settlements and industrial estates. Intensively-managed fruit-tree cultures are the main cultivation on the plain, interspersed with grasslands and various crops.

2.2. Study design

38 linear transects of 400 m length, each surrounded by a 100 m buffer (supplementary material, Table S1), were regularly scattered on the valley bottom with a minimal distance of 500 m between study sites (Brambilla et al., 2015; Assandri et al., 2016; Guyot et al., 2017). Line transects are a well-established observational method to study habitat selection of overwintering and breeding birds in open areas with a repeatable protocol (Bibby et al., 2000). Transects followed a road or a track between plantations in order to have a good view into the perpendicular tree rows. We selected the sites according to a heterogeneity gradient based on the percentage of fruit-tree culture coverage within our landscape units, as defined by our transects and their buffer zones (11 ha), from 14 % to 93 % (supplementary material, Table S1, Fig. S5). Remaining areas consisted of grasslands (meadows and pastures, mean \pm standard deviation = 12.8 % \pm 14.6 %), crop cultures (10.7 % \pm 11.2 %), old mid- and high-stem orchards (4.4 % \pm 15.6 %), private gardens (2.7 % \pm 3.8 %), woody vegetation (1.8 % \pm 4.6 %), greenhouses (1.8 % \pm 4.1 %), marshes (1.3 % \pm 6.2 %), canals (1.2 % \pm 1.8 %), isolated buildings (0.7 % \pm 0.8 %), vineyards (0.6 % \pm 2 %) and fallows (0.5 % \pm 1.3 %). The most common fruit-tree cultures were

Table 1
Landscape scale and field scale explanatory variables used for statistical analyses of species richness, Shannon index of diversity and abundance for all species and per species and species group (landscape scale) and winter and spring for all species, per species and species group (field scale).

| Analyses | Covariate | Description | Model | Recording method | Details | |
|------------------|-------------------------------|--|--------------------------------------|---------------------------|--|----------------------|
| Landscape | fruitcult | % fruit-tree plantations | species richness, abundance | QGIS | Continuous; range 14.2–93.1; mean = 56.4 | |
| | grassland | % meadows and pastures | abundance | QGIS | Continuous; range 0–60.6; mean = 12.8 | |
| | cropcult | % crop cultures | species richness, abundance | QGIS | Continuous; range 0–51.8; mean = 10.7 | |
| | garden | % gardens | abundance | QGIS | Continuous; range 0–16.6; mean = 2.7 | |
| | oldorchards | % old mid-stem and high-stem orchards | – | QGIS | Continuous; range 0–68.8; mean = 4.4 | |
| | road | % roads and paved surfaces | – | QGIS | Continuous range 0.9–13.4 mean = 4.3 | |
| | woodveg | % woody vegetation: bushes, hedges, trees and forest | species richness, abundance, Shannon | QGIS | Continuous; range 0–28; mean = 1.8 | |
| | greenhouses | % greenhouses | – | QGIS | Continuous; range 0–16.8; mean = 1.8 | |
| | marsh | % marsh, reed bed and pond | – | QGIS | Continuous; range 0–38.2; mean = 1.3 | |
| | canal | % canals | species richness | QGIS | Continuous; range 0–7.4; mean = 1.2 | |
| | buildings | % buildings | species richness | QGIS | Continuous; range 0–4.2; mean = 0.7 | |
| | vineyards | % vineyards | – | QGIS | Continuous; range 0–11.1; mean = 0.6 | |
| | fallows | % fallows | – | QGIS | Continuous; range 0–4.5; mean = 0.5 | |
| | landscape heterogeneity index | Shannon index of the different land uses on the study areas | – | R | Continuous; range 0.3–1.5; mean = 1.1 | |
| | Field | observer | observer name | species richness, Shannon | measured in the field | factorial (2 levels) |
| | | season | season (winter, spring) | winter, spring | estimated in the field | factorial (2 levels) |
| vegheight | | vegetation height between tree rows [cm] | winter, spring | measured in the field | Continuous; range 0–70; mean = 15.2 | |
| vegcover | | % vegetation under tree rows | winter, spring | estimated in the field | Continuous; range 0–100; mean = 35.8 | |
| vegtree | | vegetation height under tree rows [cm] | – | measured in the field | Continuous; range 0–80; mean = 14.1 | |
| trunkdiam | | trunk diameter [cm] | winter, spring | measured in the field | Continuous; range 0–50; mean = 14.9 | |
| fruit | | 1 = <1 fruit / row 2 = 1 fruit / row to 1 fruit / tree 3 = >1 fruit / tree | winter | counted in the field | discrete | |

apple (27.8 % ± 15.4 %), apricot (11.7 % ± 10.7 %) and pear (8.7 % ± 8.8 %). Woody vegetation consisted of hedgerows, bushes, tall trees and forest patches. Crop cultures included mainly vegetables such as asparagus, strawberries, maize or cereals. Yet, urban areas and vineyard-dominated landscapes were avoided in study site selection. North-facing slopes were excluded because the agricultural system differs from the plain with almost exclusively apricot plantations, a broader elevation range, more forests and therefore different bird communities. Along all transects, parcels and landscape structures were mapped in the field and subsequently digitalized using QGIS (QGIS Development Team, 2017) a month ahead of the first surveys. Land use was specified for all surfaces, and connected fields of the same fruit-tree culture with similar management were grouped.

2.3. Bird survey protocol

Two observers with comparable skills in bird visual and acoustic identification conducted the surveys (28 transects by Y. Rime, 10 transects by C. Luisier). Two seasons were selected: in winter, two rounds of surveys were performed between the 1st of December and the 15th of February with the objective to focus on wintering birds, while avoiding migrants and breeders. In spring, three rounds were conducted between the 1st of April and the 15th of June, thus accounting for both breeding birds and migrants. Intra-seasonal survey repetition was necessary for an optimal detection of migratory and breeding species, with at least 10 days between two surveys at the same site. As the same bird species often occurred as migratory and breeding species in the study area without reliable criteria to divide the two categories, they were analysed grouped together for the spring session. In winter, surveys were performed from 09:00 to 15:30 when bird activity peaks and in order to avoid counting birds commuting to and from roosting sites at dawn and dusk (Myczko et al., 2013; Assandri et al., 2016; Guyot et al., 2017). In spring, surveys were carried out during the 5 h immediately following dawn (Brambilla et al., 2015; Assandri et al., 2016; Guyot et al., 2017) when birds are most active. Surveys only took place under appropriate weather conditions, i.e. in the absence of rain- or snowfall and strong wind. Surveys had a standard duration of 30 ± 10 min, allowing comparisons between different surveys (Bibby et al., 2000). All birds within 100 m from the transect were recorded on a printed map during the survey, if possible specifying age, sex, number of individuals as well as atlas code for breeding species. Sightings were recorded only in one direction (no sighting was recorded on the way back along the transect after the survey) to minimize the risk of double count (Guyot et al., 2017). Birds flying low over the site (< 100 m) were included. All observations were entered into the online platform ornitho.ch (www.ornitho.ch) as precise location for every observation, with a specific report list for each survey.

For all sitting birds, precise data were recorded at the first sight of each individual or group: parcel ID, behaviour (e.g. sitting on a tree, sitting on the ground), general type of culture (e.g. fruit-tree culture, crop culture) and precise type of culture (e.g. apricot, asparagus). In intensive fruit-tree cultures, more precise information was recorded at field scale directly at the end of the survey, considering the tree row where the bird was sitting. As traditional high-stem orchards are a different and very scarcely distributed habitat, the data collected in this habitat were not taken into account at field scale. We measured trunk diameter of fruit trees as well as mean vegetation height between and under tree rows. We also estimated percentages of vegetation and bare ground underneath tree rows and counted leftover fruit on the ground or on the trees. For each precise sighting within a fruit-tree plantation, a pseudo-absence point was generated at random in the previous field in walking direction along the transect line. For the pseudo-absence field, the same variables were measured as for the presence plantation. If there was no previous field available, the field located on the opposite side of the transect line was considered. When the same species also occurred in the previous field, the closest unoccupied field was defined

Table 2

Landscape scale and field scale ranked best models ($\Delta AICc < 2$) with degrees of freedom (Df), logLik, AICc, $\Delta AICc$ and model weights for species richness, Shannon Diversity Index and abundance for all species, Chaffinch, Tree Sparrow and insectivorous species (landscape scale) and in winter and spring for all species, Chaffinch and insectivorous species (field scale).

| Rank | Model | Df | logLik | AICc | $\Delta AICc$ | Model weight |
|------|--|----|-----------|--------|---------------|--------------|
| 1 | Landscape: species richness (glmer, Poisson) season + fruitcult + cropcult + marsh + woodveg | 7 | -511.267 | 1037.1 | 0.00 | 0.284 |
| 2 | season + fruitcult + cropcult + marsh + canal + woodveg | 8 | -510.717 | 1038.2 | 1.08 | 0.165 |
| 1 | Landscape: Shannon Diversity Index (lmer, Gaussian) season + woodveg | 5 | -83.377 | 177.1 | 0.00 | 0.996 |
| 1 | Landscape: abundance (glmer, Poisson) cropcult + fruitcult + garden + marsh + woodveg | 8 | -972.150 | 1961.1 | 0.00 | 0.086 |
| 2 | cropcult + garden + marsh + woodveg + grassland | 8 | -972.210 | 1961.2 | 0.12 | 0.081 |
| 3 | garden + marsh + woodveg + grassland | 7 | -973.374 | 1961.4 | 0.27 | 0.075 |
| 4 | cropcult + fruitcult + garden + woodveg | 7 | -973.512 | 1961.6 | 0.54 | 0.065 |
| 5 | garden + marsh + woodveg | 6 | -974.669 | 1961.8 | 0.70 | 0.060 |
| 6 | fruitcult + garden + marsh + natveg | 7 | -973.705 | 1962.0 | 0.93 | 0.054 |
| 7 | fruitcult + garden + marsh + woodveg | 7 | -973.784 | 1962.2 | 1.09 | 0.050 |
| 8 | cropcult + fruitcult + garden + marsh + woodveg + grassland | 9 | -971.703 | 1962.4 | 1.31 | 0.044 |
| 9 | cropcult + garden + woodveg + grassland | 7 | -974.132 | 1962.9 | 1.78 | 0.035 |
| 10 | cropcult + garden + woodveg | 6 | -975.225 | 1962.9 | 1.81 | 0.035 |
| 1 | Landscape: Chaffinch abundance (glmer, Poisson) season + fruitcult | 5 | -623.794 | 1257.9 | 0.00 | 0.997 |
| 1 | Landscape: Tree Sparrow abundance (glmer, Poisson) season + fruitcult | 5 | -658.978 | 1328.3 | 0.00 | 0.664 |
| 2 | season | 4 | -660.849 | 1329.9 | 1.63 | 0.294 |
| 1 | Landscape: insectivorous abundance (glmer, Poisson) cropcult + fruitcult + woodveg | 6 | -324.002 | 660.8 | 0.00 | 0.288 |
| 2 | cropcult + fruitcult + marsh + woodveg | 7 | -322.984 | 661.0 | 0.24 | 0.256 |
| 3 | canal + cropcult + fruitcult + woodveg | 7 | -323.756 | 662.6 | 1.78 | 0.118 |
| 1 | Field: winter all species (glmer, binomial) fruit + trunkdiam + vegcover | 5 | -419.605 | 849.3 | 0.00 | 0.326 |
| 2 | fruit + trunkdiam | 4 | -420.716 | 849.5 | 0.19 | 0.296 |
| 3 | fruit + trunkdiam + vegheight | 5 | -420.003 | 849.5 | 0.80 | 0.219 |
| 4 | fruit + trunkdiam + vegheight + vegcover | 6 | -419.313 | 850.8 | 1.45 | 0.158 |
| 1 | Field: spring all species (glmer, binomial) trunkdiam + vegheight + vegcover | 5 | -1447.901 | 2905.8 | 0.00 | 0.864 |
| 1 | Field: winter Chaffinch (glmer, binomial) fruit | 3 | -86.442 | 179.1 | 0.00 | 0.998 |
| 1 | Field: spring Chaffinch (glmer, binomial) trunkdiam + vegcover | 4 | -459.431 | 926.9 | 0.00 | 0.755 |
| 1 | Field: spring insectivorous (glmer, binomial) vegheight + trunkdiam + vegcover | 5 | -165.868 | 342.0 | 0.00 | 0.580 |
| 2 | vegheight + trunkdiam | 4 | -167.298 | 342.7 | 0.79 | 0.391 |

as a pseudo-absence.

2.4. Statistical analyses

Analyses were conducted in R version 3.5.1 (R Core Team, 2018) and operated separately at landscape and field scales. At landscape scale, models were built with species richness (number of species per survey), bird species diversity (Shannon Index) and abundance (total count of individuals per survey) as response variables (Assandri et al., 2016; Guyot et al., 2017). We also considered the abundance per species or species group, this for the two most abundant species, Tree Sparrow *Passer montanus* and Chaffinch *Fringilla coelebs* and that of all insectivorous species grouped together (supplementary material, Table S2). Our explanatory variables were the different proportions of land use on our study sites as well as Shannon Diversity Index for landscape heterogeneity, observer identity and season (Table 1). All percentage variables were arcsin-square-root transformed to give higher importance to small proportion values (Guyot et al., 2017). Continuous explanatory variables were standardized (mean = 0, standard deviation = 1). In order to account for quadratic effects, we used for all our explanatory variables the orthogonal linear and quadratic terms from the poly function (R Core Team, 2018). Transect ID was defined as a random factor to account for repeated counts.

In a first step, we ran univariate models to select significant variables ($p < 0.05$) that would be retained for the multivariate models. We tested for collinearity among explanatory variables using Spearman's

correlation coefficient. When variables were correlated with $|r_s| > 0.7$, only those variables with the lower AIC value in univariate models were kept (Sakamoto et al., 1986; Dormann et al., 2013). Shannon index for landscape heterogeneity was negatively correlated with the proportion of fruit-tree plantations ($r_s = -0.715$) and was therefore not retained as an explanatory variable in the models. The proportion of fruit-tree plantations was therefore considered here as a proxy for landscape homogeneity. In a second step, we retained the explanatory variables that were significant in the univariate models for multivariate modelling. For species richness and abundance, we ran generalized linear mixed effect models for count data with Poisson distribution using the function glmer, R package lme4 (Bates et al., 2015). We tested for overdispersion with the function dispersion_glmer, R package blmeo (Korner-Nievergelt et al., 2015) and whenever necessary controlled for it by adding an observation level random factor giving an ID to each sighting (Harrison, 2014). For the Shannon Diversity Index, we used linear mixed effect models with Gaussian distribution applying the function lmer, R package lme4 (Bates et al., 2015). We tested for interactions between the variables and no significant interaction was found as well as no observer effect. Study sites with high proportion values for the variables woody vegetation and marshes were retained in the analyses as they were essential to evaluate the importance of such natural habitats in a region where they are actually rare. Removing these potential outliers from the analyses did not affect the main results. Using the dredge function, R package MuMIn (Bartoń, 2018), we proceeded to a model selection based on the AIC corrected for small sample

Table 3
Landscape scale and field scale model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5 % confidence intervals (CI) for species richness, Shannon Diversity Index and abundance for all species, Chaffinch, Tree Sparrow and insectivorous species (landscape scale) and winter and spring for all species, Chaffinch and insectivorous species (field scale). Significant variables are in bold.

| Term | Estimate | SE | z or t value | 2.5 % CI | 97.5 % CI |
|---|----------|-------|--------------|----------|-----------|
| Landscape: species richness | | | | | |
| cropcult | -0.065 | 0.026 | 2.516 * | -0.116 | -0.014 |
| fruitcult | -0.051 | 0.025 | 2.039 * | -0.100 | -0.002 |
| marsh | 0.047 | 0.021 | 2.280 * | 0.007 | 0.088 |
| woodveg | 0.135 | 0.023 | 5.928 *** | 0.090 | 0.180 |
| season | 0.254 | 0.043 | 5.916 *** | 0.170 | 0.338 |
| canal | 0.026 | 0.025 | 1.041 | -0.023 | 0.075 |
| Landscape: Shannon Diversity Index | | | | | |
| season | 0.351 | 0.052 | 6.769 *** | 0.249 | 0.453 |
| woodveg | 0.149 | 0.031 | 4.801 *** | 0.088 | 0.209 |
| Landscape: abundance | | | | | |
| cropcult | -0.103 | 0.062 | 1.664 | -0.224 | 0.018 |
| fruitcult | -0.101 | 0.066 | 1.526 | -0.230 | 0.029 |
| garden | 0.148 | 0.057 | 2.578 ** | 0.036 | 0.261 |
| marsh | 0.110 | 0.058 | 1.882 | -0.005 | 0.225 |
| woodveg | 0.151 | 0.065 | 2.309 * | 0.023 | 0.279 |
| grassland | 0.094 | 0.063 | 1.475 | -0.031 | 0.218 |
| Landscape: Chaffinch abundance | | | | | |
| fruitcult | 0.361 | 0.096 | 3.744 *** | 0.173 | 0.553 |
| season | -0.901 | 0.189 | -4.763 *** | -1.275 | -0.528 |
| Landscape: Tree Sparrow abundance | | | | | |
| fruitcult | -0.370 | 0.185 | 1.984 * | -0.735 | -0.004 |
| saïson | 0.558 | 0.194 | 2.863 ** | 0.176 | 0.941 |
| Landscape: insectivorous abundance | | | | | |
| cropcult | -0.324 | 0.077 | 4.122 *** | -0.478 | -0.170 |
| fruitcult | -0.168 | 0.073 | 2.274 * | -0.312 | -0.023 |
| woodveg | 0.193 | 0.071 | 2.688 ** | 0.052 | 0.333 |
| marsh | 0.091 | 0.064 | 1.416 | -0.035 | 0.218 |
| canal | 0.052 | 0.074 | 0.694 | -0.094 | 0.197 |
| Field: winter all species | | | | | |
| fruit | 0.623 | 0.086 | 7.210 *** | 0.454 | 0.792 |
| trunkdiam | 0.345 | 0.088 | 3.900 *** | 0.172 | 0.518 |
| vegcover | 0.118 | 0.086 | 1.370 | -0.051 | 0.287 |
| vegheight | 0.161 | 0.163 | 0.984 | -0.160 | 0.482 |
| Field: spring all species | | | | | |
| vegheight | -0.110 | 0.046 | -2.392 * | -0.201 | -0.020 |
| vegcover | -0.169 | 0.048 | -3.519 *** | 0.329 | 0.513 |
| trunkdiam | 0.420 | 0.047 | 8.954 *** | -0.264 | -0.075 |
| Field: winter Chaffinch | | | | | |
| fruit | 0.686 | 0.191 | 3.583 *** | 0.322 | 1.078 |
| Field: spring Chaffinch | | | | | |
| vegcover | -0.164 | 0.080 | -2.058 * | 0.173 | 0.553 |
| trunkdiam | 0.480 | 0.084 | 5.685 *** | -1.275 | -0.528 |
| Field: spring insectivorous | | | | | |
| vegheight | -0.502 | 0.170 | 2.943 ** | -0.836 | -0.168 |
| trunkdiam | 0.612 | 0.150 | 4.055 *** | 0.316 | 0.907 |
| vegcover | -0.250 | 0.149 | 1.665 | -0.543 | 0.044 |

size (Sakamoto et al., 1986) and averaged the best models within delta AICc < 2 (Burnham and Anderson, 2003) with the model.avg function, R package MuMin (Bartoń, 2018).

At field scale, separate models were built for both seasons with bird occurrence probability as response variable (presence of an individual or group = 1, absence = 0) and the paired ID of the presence and pseudo-absence as random factor. We modelled field scale habitat preferences in intensively-managed fruit-tree plantations for all species

together, for Chaffinches and for insectivorous species. For these models, explanatory variables consisted of different management variables: vegetation height between tree rows, vegetation cover under tree rows, vegetation height under tree rows, trunk diameter, amount of leftover fruit (Table 1). All percentage variables were arcsin-square-root transformed to give higher importance to small proportion values (Guyot et al., 2017) and continuous explanatory variables were standardized (mean = 0, standard deviation = 1). We tested for quadratic effects of all our explanatory variables with the orthogonal linear and quadratic terms from the poly function (R Core Team, 2018). First, we ran univariate models and retained the significant variables ($p < 0.05$) for the multivariate analyses. The Spearman's correlation coefficient was used to test for collinearity following the same procedure as for the landscape scale. Correlations were found for vegetation height under tree rows and vegetation cover under tree rows ($r_s = 0.74$) and only the latter was retained. For the multivariate analyses, we ran generalized linear mixed effect models with binomial distribution using the function glmer, R package lme4 (Bates et al., 2015) and proceeded to the same model selection and averaging process as for the landscape scale. For all effect plots, we calculated 95 % Bayesian credible intervals, which accounted for random effects and were easier to calculate for mixed models compared to the frequentist confidence intervals, both being essentially equal given the flat priors we used with simulations of the function sim from the R package arm (Gelman et al., 2018).

3. Results

Our 38 study sites were distributed along a homogeneity gradient with a proportion of fruit-tree cultures ranging 14–93 %. The rest of agricultural land consisted of crop cultures and grassland. Cultivated fields were interspersed with semi-natural and artificial habitats including woody vegetation, marshes, gardens, buildings and greenhouses. During the five surveys, 5746 observations of 15'421 individuals belonging to 106 bird species were recorded (supplementary material, Table S2); 56 species were counted in winter and 98 in spring. The most abundant species overall were Tree Sparrow ($n = 2'631$), Chaffinch ($n = 2'524$), Blackbird *Turdus merula* ($n = 1'384$), House Sparrow *Passer domesticus* ($n = 1'215$) and Starling *Sturnus vulgaris* ($n = 945$). In winter the most abundant species were Chaffinch ($n = 1'748$), Tree Sparrow ($n = 1'289$), Blackbird ($n = 895$), Alpine Chough *Pyrrhocorax graculus* ($n = 721$), House Sparrow ($n = 452$) and Fieldfare *Turdus pilaris* ($n = 352$). In spring the most recorded species were Tree Sparrow ($n = 1'342$), Starling ($n = 936$), Chaffinch ($n = 776$), House Sparrow ($n = 763$), Blackbird ($n = 489$) and Magpie *Pica pica* ($n = 302$).

3.1. Landscape scale habitat preferences

Our results highlight the detrimental effects of homogenous fruit-tree plantation landscapes on bird diversity and the beneficial effects of woody vegetation on bird abundance and diversity, even with a small proportion of cover. The mean (\pm standard deviation) number of birds per transect was 76.6 ± 72 individuals for both seasons, 90.7 ± 98 individuals in winter and 67.2 ± 46 individuals in spring. The mean number of species per transect was 12.9 ± 5 during both seasons, 11 ± 4 in winter and 14.1 ± 5 in spring. The best model for species richness (Table 2) included a strong effect of season, a linear negative effect of crop cultures and fruit-tree cultures and a linear positive effect of woody vegetation (bushes, hedgerows, trees and forest patches) and marshes (Table 3, Fig. 1). The mean Shannon index of diversity was 1.9 ± 0.4 , ranging from 0 to 3. The best model for this index (Table 2) contained only the effect of season with higher values in spring and a linear positive effect of woody vegetation (Table 3, Fig. 2). The best model for abundance (Table 2) comprised linear positive effects of private gardens and natural woody vegetation (Table 3, Fig. 3). Crop cultures had a marginally significant negative effect and fruit-tree

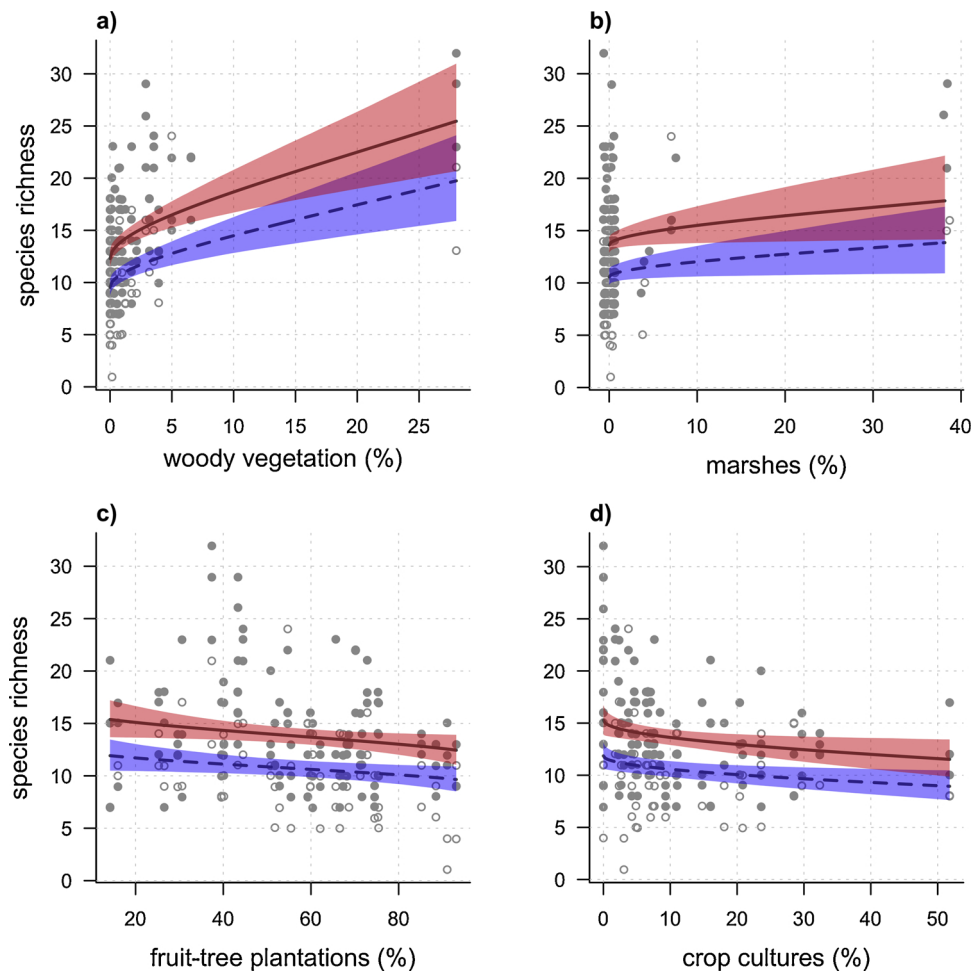


Fig. 1. Landscape scale model-averaged predictions from Poisson regression models for **species richness** in winter (dashed line) and spring (solid line) with 95 %–Bayesian credible intervals (blue areas for winter, red areas for spring) for a) woody vegetation, b) marshes, c) fruit-tree cultures and d) crop cultures. Grey dots show raw data for spring and empty dots show raw data for winter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

culture proportion was not significant in the best model for abundance.

37 insectivorous bird species were recorded in spring, with 8.1 ± 9 individuals per transect. The best model for insectivorous species (Table 2) included a linear negative effect of crop cultures and fruit-tree plantations and a linear positive effect of natural woody vegetation (Table 3, Fig. 4). Chaffinch was the second most abundant species with 13.2 ± 29 individuals overall, on average, per transect, 23 ± 39 individuals in winter and 6.8 ± 18 in spring. The species was recorded at 91 % of the surveys and seen on all 38 transects. In the best model (Table 2), fruit-tree cultures had a linear positive effect and season also had a significant effect with a higher abundance in winter (Table 3, Fig. 5). Tree Sparrow was the most abundant species with 13.9 ± 22 individuals per transect, on average, during both seasons, 17 ± 32 in winter and 11.8 ± 11 in spring. In the best model (Table 2), fruit-tree cultures had a negative effect and season was significant with a positive effect of spring (Table 3, Fig. 5). Even if the overall abundance was higher in winter, with big groups on some transects, the species was more widespread in spring (median in winter = 2 individuals, median in spring = 9 individuals).

3.2. Field scale habitat preferences

Our findings underpin a preference of the avifauna for fruit-tree plantations with thicker diameter of the fruit-tree trunks, for plantations with high amounts of left over fruit in winter and for low and

sparse ground vegetation in spring. 1'330 presence points of 51 species recorded at field scale in intensive fruit-tree cultures were retained for the analyses. Chaffinch ($n = 413$ observations) and Blackbird ($n = 274$) were the most recorded species within fruit-tree culture fields. Analyses for winter were based on 333 presence points. If the best general model for all species combined (Table 2) points to a linear positive effect of leftover fruit and fruit-tree trunk diameter, no significant effect was found for the height of the ground vegetation, neither in the inter tree-row nor under the tree rows (Table 3, Fig. 6). The analyses for spring were based on 997 presence points. The best general model for all species together (Table 2) included linear negative effects of the height of the vegetation in the inter-tree rows and of the percentage of ground vegetation cover under the tree-rows themselves, as well as, again, a linear positive effect of fruit-tree trunk diameter (Table 3, Fig. 7). Only 18 insectivorous bird species were recorded in spring within fruit-tree culture fields. In the best model (Table 2; Fig. S3, supplementary material), the height of the vegetation in the inter-tree rows had a linear negative effect while the diameter of the fruit-tree trunk had a linear positive effect (Table 3). In the best model for Chaffinches in winter (Table 2), leftover fruit had a linear positive effect (Table 3). The best model for that species in spring (Table 2) comprised a linear negative effect of vegetation cover under the fruit-tree rows and a linear positive effect of fruit-tree trunk diameter (Table 3; Fig. S4, supplementary material).

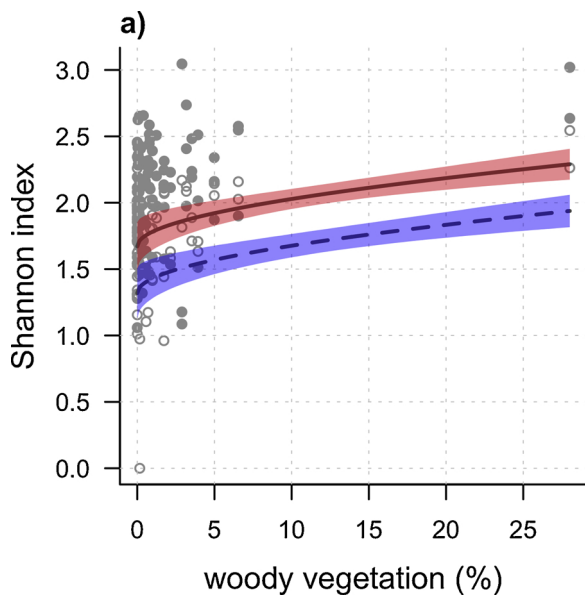


Fig. 2. Landscape scale model-averaged predictions from Gaussian regression models for **Shannon Diversity Index** for all bird species in winter (dashed line) and spring (solid line) with 95 %–Bayesian credible intervals (blue area for winter, red area for spring) for a) woody vegetation. Grey dots show raw data for spring and empty dots show raw data for winter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

4. Discussion

This study shows the importance of both habitat heterogeneity and fruit-tree plantation management practices, at landscape scale and field scale, respectively, for the assembly and fine-grained habitat selection of bird communities inhabiting that agro-ecosystem. It also establishes inter-seasonal differences in landscape and habitat use by the birds, emphasizing the negative effects that homogenous fruit-tree cultures have upon the avifauna, while semi-natural structures such as woody vegetation and marshes exert positive effects. Finally, our results show a clear preference of birds for fruit-tree plantations with older trees (thicker trunks) and low and sparse ground vegetation. These findings underline the potential for improvement of ecological conditions for the avifauna, which could be achieved through appropriate landscape planning and adapted management of the fruit-tree plantations.

Habitat heterogeneity, a key factor to enhance biodiversity in farmland in general (Benton et al., 2003; Fahrig et al., 2011; Vickery and Arlettaz, 2012), thus also plays a pivotal role for bird communities

in fruit-tree plantations. As Shannon Index for landscape heterogeneity was here negatively collinear with the proportion of intensively-managed fruit-tree cultures, we considered the latter as a good proxy for habitat homogeneity. An increased cover of intensively-managed fruit-tree cultures had negative effects on overall species richness, congruent with previous evidence on the deleterious effects of landscape homogeneity for bird diversity in other permanent cultures like vineyards (Assandri et al., 2016; Guyot et al., 2017). The abundance of insectivorous birds in our study was also negatively affected by landscape homogeneity. Surprisingly, however, diverging effects were found between the most common bird species. If chaffinches benefitted from homogeneous fruit-tree cultures, Tree Sparrows were negatively impacted. The former is a generalist species that builds its own nest in tree foliage (Glutz Von Blotzheim et al., 1966; Mouysset et al., 2011), which might enable it to use any perennial culture where inter-specific competition is low: similar results were obtained in tree-like pergola vineyards in Italy (Assandri et al., 2017a, c). Tree sparrow avoided homogeneous fruit-tree plantations, even though its density is fairly high in the central Valais lowlands with more than 20 pairs/km² (Knaus et al., 2018). The reason could be that this secondary cavity nester is more limited than the Chaffinch by breeding opportunities (nest boxes and buildings). Yet, habitat heterogeneity at landscape scale depends not only on the proportion of fruit-tree cultures, but also on the presence and arrangement of other types of habitat in the wider landscape (Devictor and Jiguet, 2007; Fahrig et al., 2011). Thus, other types of crops, cultivated grasslands and semi-natural habitats in the surroundings of fruit-tree cultures also contributed to overall habitat heterogeneity, influencing our bird communities, as is commonly observed in other sorts of agro-ecosystems (Fischer and Lindenmayer, 2007; Doxa et al., 2012). Natural woody vegetation cover such as isolated trees, hedgerows and forest patches all had positive effects on bird species richness, diversity (Shannon index) and abundance. Similar effects of bushes, hedgerows and trees were found in vineyard ecosystems (Assandri et al., 2016; Guyot et al., 2017). These natural structures offer nesting sites, perches, shelter and food to a broad variety of farmland birds (Batáry et al., 2010), e.g. declining species like the Red-Backed Shrike (Brambilla et al., 2007; Ceresa et al., 2012). However, general bird abundance was positively affected not only by natural woody elements but also by private gardens, which are small and interspersed among fruit-tree plantations and other crops. Although open fields within the fruit-tree plantations matrix might contribute to landscape heterogeneity, no effect on birds was detected for grassland whilst crops had a negative effect on overall species richness and insectivorous bird abundance. The latter can be explained by the quasi absence of vegetation except the target crop plant, i.e. a primary productivity directed exclusively to agricultural production, with thus limited support for the development of diversified arthropod prey for the birds. In a landscape

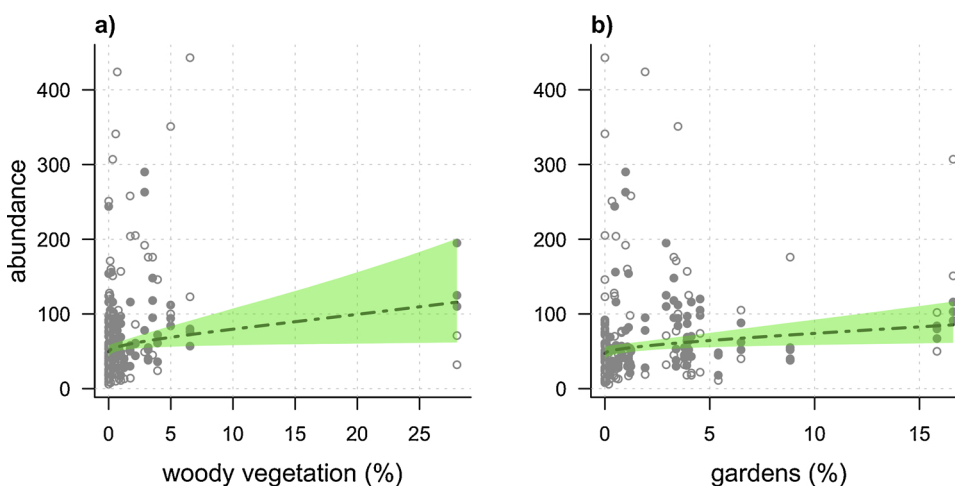


Fig. 3. Landscape scale model-averaged predictions from Poisson regression models for **all species abundance** winter and spring together with 95 %–Bayesian credible intervals (green areas) for a) woody vegetation and b) gardens. Grey dots show raw data for spring and empty dots show raw data for winter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

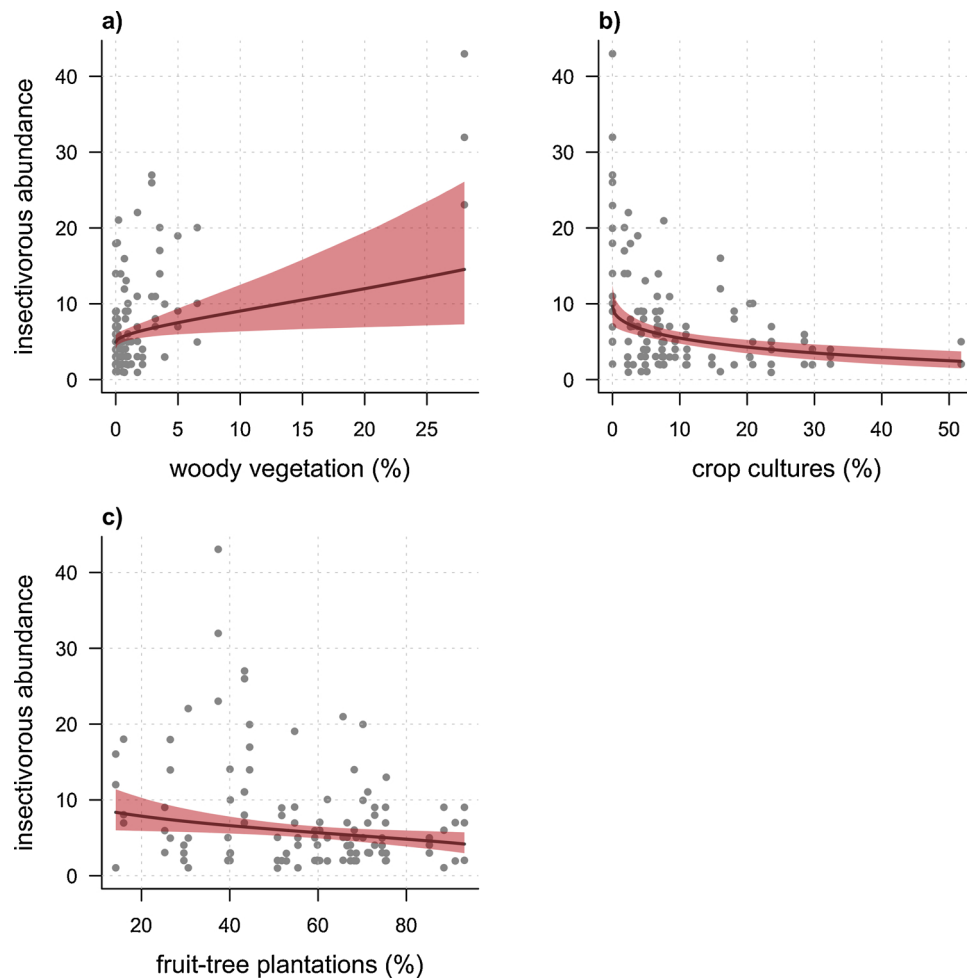


Fig. 4. Landscape scale model-averaged predictions from Poisson regression models for **insectivorous bird species abundance** in spring with 95%–Bayesian credible intervals (red areas) for a) woody vegetation, b) crop cultures and c) fruit-tree plantations. Grey dots show raw data. One data point with abundance over 43 individuals is not shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

such as ours where a regular application of pesticides upon all types of cultures is likely to greatly affect arthropod communities (Suckling et al., 1999; Epstein et al., 2000), natural woody vegetation elements may well represent unique food sources for many species of insectivorous birds. As a matter of fact, the latter were dramatically scarcely distributed in our study area. Marshes also contributed to enhance species richness on our study sites, sometimes harbouring species of high conservation concern in Switzerland. Marshes and natural woody vegetation communities are composed of either wetland or farmland and woodland species (Fuller et al., 2001; Devictor and Jiguet, 2007; Doxa et al., 2012), underlining the value of both these habitats for bird diversity (Chamberlain and Wilson, 2000; Doxa et al., 2010). All in all, our results confirm the importance of natural elements and habitats in the farmed landscape for promoting general bird abundance and diversity.

That bird communities and habitat use vary seasonally in fruit-tree plantations has been established in other types of permanent cultures, notably vineyards (Assandri et al., 2016; Guyot et al., 2017). Foraging conditions in winter rule the survival of overwintering and sedentary bird species, which often gather in large mixed-species flocks essentially focused on acquiring food (Skorka et al., 2006; Myczko et al., 2013). In contrast, in spring, priority is breeding: they thus become territorial and less mobile (Vickery and Arlettaz, 2012; Guyot et al., 2017). As most indigenous migratory species are in their winter quarters during the cold season, bird species richness and diversity within fruit-tree plantations were significantly higher in spring. If the average

number of individuals recorded was higher in winter than in spring, the occurrence of big groups in winter was fairly sporadic, with a large variation in numbers that is likely to explain why the abundance model did not include any seasonal effect. Seasonal comparative studies about bird communities in fruit-tree cultures are missing, nonetheless our results are consistent with the findings of Assandri et al. (2016) in vineyards in northern Italy. Note that no interaction was found between season and any other explanatory variables, meaning that the above respective importance of the different habitats remains constant from winter to spring.

The understanding of species-habitat associations of birds inhabiting intensively-managed fruit-tree cultures at both landscape and field scale allows the definition of conservation priorities not only for improving landscape planning but also for a more bird-friendly management of fruit-tree plantations. At field scale, preferences were driven by the age of plantations as well as food availability, the latter being abundance modified by accessibility. In both winter and spring, trunk diameter had a positive effect on field selection for bird species in general, and more specifically for Chaffinches, Tree Sparrows and insectivorous birds. This general preference for a habitat with older trees and a generally denser foliage might be due to the availability of breeding sites (Assandri et al., 2017b) and a higher arthropod abundance (Wiacek and Polak, 2008; Myczko et al., 2013), as demonstrated for Wrynecks in old pear plantations in our study area (Mermod et al., 2009). A first straightforward conservation measure for sustaining the fruit-tree bird community would therefore be to delay the replacement

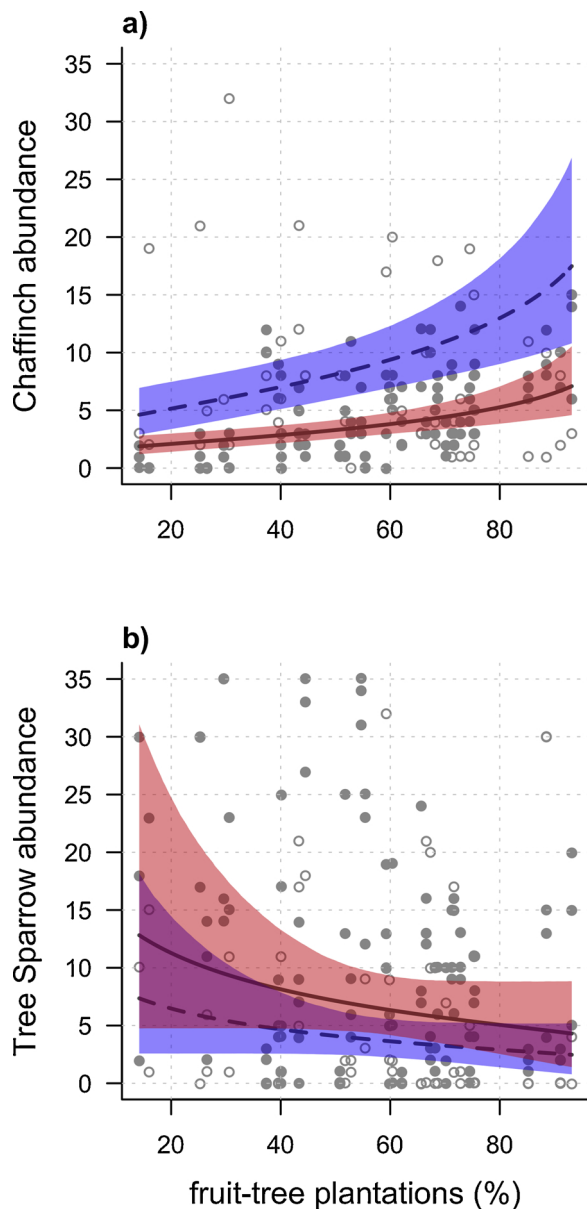


Fig. 5. Landscape scale model-averaged predictions from Poisson regression models for a) Chaffinch abundance and b) Tree Sparrow abundance in winter (dashed line) and spring (solid line) with 95%–Bayesian credible intervals (blue areas for winter and red areas for spring) for fruit-tree plantations. Grey dots show raw data for spring and empty dots show raw data for winter. Data points with abundance over 35 individuals are not shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

of old plantations as long as possible. In this respect, one should halt the conversion and destruction of the last traditional orchards, with new financial incentives for farmers to maintain them.

Foraging habitat preferences varied seasonally: in winter, field selection was driven by the presence of leftover fruit, attracting groups of fruit-eating birds, e.g. Blackbird, Fieldfare and Eurasian Jay *Garrulus glandarius*. Leaving fruit without commercial interest on the trees at harvest and disposing plucked fruit wastes on plantation ground during the cold season will provide a sustainable food resource for fruit-eating birds. In spring, a high or dense ground vegetation cover diminishes food availability for ground-feeding birds like the Common Redstart *Phoenicurus phoenicurus* (Martinez et al., 2010; Assandri et al., 2017b), which explains the preference for inter-tree rows with short sward and

scarce ground vegetation below the fruit trees, where predation risk might also be lower than where ground vegetation is dense (Moorcroft et al., 2002; Butler et al., 2005; Whittingham et al., 2006). Sparse vegetation cover providing patches of bare ground under trees particularly attracted Chaffinches, a typical ground forager. Patches of bare ground have been shown to be the main driver of foraging micro-habitat selection in several rare species of ground-feeding insectivorous birds inhabiting fruit-tree cultures such as Common Redstart, Hoopoe and Wryneck (Martinez et al., 2010; Schaub et al., 2010; Weissshaup et al., 2011; Tagmann-Ioset et al., 2012). However, weed and flower strips as well as hay flower-rich meadows are known to increase plant and arthropod diversity and abundance in farmland, with positive effects scaling up the food chain up to insectivores and even carnivorous predators (Wyss, 1996; Pfiffner et al., 2019), including species delivering pest control services (Rieux et al., 1999; Bostanian et al., 2004; Arlettaz et al., 2010a). This again stresses the necessity of providing refuges for flora and fauna in the form of tall ground vegetation areas or strips, within or adjacent to the cultivated fields, which are mown later in the season as shown for other agro-ecosystems (Buri et al., 2013, 2014; Bruppacher et al., 2016; Buri et al., 2016). The case of fruit-tree plantations is comparable to that of vineyards as cultivated plants are arranged in rows. As demonstrated for vineyard birds, alternating ground vegetation management between the inter-rows (Arlettaz et al., 2012) may represent an optimal solution for fruit-tree plantations as well: the densely vegetated inter-row offers shelter and resources for arthropods while the next short-grass or bare inter-row provides access to those prey for ground-foraging birds that avoid dense swards. A similar system could be implemented in fruit-tree plantations for the sake of biodiversity.

Not only plantation management but also landscape composition has a tremendous impact on the bird communities inhabiting areas where intensively-managed fruit-tree cultures dominate farmland. Our findings thus highlight the potential of implementing measures at the wider landscape scale to further promote the avifauna. Based on our results, landscape conservation planning should focus, first, on increasing habitat heterogeneity by preserving bushes, hedgerows, isolated trees and forest patches and re-instating such natural elements within the fruit-tree culture matrix. Second, wetlands have a positive effect on species richness and host several red-listed wetland species increasing local diversity: we thus advise to protect, restore and create ponds and marshes of sufficient size in the valley bottom, and to let the riparian vegetation of canals and ditches grow with management once a year or every second year but never in spring or summer during the breeding season. Third, as private gardens contribute to increase bird abundance, we recommend to promote their extensive management, which optimally consists of planting indigenous bushes and high-stem fruit trees and relying as little as possible on chemical applications to preserve insect populations. In that perspective, spatially combining natural woody elements, wetlands and nearby private gardens might further boost their beneficial effects for biodiversity.

First assessments, notably intense discussions with local arboriculturists and regional authorities, have showed that more extensive farming practices are particularly difficult to implement in conventional commercial fruit-tree cultures. This calls for landscape and in situ measures that offer the most optimal cost-efficiency ratios. This study paves the way towards an evidence-based catalogue of measures that may make a real difference for bird communities in that particular agro-ecosystem.

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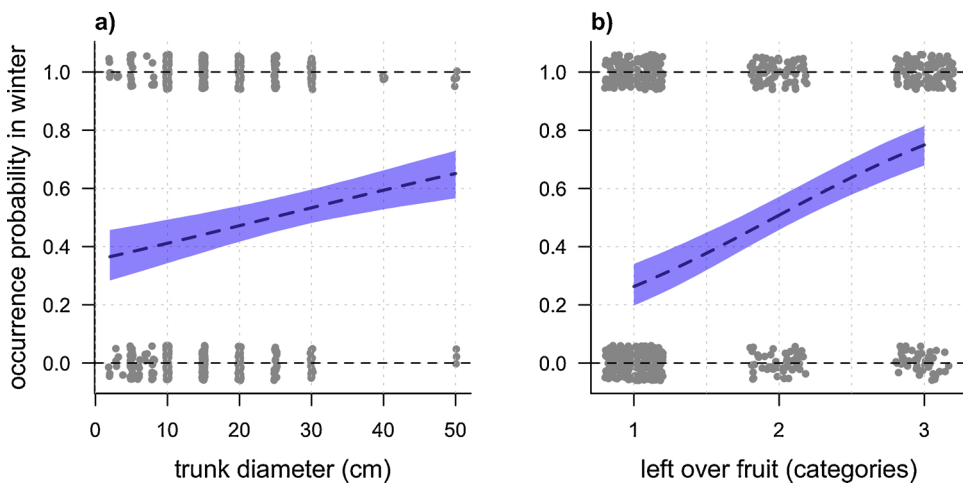


Fig. 6. Field scale model-averaged predictions from binomial regression models for **all species occurrence probability** in winter with 95%-Bayesian credible intervals (blue areas) for a) trunk diameter and b) left over fruit (1 = <1 per row, 2 = 1 per row - 1 per tree, 3 = >1 per tree). Grey dots show raw data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

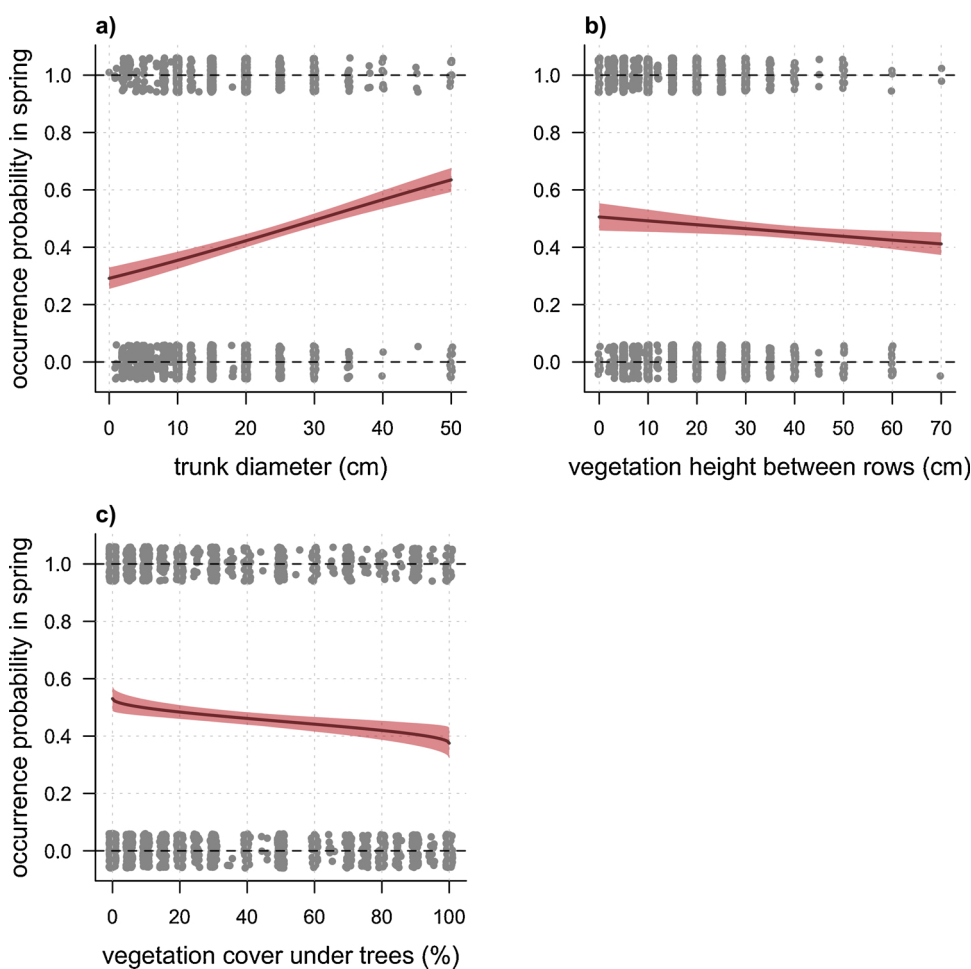


Fig. 7. Field scale model-averaged predictions from binomial regression models for **all species occurrence probability** in spring with 95%-Bayesian credible intervals (red areas) for a) trunk diameter, b) height of the vegetation in the inter-tree row and c) vegetation cover under the trees. Grey dots show raw data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.106890>.

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