Habitat preferences of wintering and breeding birds in intensively managed fruit tree plantations

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Habitat preferences of wintering and breeding birds in intensively managed fruit tree plantations

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Abstract

Intensively managed fruit tree cultures 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 by few open fields, urban areas and semi-natural structures. This observational study investigated the patterns driving landscape and field scale habitat preferences of birds in landscape units with varying fractions of fruit tree cultures. At landscape scale, habitat homogeneity, notably an increasing proportion of fruit tree cultures, 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 marshes and woody structures (hedges, isolated trees and forest patches), 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 in both seasons. In winter, leftover fruit is a crucial resource driving field selection. In spring, preferences for low and sparse ground vegetation were best explained by increased food accessibility for terrestrially foraging birds. Both landscape habitat heterogeneity and field management matter to enhance conditions for birds in this agro-ecosystem. Increasing the proportion of diverse semi-natural structures will promote wintering and breeding bird diversity and abundance. At field scale, conditions for birds can be improved by preserving old orchards and by maintaining bare ground patches and strips of low vegetation. However, given the current high-intensity management of fruit tree cultures at the study sites it is likely that measures for promoting natural features within the wider landscape matrix will be more cost-effective to enhance bird diversity and abundance.

Keywords

Intensive fruit tree cultures, landscape scale, field scale, bird communities, habitat preferences, habitat heterogeneity

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, Vickery & Norris 2007), which is mainly due to the loss of semi-natural habitats and an increase in habitat homogeneity (Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2005; Fahrig *et al.* 2011). Bird communities are particularly concerned, with massive declines in the populations of many farmland species (Tucker & Heath 1994; Chamberlain *et al.* 2000; Donald, Green & Heath 2001). 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 large intensively managed plantations of low-stem trees (Werth 1980).

Traditional orchards harbour high biodiversity through the combination of extensive grassland and perennial deciduous trees thereby supplying various structures and resources (Herzog 1998; Simon *et al.* 2010). In particular, old fruit trees with high amounts of dead wood offer breeding sites, perches and arthropods (Bailey *et al.* 2010; Vickery & Arlettaz 2012; Grüebler *et al.* 2013) whereas grasslands provide invertebrates, an important food resource for birds (Horak *et al.* 2013; Brambilla *et al.* 2015). These were prime habitats for insectivorous and cavity-breeding species that are nowadays threatened, leading for example to the extinction of the Woodchat Shrike *Lanius senator* in Switzerland (Keller *et al.* 2010; Knaus *et al.* 2011). Furthermore, habitat fragmentation and isolation are relevant problems for birds and other organisms in remaining traditional orchards (Bailey *et al.* 2010).

Intensive fruit tree cultures offer a very simplified habitat compared to traditional orchards. Vegetation is regularly cut between tree rows and treated with herbicides beneath the trees. In addition, plantations are systematically sprayed with insecticides and fungicides with more than 35 treatments per year in French apple cultures (Simon *et al.* 2010), reducing the reproductive success of nesting birds in orchards (Fluetsch & Sparling 1994; Bishop *et al.* 2000) and decreasing arthropod abundance (Suckling, Walker & Wearing 1999; Brown & Schmitt 2001; Simon, Defrance & Sauphanor 2007). The absence of chemical treatment explains the positive effects of organic orchard management for birds (Genghini, Gellini & Gustin 2006; Bouvier *et al.* 2011; MacLeod, Blackwell & Benge 2012). In intensive perennial cultures such as vineyards and fruit cultures, targeted conservation strategies 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 cultures are very homogenous and intensively managed, they provide a structured woody habitat in an open agricultural landscape, which is favourable for a broad range of species related to forest edges and open woodland (Wiacek & Polak 2008; Myczko *et al.* 2013; Brambilla *et al.* 2015), including endangered species such as Eurasian Hoopoe *Upupa epops* and Eurasian Wryneck *Jynx torquilla* (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 & Visser 2002; Mols, van Noordwijk & Visser 2005). Investigating habitat preferences of birds in fruit tree cultures is a first step before planning evidence-based conservation strategies (Arlettaz *et al.* 2010).

Habitat selection is driven by different spatial and temporal parameters. Both landscape scale (surrounding of fruit cultures) and field scale (within fruit cultures) spatial habitat criteria are relevant for conservation (Vickery & Arlettaz 2012; Gonthier *et al.* 2014). On a landscape level, availability of breeding sites, semi-natural structures and landscape heterogeneity are key for enhancing bird diversity, which has been shown for both vineyards (Assandri *et al.* 2016; Guyot *et al.* 2017) and fruit cultures (Brambilla *et al.* 2015; Assandri *et al.* 2017). At field scale, habitat selection often depends largely on foraging preferences influenced by vegetation structure and food accessibility (Vickery & Arlettaz 2012). Understanding species-specific and general preferences is essential to promote biodiversity-friendly management practices along the annual cycle. Bare ground patches are beneficial for insectivorous breeders, e.g. Hoopoe (Tagmann-Ioset *et al.* 2012) and Wryneck (Schaub *et al.* 2010; Weisshaupt *et al.* 2011) through an increase in food accessibility. Tree age (Wiacek & Polak 2008), tree height (Brambilla *et al.* 2015) and tree density (Myczko *et al.* 2013) also influence field scale habitat selection in traditional or intensive orchards. Furthermore, seasonality influences temporal bird assemblage and habitat use in permanent cultures like vineyards (Assandri *et al.* 2016; Guyot *et al.* 2017). Similar patterns are expected in fruit cultures with mobile mixed species-groups in winter and more territorial breeding pairs or colonies in spring (Wiacek & Polak 2008; Myczko *et al.* 2013). Responses to landscape characteristics are species-specific: for example, an increased proportion of hedgerows might be beneficial for structured land species like Red-Backed Shrike *Lanius collurio* (Brambilla, Rubolini & Guidali 2007; Ceresa et al. 2012), but detrimental for open land species such as Skylark (Hinsley & Bellamy 2000), both being of conservation concern in agricultural land.

Here we conduct an observational study in a landscape dominated by intensive fruit tree cultures, to highlight which habitat features influence bird communities. By accounting for fine-scaled variation in management practices, landscape composition and their seasonal effects, our study aims at providing detailed recommendations for biodiversity-promoting management in intensively managed fruit tree plantations.

Material and methods

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 section at an elevation of 455 m to 520 m above the sea level. The climate of this intra-alpine valley is characterized by continental influences with high temperatures and low precipitation in summer and relatively cold temperatures and low precipitation in winter. On south-exposed slopes, vineyards are the dominant culture, while on north-facing slopes apricots plantations prevail, interspersed by forests, open meadows and pastures. The valley bottom is dominated by intensive agriculture and human settlements. Fruit cultures are the main cultivation, intersected with meadows, pastures and diverse crop cultures within a dense network of roads and tracks.

Study design

38 linear transects of 400 m length each surrounded by a 100 m buffer (table S1) were regularly scattered in the valley bottom with a minimal distance of 500 m between 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 in the perpendicular tree rows. We selected the sites according to a heterogeneity gradient based on the percentage of fruit culture coverage from 14% to 93% (table S1, fig. S7). Remaining areas consisted of woody vegetation (mean ± standard deviation = 1.8% ± 4.6%), marshes (1.3% ± 6.2%), crop cultures (10.7% ± 11.2%), grassland (12.8% ± 14.6%), vineyards (0.6% ± 2%), gardens (2.7% ± 3.8%), fallows (0.5% ± 1.3%), canals (1.2% ± 1.8%), greenhouses (1.8% ± 4.1%) and buildings (0.7% ± 0.8%). The most common fruit cultures were apple (27.8% ± 15.4%), apricot (11.7% ± 10.7%) and pear (8.7% ± 8.8%). Woody vegetation consisted of hedges, bushes, tall trees and forest patches. Crop cultures included mainly vegetables, asparagus, strawberries, maize or cereals. Hay meadows and pastures were both considered as grassland. Urban areas and vineyard-dominated landscapes were avoided. North-facing slopes were excluded because the agricultural system differs from the plain with only apricot plantations, a broader elevation range, more forests and therefore different bird communities. On each study site, all parcels and landscape structures were mapped in the field and 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 culture with similar management were grouped.

Bird survey protocol

Two observers with equivalent knowledge in bird visual and acoustic identification carried out the surveys (28 transects by Y. Rime, 10 transects by C. Luisier). Two time windows were selected: in winter, two rounds were performed between the 1st of December and the 15th of February to consider only wintering birds but avoiding migrants or breeders. In spring, three rounds were conducted between the 1st of April and the 15th of June to account for breeding birds and migrants. Transects were surveyed twice in winter and three times in spring to allow for an optimal detection of migratory and breeding species, with at least ten days between two censuses on the same site. In winter, censuses were performed from 09:00 to 15:30 while activity is high, in order to avoid counting birds commuting to and from roosting sites after dawn or before dusk (Myczko *et al.* 2013; Assandri *et al.* 2016; Guyot *et al.* 2017). In spring, surveys were carried out during the five hours 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 without rain, snow or strong wind. Censuses had a standard duration of 30 ± 10 minutes allowing comparison between different surveys (Bibby *et al.* 2000). All birds within 100 m from the transect were recorded on a printed map, if possible specifying age, sex, number of individuals as well as atlas code for breeding species. Sightings were recorded only in one direction to minimize the risk of double count (Guyot *et al.* 2017), including birds flying low over the site (<100 m). All observations were entered in ornitho.ch (www.ornitho.ch) as precise location data within an observation list for each survey.

For all sitting birds, precise data were recorded at the first sight of each individual or group: parcel number, 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 cultures, more precise information was recorded at field scale considering the tree row where the bird was sitting. As traditional high-stem orchards are a different and scarcely distributed habitat, these data were not taken into account. We measured trunk diameter 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 field, a pseudo-absence point was recorded 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. 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 as a pseudo-absence.

Statistical analyses

Analyses were conducted in R version 3.5.1 (R Core Team 2018) and divided between landscape and field scale. For both parts, we used the Spearman's correlation coefficient to test for collinearity among explanatory variables. When variables were correlated with $|r_s| > 0.7$, only those variables with the lower AIC value in univariate models were kept (Sakamoto, Ishiguro & Kitagawa 1986; Dormann *et al.* 2013). 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). We tested for quadratic effects using orthogonal linear and quadratic terms from the poly function (R Core Team 2018), as well as for interactions between explanatory variables. Explanatory variables significant ($p < 0.05$) or marginally significant ($p < 0.1$) in the univariate analyses were retained for multivariate modelling. Marginally significant variables were excluded if still not significant in the multivariate model. Using the *dredge* function, R package *MuMIn* (Bartoń 2018), we proceeded to a model selection based on the AIC corrected for small sample size (Sakamoto, Ishiguro & Kitagawa 1986) and averaged the best models within delta AICc < 2 (Burnham & Anderson 2003) with the *model.avg* function, R package *MuMIn* (Bartoń 2018).

At landscape scale, models were built with species richness (number of species per survey), Shannon Diversity Index for bird species and abundance (total count of individuals per survey) as response variables (Assandri *et al.* 2016; Guyot *et al.* 2017). We also looked at abundance per species or species group for the two most common species and a relevant trait-specific group based on insectivorous diet. As explanatory variables, different proportions of cultures, landscape structures as well as observer, season, time after dawn and Shannon Diversity Index for landscape heterogeneity were used (table 1). Transect ID was defined as random factor to account for repeated counts. 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 over-dispersion with the function *dispersion_glmer*, R package *blmeco* (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 Shannon Diversity Index, we used linear mixed effect models with Gaussian distribution applying the function *lmer*, R package *lme4* (Bates *et al.* 2015). No observer effect was detected at landscape scale as well as no interaction regarding season and any other explanatory variable. Shannon Diversity Index for landscape heterogeneity was correlated with the proportion of fruit cultures ($r_s = -0.715$), and was therefore not retained as an explanatory variable in the models. Proportion of fruit cultures is considered here as a measure of landscape homogeneity.

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 presence-absence ID as random factor. We modelled field scale habitat preferences in intensive fruit cultures for all species and per species or species group. For these models, explanatory variables consisted of different management variables (table 2). We ran generalized linear mixed effect models with binomial distribution using the function *glmer*, R package *lme4* (Bates *et al.* 2015).

Results

Our 38 study sites were distributed along a homogeneity gradient based on fruit culture proportion from 14% to 93%. The rest of agricultural land consisted of crop cultures (0% to 52%) and grassland (0% to 60.6%). Cultivated fields were intersected with semi-natural and artificial habitats including woody vegetation (0% to 28%), marshes (0% to 38%), gardens (0% to 16.6%), buildings (0% to 4.2%) and greenhouses (0% to 4.1%). During the five survey sessions, 5'746 observations of 15'421 individuals of 106 species were recorded (table S2). 56 species were counted in winter and 98 in spring. The most common species were Tree Sparrow *Passer montanus* (n = 2'631), Chaffinch *Fringilla coelebs* (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).

Landscape scale habitat preferences

Our results highlight the detrimental effects of homogenous fruit culture 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 ± standard deviation number of birds per survey was 76.6 ± 72.3 individuals for both seasons, 90.7 ± 97.7 individuals in winter and 67.2 ± 46.6 individuals in spring. The best model for abundance (table 3) comprised linear positive effects of gardens and woody vegetation (table 7, fig. 3). Crop cultures had a marginally significant negative effect and fruit culture proportion was not significant in the best model. The number of species per survey was 12.9 ± 5.1 during both seasons, 11 ± 4.4 in winter and 14.1 ± 5.1 in spring. The best model for species richness (table 3) included a linear negative effect of crop cultures and fruit cultures and a linear positive effect of woody vegetation (bushes, hedges, trees and forest patches) and marshes (table 7, fig. 1). Season had a strong effect with higher species richness in spring. The mean of Shannon Diversity

Index was 1.9 ± 0.4, with a range from 0 to 3. The best model for Shannon Diversity Index (table 3) contained only the effect of season with higher Shannon Diversity Index in spring and a linear positive effect of woody vegetation (table 7, fig. 2).

37 insectivorous bird species were recorded in spring with 8.1 ± 9.2 individuals per survey. The best model for insectivorous species (table 4) included a linear negative effect of crop cultures and fruit cultures and a linear positive effect of woody vegetation (table 8, fig. S4). Chaffinch was the most widespread species with 13.2 ± 29.3 individuals for both seasons together, 23 ± 39.3 individuals in winter and 6.8 ± 17.6 in spring. The species was present during 91% of the surveys and seen on all 38 transects. In the best model (table 4), fruit cultures had a linear positive effect and season also had a significant effect with a higher abundance in winter (table 8, fig. S3). Tree Sparrow was the most abundant species with 13.9 ± 22.3 individuals for both seasons, 17 ± 32.4 in winter and 11.8 ± 11.1 in spring. In the best model (table 4), fruit cultures had a negative effect and season was significant with positive effect of spring (table 8, fig. S3). Even if the overall abundance was higher in winter with bigger groups on some transects, the species was more widespread in spring (median in winter = 2 individuals, median in spring = 9 individuals).

Field scale habitat preferences

Our findings underline the general importance of larger trunk diameter, the choice of fields with high amounts of left over fruit in winter and the preference for low and sparse ground vegetation in spring. 1’330 presence points and 1’512 pseudo-absence points of 51 species recorded at field scale in intensive fruit cultures were retained for analyses. Chaffinch (413 observations) and Blackbird (274 observations) were the most recorded species within fruit culture fields. Analyses for winter were based on 333 presences and 322 pseudo-absences. The best general model for all species (table 5) highlighted a linear positive effect of leftover fruit and trunk diameter but no significant effect was found for vegetation height between tree rows and percentage of vegetation under tree rows (table 9, fig. 4). Analyses for spring were based on 997 presences and 1’190 pseudo-absences. The best general model for all species (table 5) included linear negative effects of vegetation height between tree rows and percentage of vegetation under tree rows and a linear positive effect of trunk diameter (table 9, fig. 4). Only 18 insectivorous bird species were recorded in spring within fruit culture parcels. In the best model (table 6), vegetation height between tree rows had a linear negative effect and trunk diameter a linear positive effect (table 10, fig. S6). In the best model for Chaffinches in winter (table 6), leftover fruit had a linear positive effect The best model for spring (table 6) comprised a linear negative effect of vegetation cover under tree rows and a linear positive effect of trunk diameter (table 10, fig. S5).

Discussion

This study highlights the importance of both landscape habitat heterogeneity and management techniques for bird communities and their fine-scaled habitat selection. Moreover, our results suggest significant inter-seasonal differences in both landscape and field scale habitat use and emphasize the negative effects of homogenous fruit cultures, the positive effects of semi-natural structures such as woody vegetation and marshes as well as the preference for fields with older trees and low and sparse vegetation. These findings underline the potential for improvement through appropriate landscape planning and plantation management in order to promote bird diversity in an agro-ecosystem dominated by intensive fruit cultures.

Habitat heterogeneity, a key factor to enhance biodiversity in agricultural land (Benton, Vickery & Wilson 2003; Fahrig *et al.* 2011; Vickery & Arlettaz 2012), plays a pivotal role for bird communities in fruit tree plantations. As Shannon Index for landscape heterogeneity was negatively collinear with the proportion of intensive fruit cultures, we considered the latter as an indicator of habitat homogeneity. An increased cover of intensive fruit cultures had negative effects on overall species richness, congruent with previous evidences 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 was also negatively affected by landscape homogeneity. Surprisingly, opposite effects were found for the most common species. Chaffinches benefitted from homogeneous fruit cultures, while Tree Sparrows were negatively impacted. The former is a generalist species building its own nest (Glutz Von Blotzheim, Bauer & Bezzel 1966; Mouysset *et al.* 2011), apparently capable to use fruit cultures where inter-specific competition is low. The latter avoided homogenous fruit cultures, even though the density is high in central Valais lowland with more than 20 pairs/km^2 (Knaus *et al.* 2018). Limited food resources with low insect availability to feed nestlings (Field, Anderson & Gruar 2008) and a lack of breeding sites might be the cause. Habitat heterogeneity depends not only on the proportion of fruit cultures, but also on the composition of other habitats in the landscape (Devictor & Jiguet 2007; Fahrig *et al.* 2011).

Semi-natural habitats, crop cultures and grassland surrounding the fruit cultures contribute to habitat heterogeneity and influence bird communities (Fischer & Lindenmayer 2007; Doxa *et al.* 2012). Woody vegetation cover, i.e. hedges, forest patches and isolated trees had positive effects on bird species richness, Shannon Diversity Index and abundance. Similar effects of bushes, hedges and trees were found in vineyard landscape (Assandri *et al.* 2016; Guyot *et al.* 2017). These structures offer nesting sites, perches, shelter and food to a broad variety of farmland birds (Batáry, Matthiesen & Tscharntke 2010), e.g. declining species like

Red-Backed Shrike *Lanius collurio* (Brambilla, Rubolini & Guidali 2007; Ceresa *et al.* 2012). General bird abundance was affected not only by woody vegetation cover but also by gardens, generally extensive and interspersed between plantations and cultivated fields. Although open fields within the plantation matrix might structure the landscape, no effect was detected for grassland and crop culture cover had a negative effect on overall species richness and insectivorous abundance. In a landscape where regular pesticide spraying decreases arthropod densities (Suckling, Walker & Wearing 1999; Epstein *et al.* 2000), our study showed a positive effect of woody vegetation cover on insectivorous bird abundance. The latter were dramatically scarcely distributed in our study area, with a quasi absence of emblematic species such as the Common Redstart (Martinez *et al.* 2010). Marshes also contributed to enhance species richness and even harboured species of high conservation concern in Switzerland (e.g. Great Reed Warbler *Acrocephalus arundinaceus*, Little Bittern *Ixobrychus minutus*). Marshes and woody vegetation communities are composed of either wetland or farmland and woodland species (Fuller *et al.* 2001; Devictor & Jiguet 2007; Doxa *et al.* 2012), underlining the value of both these habitats for bird diversity (Chamberlain & Wilson 2000; Doxa *et al.* 2010). Brambilla *et al.* (2015) also found positive effects of wetland and semi-natural habitats on Greenfinch *Carduelis chloris* abundance and positive effects of shrubs and woodlands on Blackcap *Sylvia atricapilla* abundance in fruit cultures. Hence, our results confirm the importance of these structures for general bird abundance and diversity, with different effects depending on avian communities and seasons.

Bird communities and habitat use in permanent cultures vary between seasons (Assandri *et al.* 2016; Guyot *et al.* 2017). Winter is a sensitive period for survival of overwintering and sedentary bird species, often gathering in large mixed-species flocks focusing on foraging activities and avoidance of predation (Skorka *et al.* 2006; Myczko *et al.* 2013) while in spring, when birds are territorial and less mobile, priorities are set on breeding (Vickery & Arlettaz 2012; Guyot *et al.* 2017). Due to the absence of migrating species in winter, species richness and Shannon Diversity Index were significantly higher in spring. Mean number of individuals recorded in winter was higher, but the occurrence of big groups was sporadic with more variation in numbers than in spring, explaining why the abundance model did not include any seasonal effect. Seasonal comparative studies about bird communities in fruit cultures are missing, nonetheless our results are consistent with the findings of Assandri *et al.* (2016) in vineyards in northern Italy, even though Guyot *et al.* (2017) found a higher species richness and Shannon Diversity Index in Swiss vineyards in winter than in spring. No interaction was found between the season and any other explanatory variables, meaning that the respective importance of the different habitats remains similar through winter and spring. Knowing habitat preferences of birds in intensive fruit cultures on a landscape scale allows the definition of conservation priorities for landscape planning, however, a multi-scale approach accounting also for habitat selection within fruit culture fields provides complementary information on fine-scale preferences.

On a field scale, preferences were driven by the age of plantations as well as food accessibility and availability. In winter and spring, trunk diameter had a positive effect on field selection for all species and specifically for Chaffinches, Tree Sparrows and insectivorous birds. This general preference for older woodland-like habitat might be linked with arthropod density (Wiacek & Polak 2008; Myczko *et al.* 2013), as it is the case in old pear orchards where Wrynecks benefit from an increased ant prey availability and accessibility (Mermod *et al.* 2009). Foraging habitat preferences showed more seasonal variation. 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*. In spring, high or dense vegetation decreases food accessibility, which explains why birds preferred to forage in fields with low or scarce ground vegetation, where predation risk might also be lower than in dense vegetation (Moorcroft *et al.* 2002; Butler *et al.* 2005; Whittingham *et al.* 2006). For insectivorous species, vegetation height between tree rows is also a relevant criterion with preference for plantations with short sward rather than high grass. Sparse vegetation cover under trees with bare ground patches attracted Chaffinches, although Brambilla *et al.* (2015) found densely vegetated fruit cultures to be more beneficial for this species on a landscape level than plantations with bare ground. Open ground patches are also known to promote rare insectivorous birds such as Common Redstart, Hoopoe and Wryneck (Martinez *et al.* 2010; Schaub *et al.* 2010; Weisshaupt *et al.* 2011; Tagmann-Ioset *et al.* 2012). These ground vegetation results are independent of any consideration about food availability and only apply to resource accessibility. Weed and flower strips harbour high arthropod densities (Wyss 1996), including beneficial species for pest control (Rieux, Simon & Defrance 1999; Bostanian *et al.* 2004), supporting the necessity of leaving alternate un-mown grass strips as a refuge for arthropods, which might then be accessible for birds on adjacent mown or bare surfaces (Arlettaz *et al.* 2012). Both landscape heterogeneity and plantation management matter for habitat selection of birds, although a relatively low number of species use intensive fruit cultures compared to semi-natural structures in the surrounding landscape. Hence, our results highlight the potential effectiveness of implementing measures at the landscape level in order to enhance overall habitat quality promoting bird diversity, while adapting field scale management within intensive fruit tree plantations will primarily benefit a subset of species adapted to this habitat.

Recommendations and conclusion

Based on our results, we recommend actions on both landscape composition and plantation management. Landscape conservation planning should focus on increasing habitat heterogeneity by preserving bushes, hedges, isolated trees and forest patches and inserting such structures within the fruit culture matrix. Furthermore, marshes have a positive effect on species richness and host several red-listed wetland species increasing local diversity: we advise to protect but also to restore and create ponds and marshes of sufficient size in the valley bottom. As this habitat increases bird abundance, we recommend an extensive management of gardens preferably with diverse indigenous bushes and high-stem fruit trees. Mixing woody vegetation and wetlands might be an optimal solution, with the option of revitalizing existing canals. Field scale results show a clear preference for older plantations; we therefore propose to delay replacement of old plantations as long as possible. As food availability drives foraging habitat selection in winter, leaving fruit after harvest and disposing fruit wastes regularly during the cold season will provide a sustainable food resource for fruit-eating birds. In spring, food accessibility prevails and vegetation management has to be adapted consequently. Our findings highlight the importance of keeping low vegetation strips in spring to facilitate access to arthropod prey, however vegetation should not be mown totally. Bare ground patches should be maintained mechanically, as they are driving spring field scale habitat selection for all species and more specifically for Chaffinch, the most common breeding species in fruit cultures.

Destruction of the last traditional orchards is still ongoing, requesting urgent conservation measures for these remaining parcels. A restoration of this habitat is unlikely to happen at a sufficient scale and fruit cultures are still expanding with an increasingly intensive management. As more extensive practices are difficult to implement in conventional commercial fruit cultures, measures on ground vegetation management and landscape structures with a good cost-efficiency ratio should be a priority to improve the situation for birds in an area dominated by intensive fruit tree plantations. This study emphasizes the importance of combining landscape and fine scale approaches considering seasonal variation to understand habitat use of bird communities in order to improve the situation for biodiversity in permanent cultures.

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Table 1. ***Landscape scale*** *explanatory variables used for statistical analyses of species richness, Shannon Diversity Index and abundance*

Covariate	Description	Model	Recording method	Details
fruitcult	% fruit cultures	species richness, abundance	QGIS	continuous range 14.2 – 93.1 mean = 56.4
cropcult	% crop cultures	species richness, abundance	QGIS	continuous range 0 – 51.8 mean = 10.7
grassland	% meadows and pastures	abundance	QGIS	continuous range 0 – 60.6 mean = 12.8
garden	% gardens	abundance	QGIS	continuous range 0 – 16.6 mean = 2.7
marsh	% marsh, reed bed and pond	species richness	QGIS	continuous range 0 – 38.2 mean = 1.3
woodveg	% woody vegetation: bushes, hedges, trees and forest	species richness, abundance, Shannon	QGIS	continuous range 0 – 28 mean = 1.8
canal	% canals	species richness	QGIS	continuous range 0 – 7.4 mean = 1.2
observer	observer (Yann Rime, Célestin Luisier)			factorial (2 levels)
season	season (winter, spring)	species richness, Shannon		factorial (2 levels)

*Table 2. **Field scale** explanatory variables used for statistical analyses for winter and spring.*

Covariate	**Description**	**Model**	**Recording method**	**Details**
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
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

*Table 3. **Landscape scale** ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLink, AICc, ΔAICc and model weights for species richness, Shannon Diversity Index and abundance.*

Rank	Model	Df	logLik	AICc	ΔAICc	Model weight
	***species richness** (glmer, Poisson)*					
1	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
	***Shannon** (lmer, Gaussian)*					
1	season + woodveg	5	-83.377	177.1	0.00	0.996
	***abundance** (glmer, Poisson)*					
1	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 + grass	7	-974.132	1962.9	1.78	0.035
10	cropcult + garden + woodveg	6	-975.225	1962.9	1.81	0.035

Table 4. ***Landscape scale*** *ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLink, AICc, ΔAICc and model weights per species and species groups.*

Rank	Model	Df	logLik	AICc	ΔAICc	Model weight
	Chaffinch abundance *(glmer, Poisson)*					
1	season + fruitcult	5	-623.794	1257.9	0.00	0.997
	Tree Sparrow abundance *(glmer, Poisson)*					
1	season + fruitcult	5	-658.978	1328.3	0.00	0.664
2	season	4	-660.849	1329.9	1.63	0.294
	insectivorous abundance *(glmer, Poisson)*					
1	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

Table 5. ***Field scale*** *ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLink, AICc, ΔAICc and model weights for all species in winter and spring.*

Rank	Model	Df	logLik	AICc	ΔAICc	Model weight
	winter all species *(glmer, binomial)*					
1	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
	spring all species *(glmer, binomial)*					
1	trunkdiam + vegheight + vegcover	5	-1447.901	2905.8	0.00	0.864

Table 6. ***Field scale*** *ranked best models (Δ AICc < 2) with degrees of freedom (Df), logLink, AICc, ΔAICc and model weights per species or species group in winter and spring.*

Rank	**Model**	**Df**	**logLik**	**AICc**	**ΔAICc**	**Model weight**
	Chaffinch winter *(glmer, binomial)*					
1	fruit	3	-86.442	179.1	0.00	0.998
	Chaffinch spring *(glmer, binomial)*					
1	trunkdiam + vegcover	4	-459.431	926.9	0.00	0.755
	insectivorous spring					
1	vegheight + trunkdiam + vegcover	5	-165.868	342.0	0.00	0.580
2	vegheight + trunkdiam	4	-167.298	342.7	0.79	0.391

*Table 7. **Landscape scale** model-averaged conditional estimates, standard errors (SE), z or t values and lower and upper 2.5% confidence intervals (CI) species richness, Shannon Diversity Index and abundance. Significant variables are in bold.*

Term	Estimate	SE	z or t value	2.5% CI	97.5% CI
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
Shannon					
season	**0.351**	**0.052**	**6.769 *****	**0.249**	**0.453**
woodveg	**0.149**	**0.031**	**4.801 *****	**0.088**	**0.209**
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

Table 8. ***Landscape scale*** *model-averaged conditional estimates, standard errors (SE), z values and lower and upper 2.5% confidence intervals (CI) for species and species groups. Significant variables are in bold.*

Term	Estimate	SE	z value	2.5% CI	97.5% CI
Chaffinch abundance					
fruitcult	**0.361**	**0.096**	**3.744 *****	**0.173**	**0.553**
season	**-0.901**	**0.189**	**-4.763 *****	**-1.275**	**-0.528**
Tree Sparrow abundance					
fruitcult	**-0.370**	**0.185**	**1.984 ***	**-0.735**	**-0.004**
saison	**0.558**	**0.194**	**2.863 ****	**0.176**	**0.941**
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

Table 9. ***Field scale*** *model-averaged conditional estimates, standard errors (SE), z values and lower and upper 2.5% confidence intervals (CI) for all species in winter and spring. Significant variables are in bold.*

Term	**Estimate**	**SE**	**z value**	**2.5% CI**	**97.5% CI**
winter					
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
spring					
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**

*Table 10. **Field scale** model-averaged conditional estimates, standard errors (SE), z values and lower and upper 2.5% confidence intervals (CI) per species or species groups in winter and spring. Significant variables are in bold.*

Term	Estimate	SE	z value	2.5% CI	97.5% CI
Chaffinch winter					
fruit	**0.686**	**0.191**	**3.583 *****	**0.322**	**1.078**
Chaffinch spring					
vegcover	**-0.164**	**0.080**	**-2.058 ***	**0.173**	**0.553**
trunkdiam	**0.480**	**0.084**	**5.685 *****	**-1.275**	**-0.528**
insectivorous spring					
vegheight	**-0.502**	**0.170**	**2.943 ****	**-0.836**	**-0168**
trunkdiam	**0.612**	**0.150**	**4.055 *****	**0.316**	**0.907**
vegcover	-0.250	0.149	1.665	-0.543	0.044

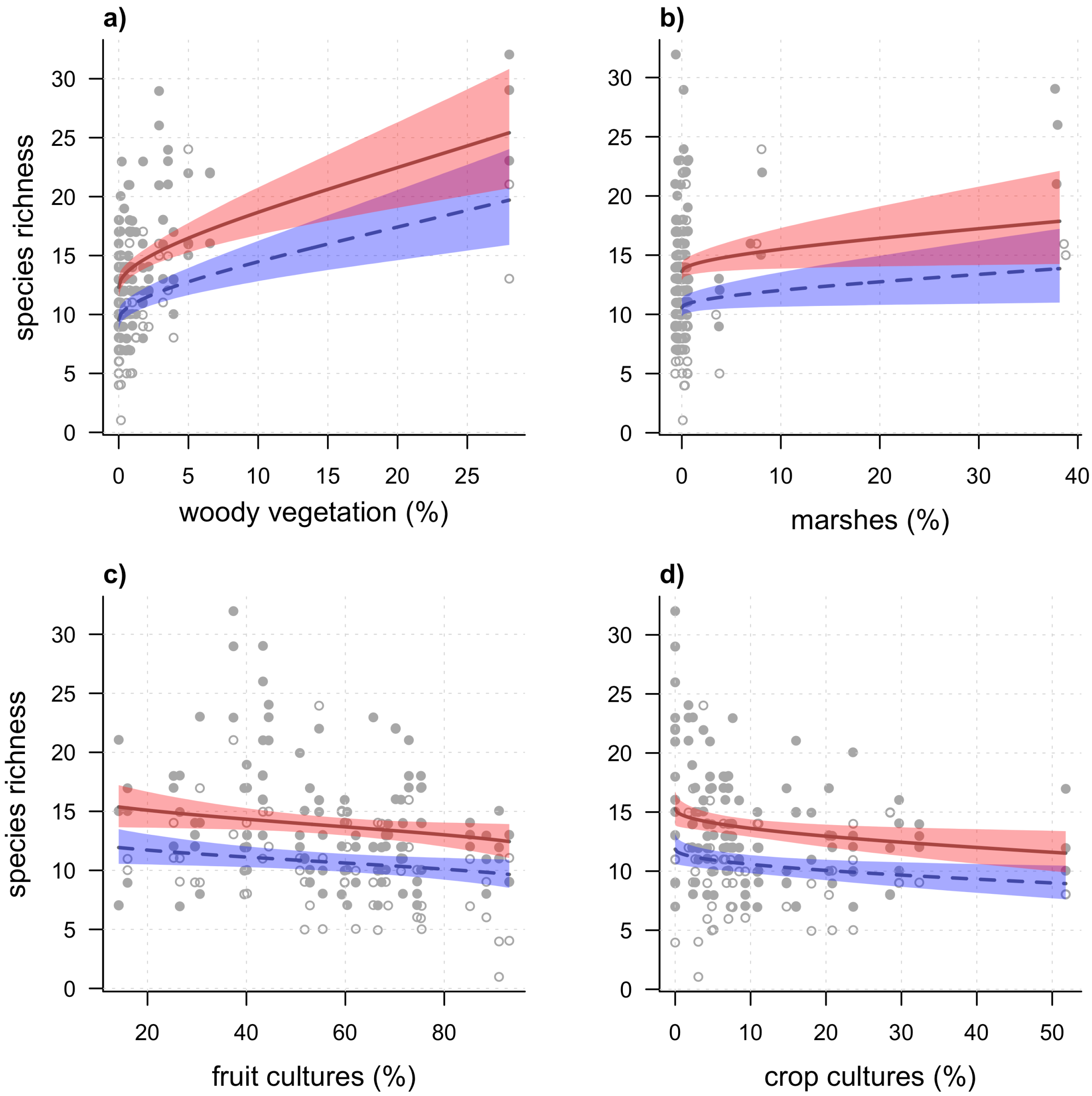

Fig. 1. Landscape scale model-averaged predictions from Poisson regression models for ***species richness*** *in winter (dashed line) and spring (solid line) with 95%–Bayesian credible intervals (blue areas for winter, red areas for spring) for a) woody vegetation, b) marshes, c) fruit cultures and d) crop cultures. Grey dots show raw data for spring and empty dots show raw data for winter.*

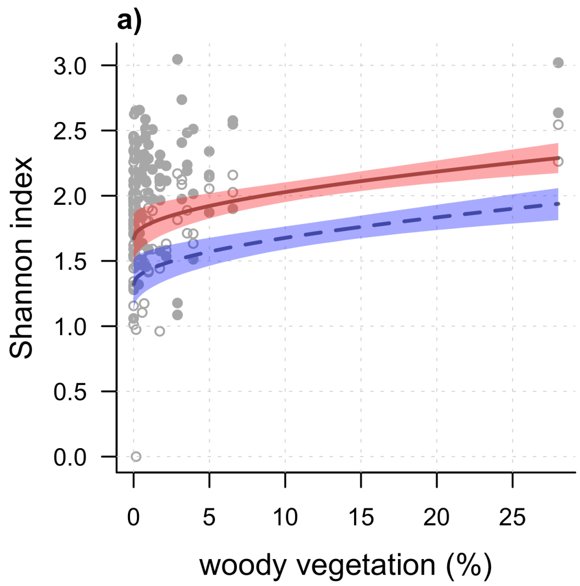

Fig. 2. Landscape scale model-averaged predictions from Gaussian regression models for ***Shannon Diversity Index*** *for all bird species in winter (dashed line) and spring (solid line) with 95%–Bayesian credible intervals (blue area for winter, red area for spring) for a) woody vegetation. Grey dots show raw data for spring and empty dots show raw data for winter.*

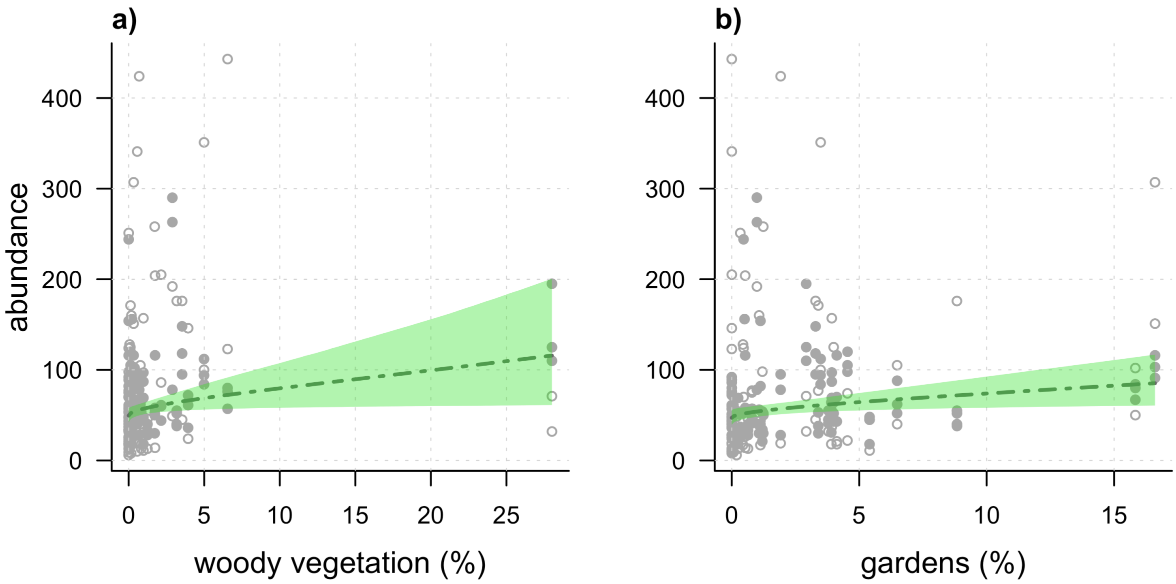

*Fig. 3. Landscape scale model-averaged predictions from Poisson regression models for **all species abundance** winter and spring together with 95%–Bayesian credible intervals (green areas) for a) woody vegetation and b) gardens. Grey dots show raw data for spring and empty dots show raw data for winter.*

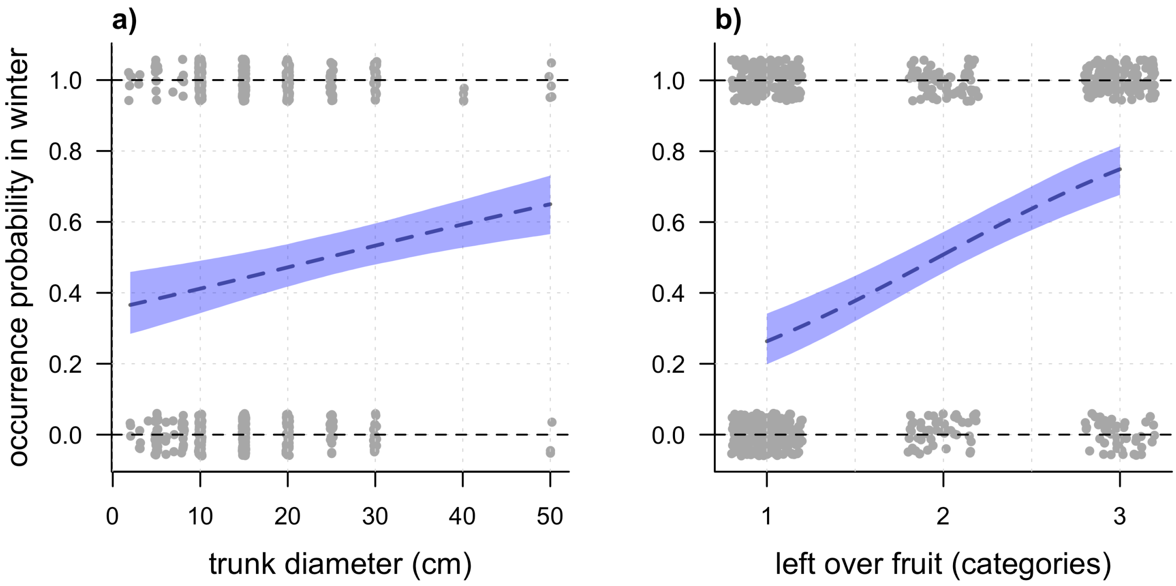

Fig. 4. Field scale model-averaged predictions from binomial regression models for ***all species occurrence probability*** *in winter with 95%–Bayesian credible intervals (blue areas) for a) trunk diameter and b) left over fruit (1 = <1 per row, 2 = 1 per row - 1 per tree, 3 = >1 per tree). Grey dots show raw data.*

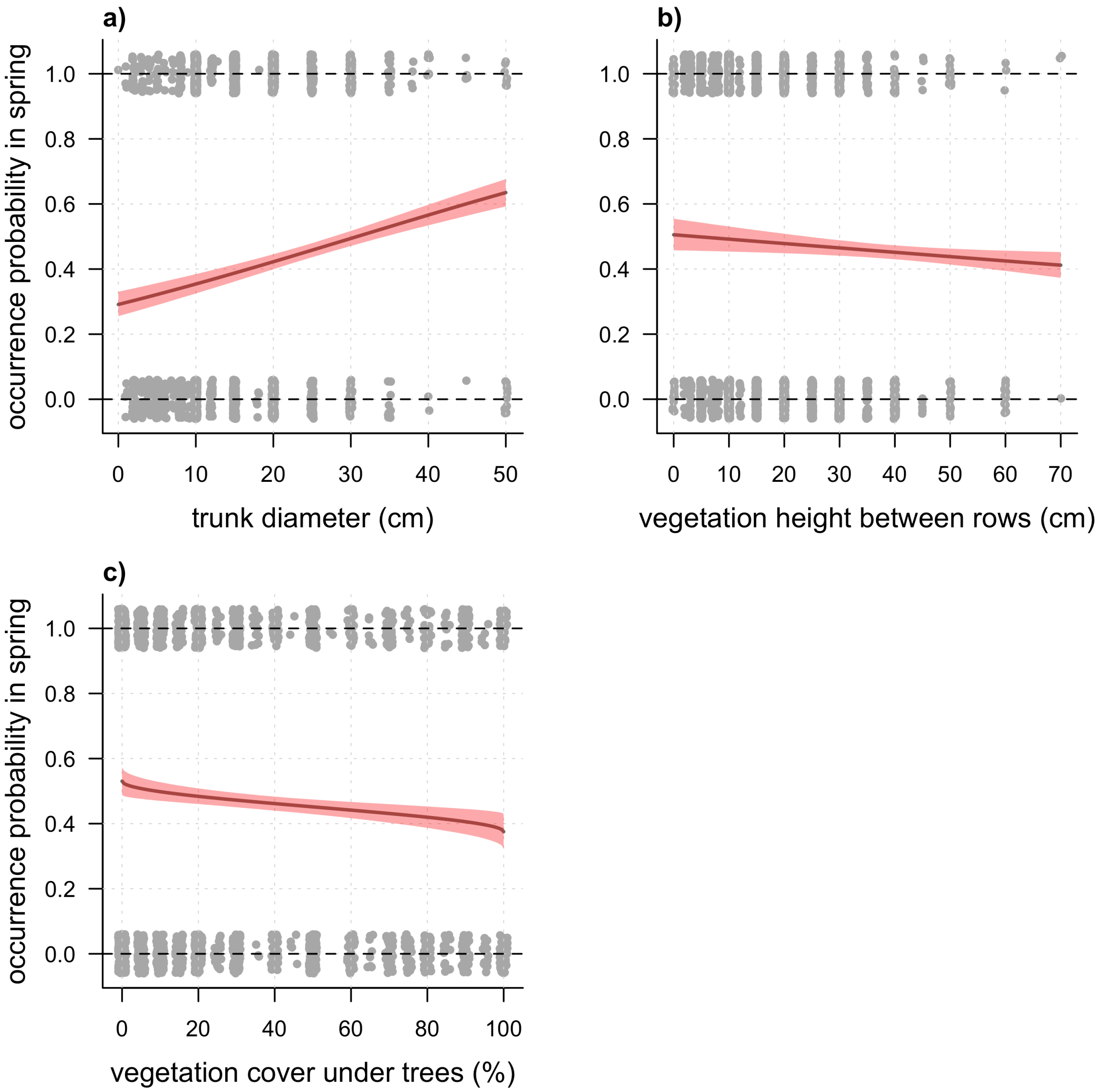

Fig. 5. Field scale model-averaged predictions from binomial regression models for ***all species occurrence probability*** *in spring with 95%–Bayesian credible intervals (red areas) for a) trunk diameter, b) vegetation height between rows and c) vegetation cover under trees. Grey dots show raw data.*

Supplementary material

Table S1. List of 38 study sites with transect ID, total surface within the 100 m buffer area (m^2), length (m), fruit culture proportion and coordinates (N latitude and E longitude).

Transect ID	Surface (m^2)	Length (m)	% fruit cultures	Coordinates	
01	110863	402	62.11	46.12756	7.05339
02	111636	404	67.33	46.11809	7.06004
03	111129	402	40.05	46.11213	7.07992
04	107021	399	29.60	46.11768	7.09163
05	113369	404	25.28	46.12242	7.09566
06	111040	401	68.19	46.11068	7.10930
07	100924	401	14.17	46.11747	7.11341
08	110838	401	71.25	46.11394	7.11856
09	111288	402	75.29	46.12662	7.10984
10	110335	398	43.30	46.12105	7.12337
12	110870	401	60.38	46.13036	7.12985
13	106193	396	59.26	46.12931	7.14041
14	110785	400	74.51	46.13795	7.13941
16	110979	406	59.86	46.14550	7.13952
17	106326	402	54.69	46.13604	7.15136
18	110821	400	66.57	46.14314	7.14943
19	111365	403	68.65	46.15182	7.15023
20	110239	397	51.77	46.15039	7.16371
23	110162	397	70.17	46.16222	7.18378
24	111059	401	93.15	46.15585	7.19876
25	110860	400	52.83	46.16856	7.19522
26	111719	404	88.50	46.16306	7.21309
27	110822	400	85.21	46.17284	7.20970
28	111133	402	75.43	46.17844	7.23473
29	106106	398	65.66	46.18792	7.25247
30	111613	400	43.34	46.19410	7.25529
31	110985	401	72.84	46.19950	7.26246
32	112521	408	91.07	46.19741	7.27064
34	109059	401	39.58	46.20900	7.28941
35	110444	398	30.60	46.21569	7.28555
36	111166	402	40.13	46.21003	7.30412
38	111037	405	26.53	46.22818	7.38961
39	110100	400	44.50	46.24279	7.38923
40	111234	402	15.96	46.24004	7.40347
42	110278	397	71.63	46.25677	7.43989
45	110769	403	37.38	46.26840	7.48897
46	108178	405	50.80	46.27038	7.49809
47	109300	393	55.43	46.27724	7.52567

Table S2. List of all species recorded during winter and spring with total count

Species (English)	**Species (Latin)**	**Total count**
Tree Sparrow	*Passer montanus*	2631
Common Chaffinch	*Fringilla coelebs*	2524
Eurasian Blackbird	*Turdus merula*	1384
House sparrow	*Passer domesticus*	1215
Common Starling	*Sturnus vulgaris*	945
Alpine Chough	*Pyrrhocorax pyrrhocorax*	871
Eurasian Magpie	*Pica pica*	582
Fieldfare	*Turdus pilaris*	528
Carrion crow	*Corvus corone*	448
Raven	*Corvus corax*	386
Great Tit	*Parus major*	349
European Goldfinch	*Carduelis carduelis*	342
European Greenfinch	*Carduelis chloris*	339
Brambling	*Fringilla montifringilla*	328
White Wagtail	*Motacilla alba*	278
Eurasian Jay	*Garrulus glandarius*	186
European Serin	*Serinus serinus*	168
Blue Tit	*Cyanistes caeruleus*	145
Barn Swallow	*Hirundo rustica*	144
Mistle Thrush	*Turdus viscivorus*	115
Long-tailed Tit	*Aegithalos caudatus*	104
Common Linnet	*Carduelis cannabina*	88
Eurasian Blackcap	*Sylvia atricapilla*	80
House Martin	*Delichon urbicum*	75
Song Thrush	*Turdus philomelos*	72
Water Pipit	*Anthus spinoletta*	67
Common Swift	*Apus apus*	58
Black Redstart	*Phoenicurus ochruros*	48
Wood Pigeon	*Columba palumbus*	41
Alpine Swift	*Tachymarptis melba*	40
Rook	*Corvus frugilegius*	37
Common Buzzard	*Buteo buteo*	34
Eurasian Siskin	*Carduelis spinus*	33
Eurasian Skylark	*Alauda arvensis*	33
Eurasian Reed Warbler	*Acrocephalus scirpaceus*	32
European Robin	*Erithacus rubecula*	31
Marsh Tit	*Poecile palustris*	28
Hawfinch	*Coccothraustes coccothraustes*	27
European Stonechat	*Saxicola rubicola*	25
Grey Heron	*Ardea cinerea*	25
Eurasian Wryneck	*Jynx torquila*	24
Great Spotted Woodpecker	*Dendrocopos major*	24

Species (English)	Species (Latin)	Total count
Mallard	*Anas platyrhynchos*	24
Yellowhammer	*Emberiza citrinella*	24
Eurasian Hoopoe	*Upupa epops*	22
Green Woodpecker	*Picus viridis*	21
Common Reed Bunting	*Emberiza schoeniclus*	20
Redwing	*Turdus iliacus*	20
Lesser Redpoll	*Acanthis (flammea) cabaret*	19
Rosy Starling	*Pastor roseus*	16
Yellow Wagtail	*Motacilla flava*	16
Common Kestrel	*Falco tinnunculus*	15
Eurasian Coot	*Fulica atra*	15
Short-toed Treecreeper	*Certhia brachydactyla*	15
Black Kite	*Milvus migrans*	14
Eurasian Wren	*Troglodytes troglodytes*	14
Red-backed Shrike	*Lanius collurio*	12
Rock Bunting	*Emberiza cia*	12
Tree Pipit	*Anthus trivialis*	12
Crag Martin	*Ptyonoprogne rupestris*	11
Eurasian Sparrowhawk	*Accipiter nisus*	11
Whinchat	*Saxicola rubetra*	11
Collared Dove	*Streptopelia decaocto*	10
Dunnock	*Prunella modularis*	10
Eurasian Nuthatch	*Sitta europaea*	10
Grey Wagtail	*Motacilla cinerea*	9
Common Chiffchaff	*Phylloscopus collybita*	7
Meadow Pipit	*Anthus pratensis*	7
Common Nightingale	*Luscinia megarhynchos*	6
Grasshopper Warbler	*Locustella naevia*	6
White-throated Dipper	*Cinclus cinclus*	6
Eurasian Bullfinch	*Pyrrhula pyrrhula*	5
Peregrine Falcon	*Falco peregrinus*	5
Pied Flycatcher	*Ficedula hypoleuca*	5
Common Moorhen	*Gallinula chloropus*	4
Eurasian Kingfisher	*Alcedo atthis*	4
Sand Martin	*Riparia riparia*	4
Turtle Dove	*Streptopelia turtur*	4
Willow Warbler	*Phylloscopus trochilus*	4
Wood Warbler	*Phylloscopus sibilatrix*	4
Black Woodpecker	*Dryocopus martius*	3
Coal Tit	*Periparus ater*	3
Common Redstart	*Phoenicurus phoenicurus*	3
Crested Tit	*Lophophanes cristatus*	3
European Bee-eater	*Merops apiaster*	3
Golden Oriole	*Oriolus oriolus*	3

Species (English)	Species (Latin)	Total count
Great Cormorant	*Phalacrocorax carbo*	3
Great reed Warbler	*Acrocephalus arundinaceus*	3
Little Egret	*Egretta garzetta*	3
Red Kite	*Milvus milvus*	3
Common Firecrest	*Regulus ignicapilla*	2
Common Whitethroat	*Sylvia communis*	2
Eurasian Goshawk	*Accipiter gentilis*	2
Eurasian Hobby	*Falco subbuteo*	2
Hybrid Carrion x Hooded Crow	*Corvus corone x cornix*	2
Little Grebe	*Podiceps cristatus*	2
Marsh Warbler	*Acrocephalus palustris*	2
Goldcrest	*Regulus regulus*	1
Green Sandpiper	*Tringa ochropus*	1
Little Bittern	*Ixobrychus minutus*	1
Marsh Harrier	*Circus aeroginosus*	1
Montagu's Harrier	*Circus pygargus*	1
Ring Ouzel	*Turdus torquatus*	1
Spotted Flycatcher	*Muscicapa striata*	1
Stock Dove	*Columba oenas*	1
Western Jackdaw	*Corvus monedula*	1

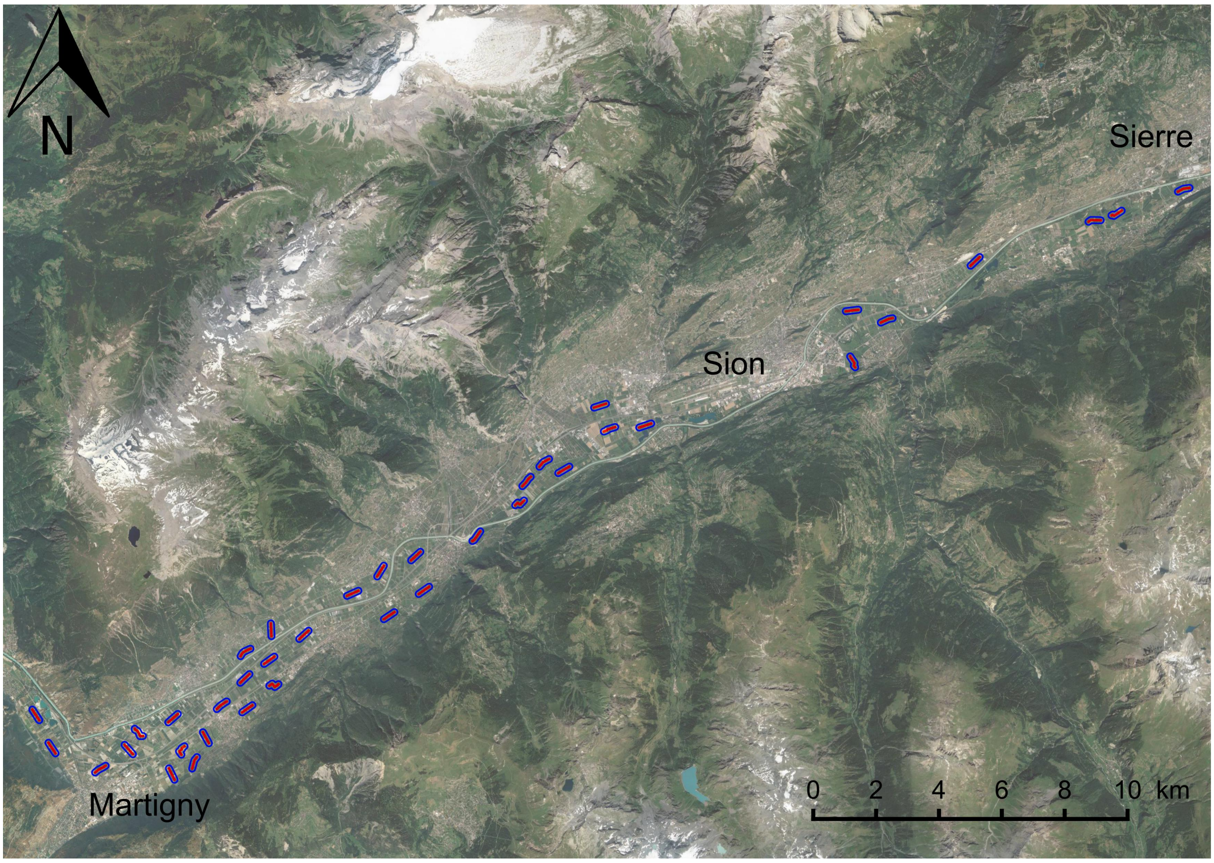

Fig. S1. Map of the 38 transects between Sierre (46°16’39.7”N 7°31’43.5”E) and Martigny (46°07’15.5”N 7°03’26.2”E), Valais, Swizerland (© Google Earth).

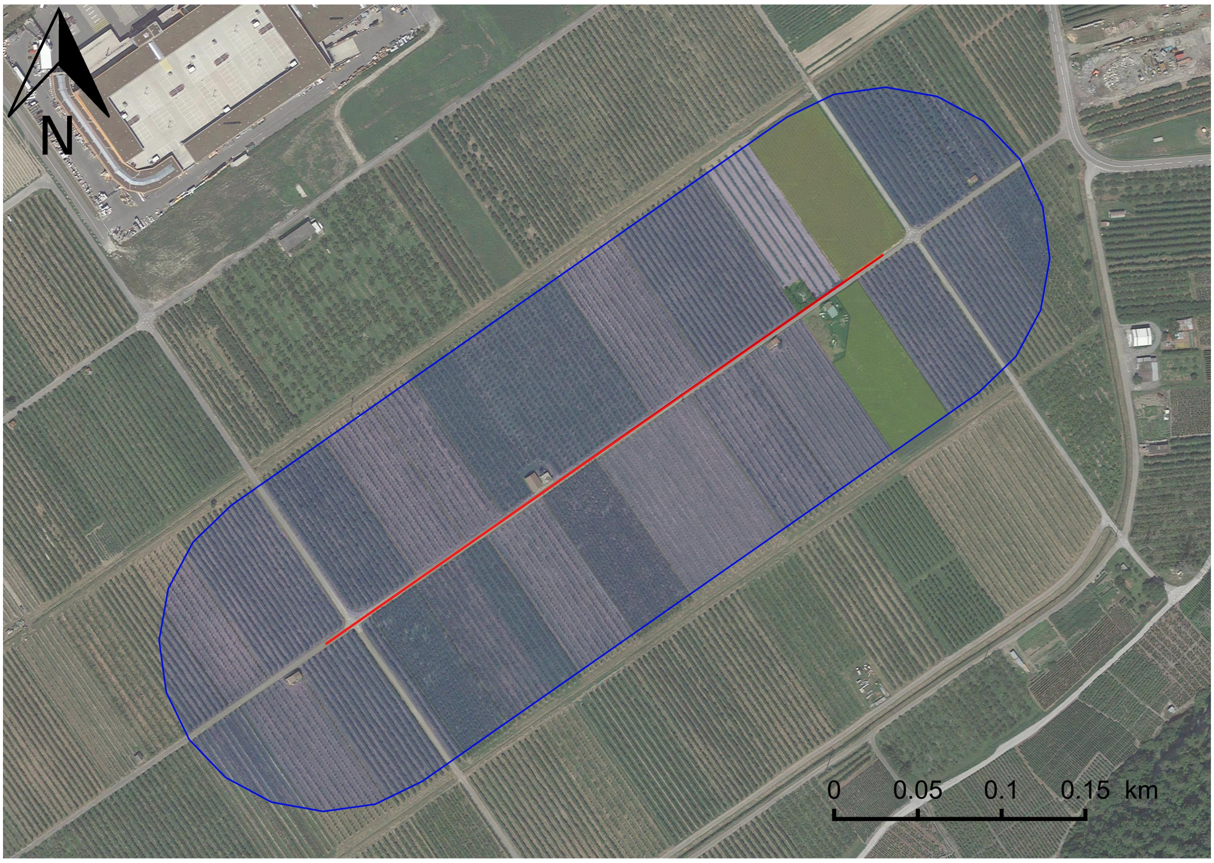

Fig. S2. Example of a 400 m transect (red line) with the 100 m buffer area delimited by the blue line. Study site shown is transect 26 in Riddes, 46°09'47.0"N, 7°12'47.1"E. Fruit cultures are in blue, roads in grey, gardens and woody vegetation in deep green, meadows in light green and crop or vegetable cultures in light brown (© Google Earth).

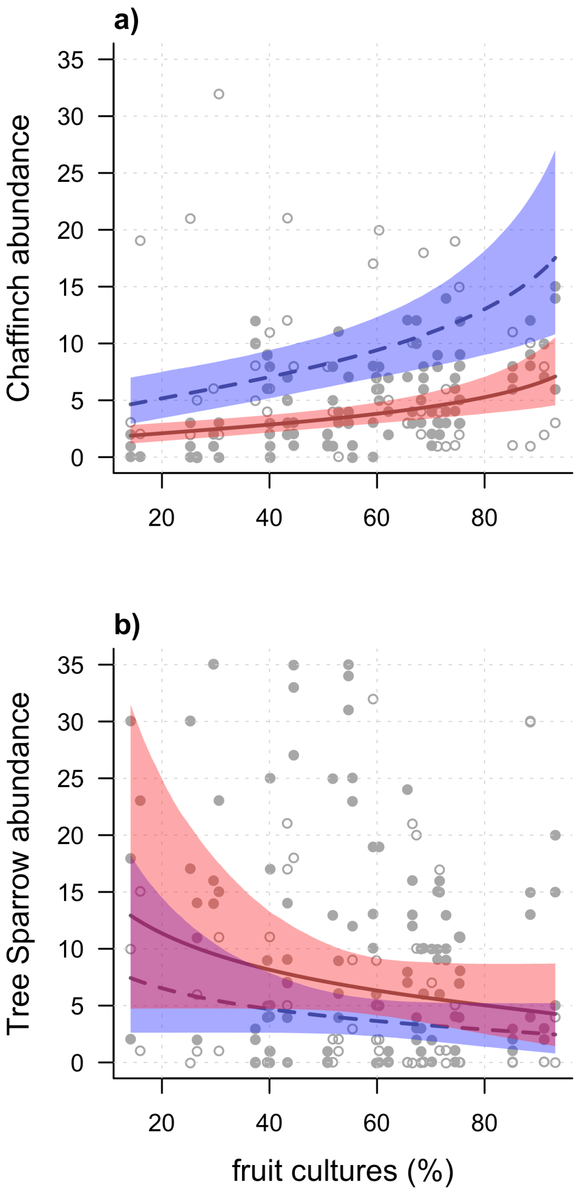

Fig. S3. Landscape scale model-averaged predictions from Poisson regression models for a) ***Chaffinch abundance*** *and b)* ***Tree Sparrow abundance*** *in winter (dashed line) and spring (solid line) with 95%–Bayesian credible intervals (blue areas for winter and red areas for spring) for fruit cultures. 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.*

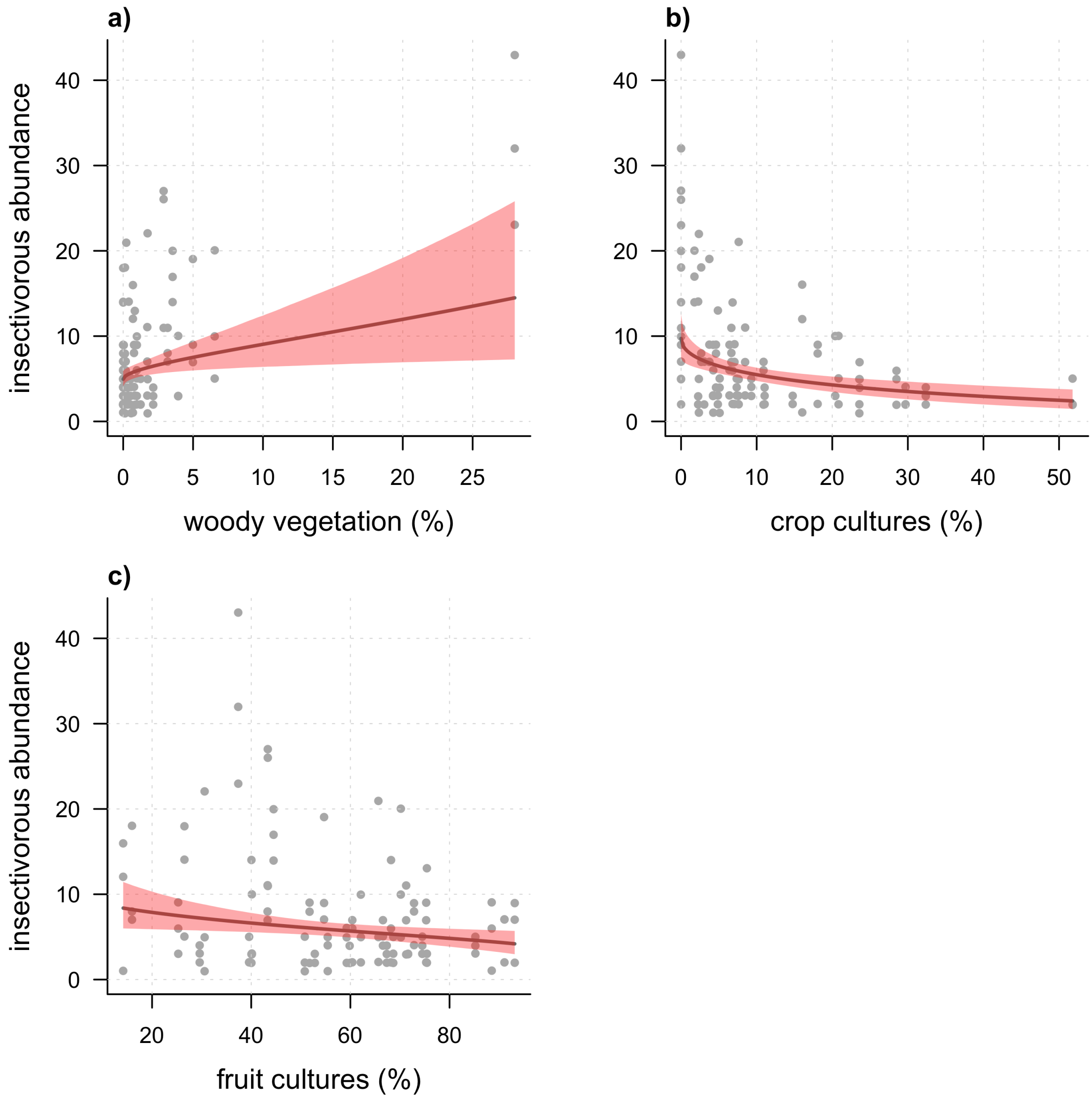

*Fig. S4. Landscape scale model-averaged predictions from Poisson regression models for **insectivorous bird species abundance** in spring with 95%–Bayesian credible intervals (red areas) for a) woody vegetation, b) crop cultures and c) fruit cultures. Grey dots show raw data. One data point with abundance over 43 individuals is not shown.*

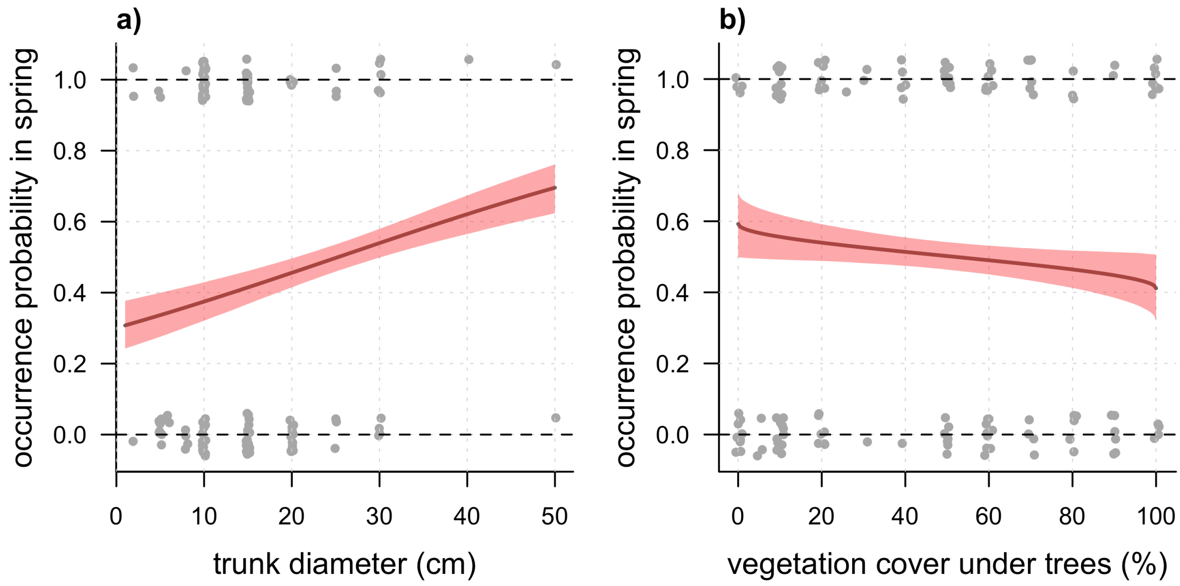

*Fig. S5. Field scale model-averaged predictions from binomial regression models for **Chaffinch occurrence probability** in spring with 95%–Bayesian credible intervals (red areas) for a) trunk diameter and b) vegetation cover under trees. Grey dots show raw data.*

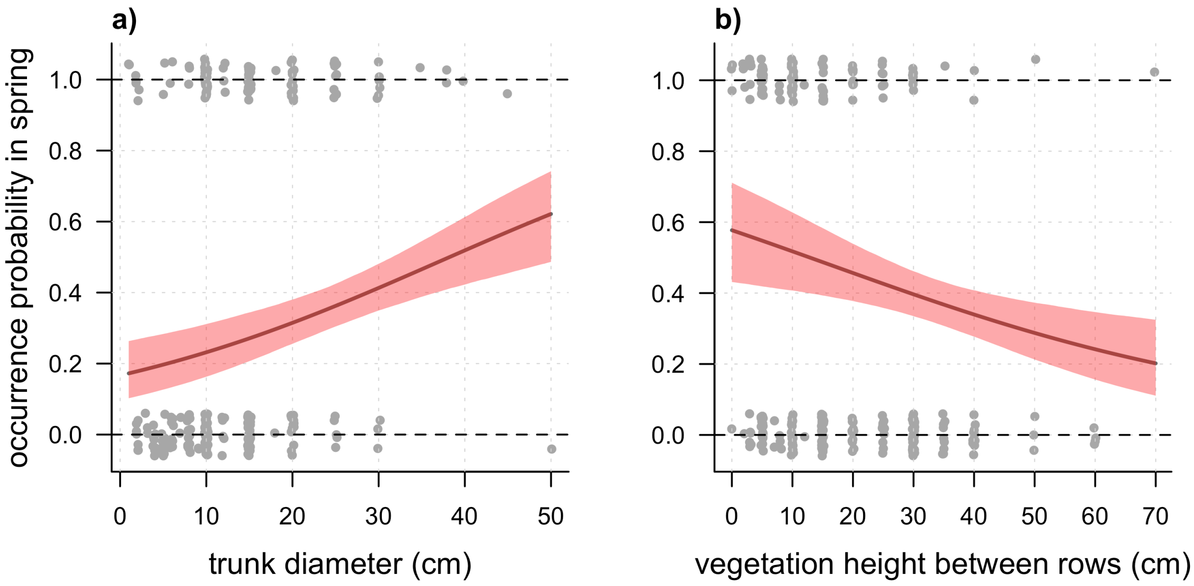

Fig. S6. Field scale model-averaged predictions from binomial regression models ***insectivorous bird species occurrence probability*** *in spring with 95%–Bayesian credible intervals (red areas) for a) trunk diameter and b) vegetation height between rows. Grey dots show raw data.*

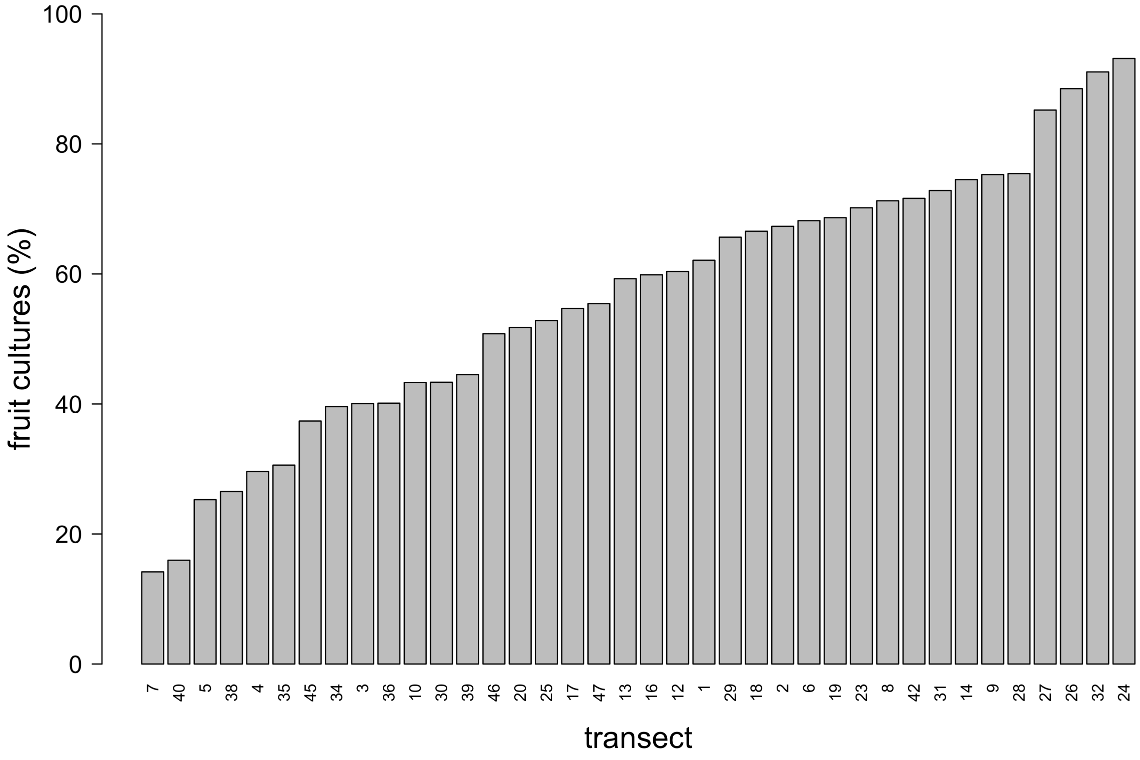

Fig. S7. Distribution of the fruit culture proportion gradient along the 38 transects.