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Are vineyards important habitats for birds at local or landscape scales?

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Abstract

In Europe, monitoring indicates that farmland bird populations are declining. Numerous studies at different spatial scales have considered bird ecology in farmland, but viticulture has received little attention. We carried out bird surveys at two spatial scales over two years in western France. We assessed the contribution of vineyards to bird diversity at landscape scale and undertook plot-scale analyses of habitat selection in vineyards and their associated semi-natural habitats. We detected a strong negative relationship between vineyard cover and both abundance and species richness of birds. Only two species responded positively to vineyards: Woodlark *Lullula arborea* and Skylark *Alauda arvensis*. Of the 93 species detected at landscape scale, only 16 were frequent users of vine plots. The majority of these species were found to select semi-natural habitats adjacent to grapevines, in particular areas with trees. Only Woodlarks positively selected vineyards as opposed to semi-natural habitats but no consistent selection criteria between different vineyard habitat variables could be detected. Our study shows that, although wine-growing landscapes may be species-rich, fewer species use vineyards themselves, and at low levels of abundance. Planting or maintaining semi-natural woody vegetation are popular management approaches, which our data suggest may encourage generalist species without improving vineyard habitats for open farmland specialists.

Zusammenfassung

Erfassungen von Vögeln der Agrarlandschaft zeigen, dass deren Populationen in Europa zurückgehen. Zahlreiche Untersuchungen haben sich mit der Ökologie der Vögel von landwirtschaftlichen Nutzflächen befasst, aber Weinbauflächen wurden wenig beachtet. Wir führten zwei Jahre lang Vogelerfassungen auf zwei räumlichen Ebenen in Westfrankreich durch. Wir bestimmten auf der Landschaftsebene den Einfluss von Weinbauflächen auf die Vogeldiversität und analysierten auf der Ebene von Probeflächen die Habitatwahl auf Weinbauflächen und in angegliederten halb-natürlichen Habitaten. Wir stellten einen stark negativen Zusammenhang zwischen Deckungsanteil der Weinbauflächen und Abundanz bzw. Artenreichtum der Vögel fest. Nur zwei Arten reagierten positiv auf Weinbauflächen: Heidelerche (*Lullula arborea*) und Feldlerche (*Alauda arvensis*). Von den 93 in der Landschaft nachgewiesenen Arten traten nur 16 häufig in Weinbauflächen auf. Die Mehrzahl dieser Arten wählten halb-natürliche Habitate in der Nähe zum Wein, insbesondere Flächen mit Bäumen. Nur die Heidelerche bevorzugte Weinbauflächen gegenüber halb-natürlichen Habitaten; es konnten aber keine konsistenten Selektionskriterien zwischen verschiedenen

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Habitatvariablen der Weinbauflächen ermittelt werden. Unsere Untersuchung zeigt, dass, auch wenn Weinbaulandschaften artenreich sein können, nur wenige Arten die Weinanbauflächen selbst nutzen und das auch nur in geringer Abundanz. Neuanlage oder Erhalt von halb-natürlicher Gehölzvegetation sind populäre Managementmaßnahmen, die, wie unsere Daten nahelegen, generalistische Arten fördern können, ohne dass Weinbauhabitate für Spezialisten der offenen Agrarflächen verbessert werden.

Keywords: Farmland; Bird; Vineyard; Landscape; Habitat selection; *Lullula arborea*

Introduction

Declines in European farmland biodiversity observed over the past three or four decades are clearly attributable to the combined effects of homogenisation of rural landscapes and widespread intensification of farming practises (Chamberlain, Fuller, Bunce, Duckworth, & Shrubb, 2000). In France, as elsewhere in Europe, farmland bird monitoring indicates that even the populations of common bird species associated with farmland habitats have steeply declined (Siriwardena et al., 1998; Donald, Green, & Heath, 2001b; Voříšek et al., 2010). Twenty species that form the French farmland bird index declined by 25% between 1989 and 2009 (Jiguet, 2010). A growing body of evidence suggests that in general, farmland biodiversity will benefit from increasing heterogeneity in farmland landscapes (Benton, Vickery, & Wilson, 2003), particularly through the maintenance, creation and management of semi-natural habitats surrounding land used for agricultural production (Fuller, Hinsley, & Swetnam, 2004; Haslem & Bennett, 2008). In the case of birds, careful management of such habitats can help to alleviate the key problems of limited food resources and breeding sites for farmland bird populations (Wilson, Evans, & Grice, 2009). Most of this work on the relationships between wildlife conservation and farming has focused on the flora and fauna of annual crops, grassland and their associated semi-natural habitats while certain forms of agriculture and in particular viticulture have received less attention.

In parts of southern Europe viticulture is a dominant form of agriculture and in France 3.7% of agricultural land (about 800,000 ha) is used for wine-growing (OIV, 2012). This type of production presents a particular set of opportunities and challenges for the preservation of biodiversity. Vineyards tend to be intensively managed; it has been shown that 20% of all pesticides used in France are consumed by viticulture alone, 80% of which are fungicides, which in turn represent 30% of fungicides used at national level (Aubertot et al., 2005). Studies of vineyard biodiversity have often focused on potentially beneficial organisms in the context of conservation biological control (Begum, Gurr, Wratten, Hedberg, & Nicol, 2006; Thomson & Hoffmann, 2009, 2013) but studies on the specific role of viticulture in the maintenance of farmland biodiversity are relatively rare (Bruggisser, Schmidt-Entling, & Bacher, 2010; Tanadini, Schmidt, Meier, Pellet, & Perrin, 2012). Studies of birds in vineyards tend to focus on bird damage to grapes (Somers & Morris, 2002; Kross, Tylianakis, & Nelson, 2012), or on the possible role of birds themselves as agents of insect biological control (Jedlicka, Greenberg, & Letourneau, 2011). Therefore, we know little about the contribution vineyards make to maintaining biodiversity in general, although they have some potential advantages to offer. They provide woody cover all year round and sometimes green cover in between the rows of grapevines and, like other types of farmland, they contain a range of associated semi-natural habitats outside of the areas strictly used for production, such as grassy turning bays, scrub, woodland patches and isolated trees. Only a few authors have pointed out the use of vineyards as corridors by woodland bird species (Brotons & Herrando, 2001) or have demonstrated the positive effects of green cover for certain species (Sierro & Arlettaz, 2003; Arlettaz et al., 2012).

Wine-growers are increasingly interested in the question of biodiversity management on their farms and collective action is being taken to reintroduce biodiversity or to promote “green” vineyards (Gillespie & Wratten, 2012; Van Helden, Guenser, & Fulchin, 2012). A major reason is that biological diversity may help reduce pesticide use through natural regulation of grapevine pests, while also enhancing a range of other ecosystem services such as weed suppression, plant and insect conservation and ecotourism (Fiedler, Landis, & Wratten, 2008). In response to urbanisation in wine-growing areas or market globalisation, an increasing number of wine producers aim to sell their produce on site or locally (Jarrige, 2004; Brugarolas, Martinez-Carrasco, Bernabeu, & Martinez-Poveda, 2010). After large-scale loss of hedgerows in Europe over the past few decades (Petit, Stuart, Gillespie, & Barr, 2003; Pointereau, 2001), and because hedgerows can perform multiple agro-ecological functions (Baudry, Bunce, & Burel, 2000), incentives for farmers to adopt environmentally or wildlife friendly farming now often focus on hedge-planting. Such schemes are often applied in a standardised manner over wide areas and local planters may be unaware of the potential consequences of planting (Busck, 2003). If viticulturists are to respond to the demand for a more environmentally conscious approach to wine-growing, better knowledge of the relationships between vineyard management and wildlife is needed. Within this context, and basing our research on birds, often used as indicators of farmland biodiversity, and well-studied in other agricultural systems, our aims were to

(a) compare the diversity of bird communities in different landscape contexts that include vineyards
(b) assess the particular influence of vineyards on the richness and abundance of bird communities
(c) undertake a fine-scale analysis of habitat selection by those bird species able to use vineyards and their associated semi-natural habitats.

Throughout this study we paid particular attention to bird species that are typical of open farmland habitats and which are therefore particularly likely to be experiencing declines at national and European levels.

Materials and methods

Study area

In the Loire valley, the wine-growing area corresponding to the Saumur–Champigny controlled origin appellation was chosen for this study (Fig. 1), as since 2004 it has been involved in a major "biodiversity and landscape" project initiated by local wine producers (Sigwalt, Pain, Pancher, & Vincent, 2012). This area to the south-east of the town of Saumur is limited to the north by the Loire River and to the west by the Thouet River and covers around 5900 ha, 1600 of which are devoted to vineyards belonging to approximately 120 viticulturists. Although vineyards occupy a large part of this area, a diversity of other adjacent land cover types form the landscape: mainly woodland (24%), other crops (17%) and built-up areas (16%). In and around the grapevines a diversity of semi-natural non-cropped habitats occur, such as isolated trees (mainly walnut and other fruit trees), hedges, ditches (rarely), dry limestone walls, grassy margins and green cover.

Bird sampling at two spatial scales: landscape and vine plot

Using a simple map based on 5 habitat classes, a moving window analysis was carried out to select 1 × 1 km square areas containing at least 25% vines. From around 650 windows that met this criterion we selected twelve to represent contrasting landscape contexts found within the study area: wooded (>30% woodland cover), built-up (>20% built-up), mainly vine (>66% vine) and mixed situations (>8% woodland and >8% built-up), with three landscapes per context distributed in different parts of the study area (Fig. 1).

Within each of these study landscapes, two transects of 1 km were traced at 250 m from the window edge and 500 m apart in such a way as to sample the entire landscape unit.

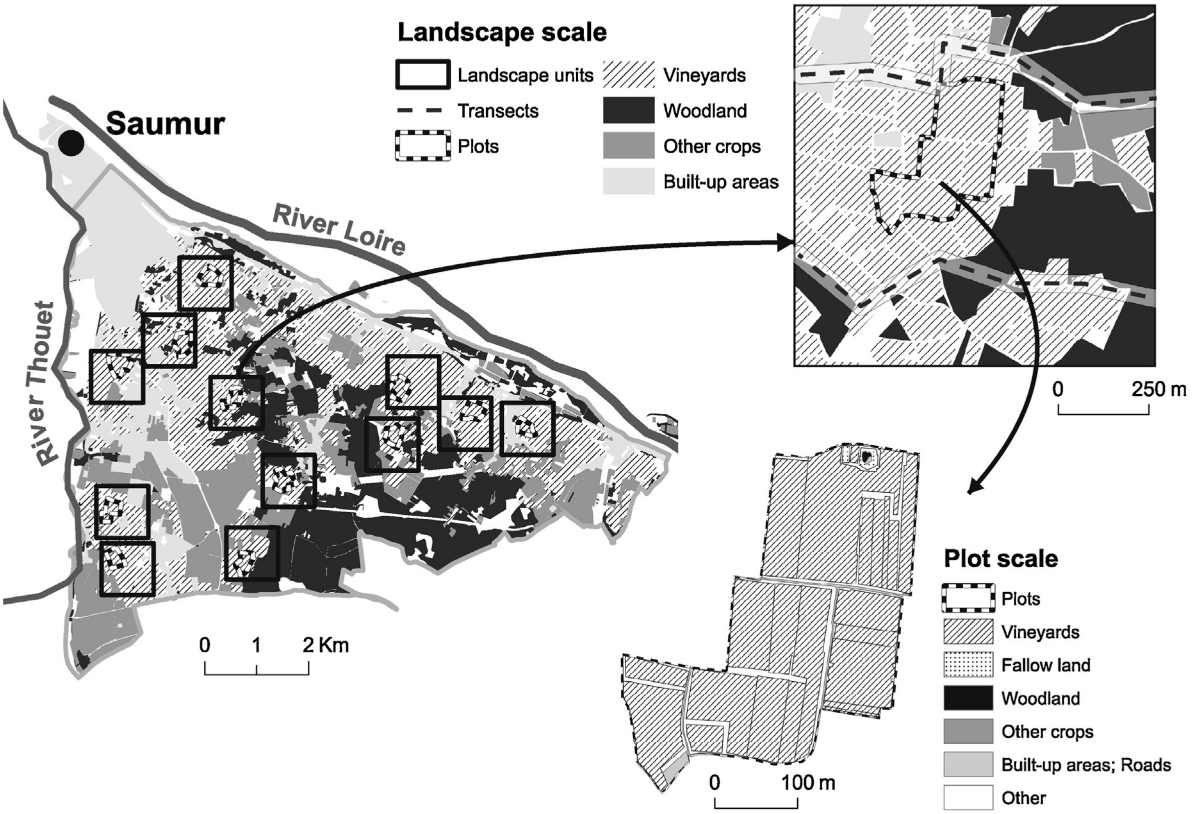

Fig. 1. Map of the study area near Saumur in the Loire valley in France. The three sampling scales are represented: 1 km × 1 km study windows and within these, 1 km × 50 m transects and 10 ha plots.

These were marked using a GPS with about half oriented N–S and the other half E–W. The 24 km of transect thus obtained were sampled using standard line transect methodology (Bibby, Burgess, Hill, & Mustoe, 2000) during two consecutive breeding seasons (2009–2010) with two visits per season: between early April and mid-May for resident species and between mid-May and end of June to detect summer visitors. Two detection bands were used: <25 m, 25 m–250 m. As detection probabilities vary between habitats and species, in certain analyses only the data from the first and most reliable detection band (25 m either side of each transect) were retained for analysis. This sampling unit is referred to as the transect scale.

In the centre of each landscape unit we also searched for a continuous area dominated by vines, around 10 ha in size, within which to carry out finer-scale bird surveys using territory mapping methods (Bibby et al., 2000). Each plot was composed of several fields of vineyards, always associated with a number of different land owners and wine growers. The twelve plots covering a total surface area of 126 ha were visited 8 times per breeding season in two years (between mid-March and mid-June), allowing at least two weeks between visits. On each plot, a route was defined, which approached to within 50 m of every point. This route was walked slowly while exact positions of all birds detected were mapped on the 1:2500 habitat maps along with information about territorial behaviour as well as any observed feeding behaviour or movements. Each visit lasted at least 45 min. All bird surveys were carried out between 1 and 4 h after sunrise on days without continuous rain or wind.

Habitat and vine management survey

We combined existing local land cover data, based on classification of orthophotographs and fieldwork, to produce a land cover map of the study area. From this, the proportions of four main land cover types (vineyard, woodland, built-up, other crops) were calculated (using ArcGis 9.3) for each landscape unit (1 × 1 km) and for each transect (1 × 50 m bird sampling unit). For each plot a detailed 1:2500 habitat map was digitised from field surveys carried out in the summer of the first year of the study. Within the plots habitat variables relating to vine management were surveyed using visible criteria i.e. spacing between vine rows, ratio of bare ground to green cover, proportion of dicotyledonous or monocotyledonous plants, chemical v. mechanical weeding (on alternate rows), grapevine age class and proportion of stony ground. Using a detailed classification (10 habitat features; Table 1), all non-cropped habitats were also mapped in the

Table 1. Habitat types and variables used in analyses of bird–habitat relationships at the plot scale. * d_ indicates "distance to the nearest".

Habitat type	Habitat types for compana	Habitat variables for k-select	Detailed habitat descriptions
Vineyard	Vine	vine_age	Vine age (young, mature, old)
		weed_method	Weeding method on rows (mechanical/chemical)
		p_grass	Proportion of grasses between rows (<20%, 20–80%, >80%)
		p_dicots	Proportion of dicotyledons between rows (<20%, 20–80%, >80%)
		p_baresoil	Proportion of bare soil between rows (none, 1–80%, >80%)
		ploughed_strip	Strip between rows mechanically ploughed (yes/no)
		stones	Quantity of stony ground in the plot (none or dispersed, abundant)
		gr_cover_width	Green cover width
Associated uncropped semi-natural habitats	Grassy patch	*d_grass	Area of grassy or herbaceous vegetation
	Grassy bank/ditch	d_bank_ditch	Area of grassy or herbaceous vegetation with a bank or ditch
	High tree cover	d_high_trees	Trees > 7 m
	Low tree cover	d_low_trees	Trees < 7 m
	Shrub cover	d_shrubs	Area with shrub cover
		d_building	Building
		d_crops	Crop (other than vine)
		d_man-made	Man-made objects (wall, pylon. . .)
	Wall with vegetation	d_wall_veg	Wall with vegetation (mostly ivy)
		d_roadside	Roadside vegetation

field and digitised. Table 1 shows the list of habitat variables retained for the spatial analyses of bird–habitat relationships. Appendix A: Table 1 provides land cover proportions measured at landscape (1 km^2) and transect scales.

Data analysis

Prior to analysis of the transect data we excluded species for which this survey method was not appropriate: highly mobile species or birds of prey, migratory species on passage, species not directly associated with on-site habitats and domesticated species as well as large flocks (>8 individuals). For each species the maximum number of individuals recorded per 1 km transect was used. First, cumulative species richness in the different landscape contexts was compared using bird data from both detection bands (up to 250 m from the observer). In subsequent analyses only the data from the transect scale were retained for analysis.

We carried out canonical correspondence analysis (CCA) using CANOCO 4.53 (Ter Braak & Smilauer, 2002) to detect patterns in species assemblages related to land cover type (vine, crop, woodland, built-up areas) at landscape (1 km × 1 km) and transect (1 km × 50 m) scales. Rare species were down-weighted for the analysis (see Ter Braak & Smilauer, 2002 for details) and species with less than 3 occurrences were removed from the data set to prevent distortion. The relative influence of the two sets of land cover variables, corresponding to landscape or transect scales, on bird communities observed on transects was investigated using partial canonical correspondence analysis (CCA). The fraction of variation explained by one set of variables, and not shared by the other set, was assessed, using the first set as constrained variables, and the second set as covariables (Le Coeur, Baudry, & Burel, 1997; Leps & Smilauer, 2003). We subsequently carried out a constrained ordination using only one set of land cover variables corresponding to the spatial scale which best explained bird community structure.

In order to test the effect of proportion of vineyard within transects on total bird abundance, bird species richness and on the abundance of species associated with vineyard habitats at the finer territory mapping scale, we used generalised linear mixed models. This approach is appropriate for analysing non-normal data involving random effects (Bolker et al., 2009), such as the potential influence of our choice of study landscapes. The fixed effect variable was the proportion of vineyard habitat on the transect and the dependent variables (count data) were assumed to be Poisson distributed. The analyses were carried out using the glmm function of the MASS package in R (Venables & Dichmont, 2004).

In order to study habitat selection at the finer plot scale, we needed to compare habitat use as a function of its availability using standard compositional analyses such as those developed by Aebischer, Robertson, and Kenward (1993). For both of the following analyses, we opted for a type III design, which takes individual responses to habitat availability into consideration as well as the habitat available to each individual, as opposed to type I or II designs which consider the response of an entire population to habitat availability (Thomas & Taylor, 1990). Therefore, the only habitats considered available to an individual bird, were those found within the plot in which it was recorded. A plot represented a data unit and for each we computed the proportion of each habitat available as well as the proportion used by each study species (the proportion of individuals recorded in a particular habitat). We retained all species with >30 registrations over the two sampling years for analysis, whether or not they displayed territorial behaviour and we pooled the two years' data. Although detection probability must vary to some extent between trees, bushes and open habitats, we considered this bias to be negligible, as the habitats we sampled were relatively homogeneous in structure and the birds using them very accustomed to regular human disturbance. We also relied on our high sampling intensity, assumed to produce density estimates very close to the actual abundances (see Svensson, 1979). Using GIS, we projected bird locations onto vector maps derived from field surveys. The number of bird contacts occurring on each habitat type, as a function of its availability in a given plot, could then be computed. The compositional analyses were carried out in two steps: first, the significance of habitat selection was tested using a Wilks lambda randomisation test and then a ranking matrix was built to compare each habitat's use with its availability.

First, we analysed which species selected vineyards themselves as opposed to six types of associated semi-natural habitats within the plots. These habitat types were: grassy patch, grassy bank/ditch, high or low tree cover, shrub cover and wall with vegetation. These compositional analyses (compana function) were carried out using the adehabitat package developed by Calenge (2006) within R (R Development Core Team, 2008).

For species selecting vineyards a K-select analysis was used to examine how management of the vineyard and/or distance to semi-natural habitats might explain those species' habitat selection at the plot scale. This type of analysis allowed us to include a greater number as well as a mix of both continuous (distance) and discrete (management) habitat variables in the same analysis (Calenge, Dufour, & Maillard, 2005). In order to calculate the distance variables, maps with a 6 × 6 m resolution were prepared by rasterisation of vector maps of management variables. The chosen resolution was fine enough to detect differences in these variables at the broader parcel scale without overly increasing the total number of pixels and hence total calculation times for the analysis. For each pixel, the distance to the nearest non-cropped habitat was calculated. Distance variables were transformed using the formula: $\exp(-0.00003 \times \text{distance}^2)$ to correct for the fact that birds would be more strongly influenced by habitats at shorter distances than by those further away (Calenge, 2005). Field checks were carried out to determine the nearest habitat feature if none was present in the originally surveyed vine plot.

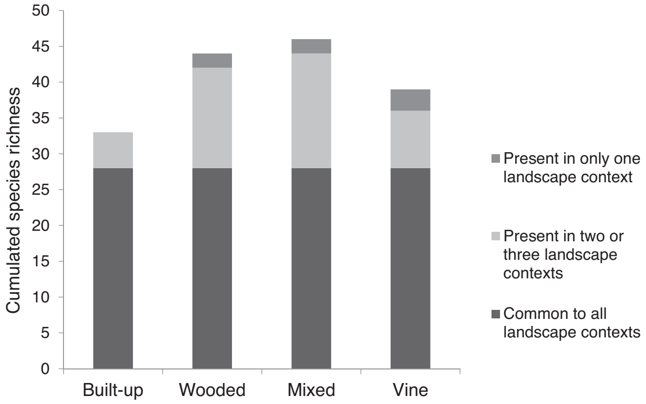

Fig. 2. Cumulated species richness in the four landscape contexts; the proportions of species occurring in all contexts, two or three contexts or only one context are shown. All observations at window scale (up to 250 m from transect routes) are included, for 45 species retained in the analysis (see text).

Results

Bird communities of the wine-growing landscape

During the study, 93 species of bird were observed either on transects or in the plots. This represents around half of the total number of species (188) that regularly nest in the "Pays de la Loire" region (Marchadour & Séchet, 2008). Of the 79 species observed on transects, 45 were retained in the analysis. As Fig. 2 shows, species richness of landscapes in a woodland context, or containing a proportion of woodland (mixed) was higher than in landscapes dominated by either vineyards or built-up land. However, three species were only detected in landscapes dominated by vineyard cover and these were Stone curlew *Burhinus oedicnemus*, Corn bunting *Miliaria calandra* and Lapwing *Vanellus vanellus*.

Thirty four species were retained for CCA (see Appendix A: Table 2 for species names and codes). Bird community composition was better explained by transect scale than by landscape scale land cover variables; the fraction of variation explained by transect scale variables and not shared by landscape scale variables was 45.8% of the total inertia, whereas the fraction of variation explained by the landscape scale variables and not shared by transect scale variables was only 26.7%. A constrained ordination was subsequently carried out including only transect land cover variables (Fig. 3). The eigenvalues of the first and second axes were 0.176 and 0.146, respectively. The first axis was clearly associated with vineyard cover and with open farmland species such as the Skylark, Woodlark, Linnet *Carduelis cannabina* and Red-legged partridge *Alectoris rufa*. The second axis separated woodland and built-up land cover. A group of mainly generalist species, but also some woodland specialists, such as the Great spotted woodpecker *Dendrocopos major* and the Short-toed treecreeper *Certhia brachydactyla*, were associated with woodland while a typically urban group of species including House sparrow *Passer domesticus*, Collared dove *Streptopelia decaocto* and Black redstart *Phoenicurus ochruros* were associated with built-up areas. Transects were well grouped according to their dominant land cover, on this factorial map, irrespective of their landscape context.

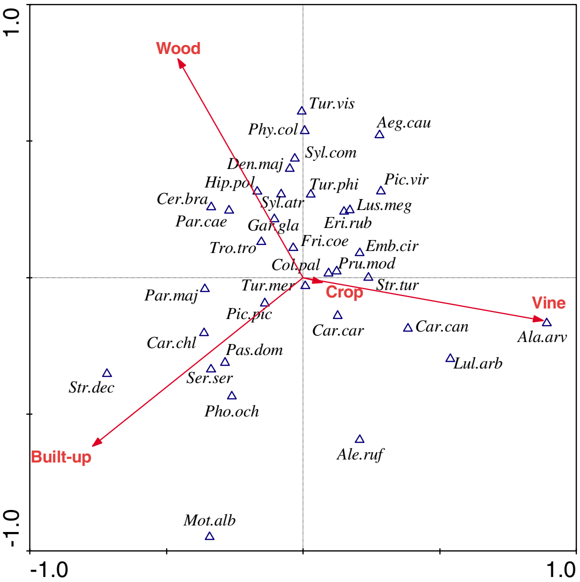

Fig. 3. First factorial map of the canonical correspondence analysis (CCA) with land cover proportions at the transect scale as environmental variables. Biplot representing land cover variables and species positions; bird name abbreviations are given in Appendix A: Table 2.

Effect of vineyard cover on bird richness and abundance at the transect scale

There was a strong negative relationship between the proportion of vineyard cover per transect and both total abundance and species richness of birds (Table 2, Fig. 4). Among the 16 species that made regular use of vineyard habitats at the plot scale, 13 were also detected on transect routes. Of these, only two, Woodlark and Skylark showed a significantly positive response to increasing proportion of vineyard. Four species followed the general trend and were significantly less abundant in vine-dominated areas while the majority of species analysed showed a non-significant negative relationship with vineyard cover, with the exception of the Linnet, whose response was weakly positive. Only the abundance of both Cirl bunting and Skylark were influenced by the random effect of landscape unit.

The contribution of vineyard habitats to bird diversity was therefore weak in terms of species richness and overall abundance. Even species that were relatively abundant at the plot scale were negatively affected by increasing vineyard cover. However, for a small number of farmland specialists, vineyard cover had a positive influence on abundance at this landscape scale.

Table 2. Summary of generalised linear mixed models exploring the response of species richness, total abundance and abundance of 13 vineyard species to proportion of vineyard cover at the 1 km transect scale. The species are listed in decreasing order of relative abundance [within transects].

Dependent variable	Slope ± S.E.	*t*-Value	*p*-Value	Percentage of random effects explained by landscape unit
Species richness	−1.66 ± 0.42	−3.99	<0.01	<1
Total abundance	−2.53 ± 0.52	−4.91	<0.001	<1
Blackbird	−2.69 ± 0.66	−4.05	<0.01	<1
Woodpigeon	−1.20 ± 0.75	−1.61	NS	<1
Linnet	0.14 ± 0.99	0.14	NS	<1
Chaffinch	−3.32 ± 0.88	−3.78	<0.01	<1
Goldfinch	−0.83 ± 1.22	−0.68	NS	<1
Blackcap	−4.10 ± 1.12	−3.66	<0.01	<1
Cirl bunting	−1.43 ± 0.94	−1.52	NS	41.64
Woodlark	2.59 ± 1.11	2.33	<0.05	5.76
Magpie	−2.04 ± 1.97	−1.03	NS	<1
Melodious warbler	−6.28 ± 1.36	−4.62	<0.001	<1
Dunnock	−1.16 ± 1.54	−0.76	NS	<1
Skylark	12.11 ± 3.59	3.37	<0.01	77.73
Song thrush	−2.75 ± 2.18	−1.26	NS	<1

Habitat selection at the plot scale

In the plots 60 species were observed but only 16 of these were recorded more than 30 times over 2 years and were retained for compositional analyses. These 16 species, most clearly associated with vineyard habitats in our study, we shall call vineyard species (see Appendix A: Table 3). In terms of habitat availability, vineyards occupied around 100 ha or 82% of the sampled plots with only a small surface area of associated semi-natural, non-cropped habitats available to

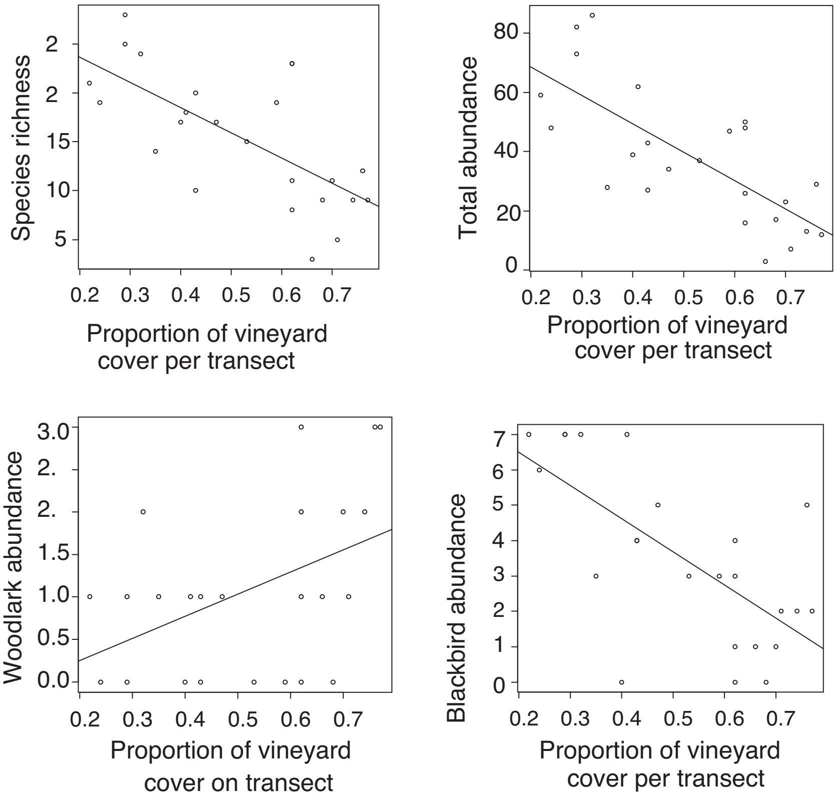

Fig. 4. Reponse of species richness, total abundance and abundance of a farmland specialist, Woodlark *Lullula arborea*, and a habitat generalist, Blackbird *Turdus merula*, to increasing proportion of vineyard cover at the 1 km transect scale ($n = 24$).

Table 3. Habitat selection by 16 abundant species in vineyards as revealed by compositional analysis of habitat use compared with availability. Habitats used significantly more or less than at least three other habitats are indicated; + indicates positive selection and − negative selection and the numbers in brackets indicate the number of other habitats more or less significantly used. Example: +(3) means that Woodlark uses vineyards significantly more than 3 other habitat types out of a total of seven.

Species	Number of contacts	Lambda	*p* Value	Habitats selected						
				Vineyard	High tree cover	Low tree cover	Shrub cover	Grassy patch	Grassy bank or ditch	Wall with vegetation
Woodlark	368	0.0534	0.014	+(3)				+(5)		
Blackbird	255	0.0466	0.004	−(5)	+(5)	+(4)				
Woodpigeon	239	0.09376	0.016	−(4)	+(5)	+(4)				
Cirl bunting	215	0.0320	0.004	−(6)		+(3)				
Chaffinch	196	0.0083	0.004	−(6)	+(5)	+(3)	−(4)			
Linnet	164	NS	NS							
Goldfinch	82	0.1225	0.030	−(3)	+(3)	+(4)	−(4)	+(3)		−(3)
Skylark	75	NS	NS							
Carrion crow	69	NS	NS							
Magpie	60	0.0688	0.008	−(5)	+(3)					+(4)
Melodious warbler	58	0.0088	0.004	−(6)	+(3)	+(4)			−(4)	
Blackcap	57	0.0068	0.002	−(6)	+(3)	+(5)			−(4)	
Meadow pipit	54	NS	NS							
Starling	44	NS	NS							
Song thrush	41	0.0536	0.002	−(6)	+(3)	+(3)		−(4)		
Dunnock	39	0.0345	0.002	−(6)	+(6)	+(4)				

birds (see Appendix A: Table 4). This result strengthened our assumption that detection probability would vary little in response to vegetation structural heterogeneity. Within the vineyard, grapevine age varied. The green cover between vine rows was dominated by grasses, though situations with more bare soil or dicotyledonous species did exist. Around half the grapevines were on stony ground and most of the space between vine rows had not been recently ploughed. A majority of weeding appeared to be carried out using mechanical rather than chemical methods.

Despite the wide availability of vineyard habitat, compositional analysis showed that only one species, Woodlark, showed a rather weak preference for vineyards as opposed to the six non-cropped habitats included in the analysis (Table 3). Five other species used both vineyard and non-cropped habitats indiscriminately: Linnet, Carrion crow *Corvus corone*, Skylark, Meadow pipit *Anthus pratensis* and Starling *Sturnus vulgaris*. The remaining species positively selected semi-natural non-cropped habitats adjacent to the grapevines and, although preferences varied, most species selected areas with trees. At this finer scale it was apparent that, even among species using vineyard habitats, the grapevines themselves were avoided by all but 5 species. Most species selected much less abundant semi-natural habitats, within the plots.

As the Woodlark was the only species showing any positive selection for vineyards themselves, the k-select analysis was carried out on this species alone. Although observations of Woodlarks were numerous, the analysis failed to detect any consistent habitat selection within plots. In some plots habitat selection was strong, i.e. habitat use was not correlated with its availability, but the direction of habitat selection could be opposite for two different plots. In other plots, no clear habitat preferences were apparent. In view of these weak and/or contradictory findings, we concluded that the set of habitat variables measured were not able to explain the distribution of this species.

Discussion

This study has shown that a landscape mosaic including vineyards can support a diverse avifauna. Landscape contexts with a proportion of woodland tended to be more species-rich. The three species found only in landscape contexts with a high proportion of vineyard (Stone curlew, Corn bunting and Lapwing) were all very infrequent at the study site and are farmland specialists with declining populations at national and European levels. A more heterogeneous landscape context did not influence community composition in vineyard habitats and it seemed that local land cover types largely determined bird communities in vineyards while interactions with neighbouring types were limited. It should be noted, however, that the relatively small sample size of 12 landscape units limited analysis at this scale. Woodland bird communities were very distinct from farmland communities of crops and vineyards, as were the bird communities of built-up areas. In terms of species richness, while overall community richness was relatively high at the landscape scale, vineyards themselves were regularly used by only a small proportion of the bird species. Five of the 16 species we found to be frequent users of vineyards are considered to be farmland specialists, two are associated with built-up areas, one with woodland or forest and the rest are generalists (Jiguet, 2010). Of the five farmland specialists, Skylark, Meadow pipit and Linnet are experiencing declines at national and European level, while the population trend of the Woodlark is uncertain, and only the Cirl Bunting is moderately increasing. Most of the species using vineyards were more abundant in adjacent semi-natural habitats. This provides further evidence that vineyards do not generally support a high diversity of birdlife (Sierro & Arlettaz, 2003). However, the Woodlark and the Skylark responded positively to increasing vineyard cover in the landscape. The Skylark, in particular, is known to prefer open landscapes and to avoid tall, dense vegetation cover on field boundaries (Donald, Evans, Buckingham, Muirhead, & Wilson, 2001a). It is interesting to note that the species appeared to perceive vineyard cover as attractive open habitat at this scale, despite the presence of the rows of grapevine trees.

At the plot scale, it was clear that species which were abundant tended to be common, generalist species using semi-natural habitats in the vicinity of the grapevines. As Filippi-Codaccioni, Devictor, Bas, and Julliard (2010) have shown, habitat heterogeneity, i.e. increasing proportion of woody or scrubby habitats in crop-dominated French farmland contexts, may indeed lead to increases in overall species richness and abundance, but often to the detriment of open farmland habitat specialists. These species may therefore benefit from the maintenance of homogeneous areas of open farmland. Incentives to farmers to plant hedges potentially lead to the creation of hedgerow networks in agricultural areas where they have never previously existed. In a wine-growing context, planting hedges may be the last thing a viticulturist feels able to invest in, as sunlight reaching the grape crop is key to the success of his farm. Our results suggest that such schemes may also not be appropriate in conservation terms, if the objective is to improve habitats for declining specialists of open farmland. Functional homogenisation, whereby generalist species do better than specialists, is just one component of a more general process of biotic homogenisation, currently observed in many natural communities impacted by human activities (McKinney & Lockwood, 1999), including French bird communities in disturbed landscapes (Barnagaud, Devictor, Jiguet, & Archaux, 2011).

Some of the species using the Saumur vineyards were too rare to be included in the analysis of bird–habitat relationships. Species like the Stone curlew or the Corn bunting, found predominantly in vineyard-dominated study landscapes, might also benefit from wildlife-focused vineyard management. For these relatively rare species, at least at local scale, the study of their habitat requirements is complicated. In the case of the Stone curlew, diurnal sampling is not the optimal technique to obtain abundance estimates, and indeed crepuscular and nocturnal sampling could complete this inventory of the Saumur vineyards' breeding avifauna.

At the plot scale, the Skylark selected neither vineyard habitats nor non-cropped habitats, using both indiscriminately. At the transect scale, it may have been simply selecting open areas that include both grapevine crops and other arable crops, more suitable for its breeding ecology. Territory densities within the twelve vine plots averaged 0.6 pairs/10 ha, with a maximum of 5 pairs/10 ha (data not shown; see Pithon, Fréville, Pain, and Vallet (2012)), which is comparable with densities in Great Britain (Mason & Macdonald, 2000), but rather lower than estimates from French set-aside (Eraud, Boutin, & Roux, 2000) or from arable farmland in Germany (Schön, 2011). Vineyards therefore possibly constitute a suitable but slightly suboptimal habitat for this species.

Woodlark was therefore the only abundant species to actively use vine plots. Studies of fine-scale habitat selection by this species have usually been carried out in other types of farmland (Sirami, Brotons, & Martin, 2011) or heathland habitats (Mallord, Dolman, Brown, & Sutherland, 2007), where the species favours a mix of sparsely vegetated areas and bare ground. In southern Switzerland, where the species occurs mostly in vineyards, radio-tracking has shown that woodlarks prefer vegetated vineyards that provide a mix of grasses and herbs interspersed with bare ground, the former providing food supply and nesting opportunities, the latter foraging grounds (Arlettaz et al., 2012). Situations with either very high grass cover (organic vineyards) or completely bare ground (vineyards with heavy use of herbicides) were both avoided. We found no consistent relationships between woodlark abundance and proportion of grasses, dicotyledonous plants or bare ground. Arlettaz et al. (2012) also noted a negative relationship with vineyard age, with woodlarks preferring the more open canopies offered by younger grapevines, however, vine age did not clearly influence woodlarks in Saumur either. The difficulty we experienced in explaining this species' distribution may be due to fine-scale heterogeneity in farming practises. Interviews with farmers to obtain information about chemical weed control, use of fungicides and insecticides and other practices not visible in the field could have completed our set of explanatory variables. However, as Sigwalt et al. (2012) showed, in the Saumur–Champigny wine-growing context, land ownership and management is remarkably fragmented. In a single vine plot, as many as ten viticulturists could be involved in vine cultivation, while as few as two or three rows, in what appears to be a vine plot, may be managed in a very different way to the rest of the plot. This is not unusual in wine-growing areas and will make the study of vineyard biodiversity more complex for organisms perceiving and selecting habitat at relatively broad scales.

To conclude, the possible contribution that viticulture could make to bird conservation would involve tailoring vineyard management to benefit farmland specialists, and the challenge for future studies of bird–vineyard relationships will be to produce more detailed and constructive management advice to wine-growers interested in wildlife enhancement. As studies of this kind accumulate, allowing more comparisons between wine-growing areas, and with more analysis of bird–vineyard relationships at regional and national scales, this should become possible. In the meantime, we have shown, again, that the maintenance of open habitats, including vineyards, is important for declining farmland specialists, and that planting hedges may not always be the most suitable wildlife conservation approach in wine-growing areas.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.12.004.

References

Aebischer, N. J., Robertson, P. A., & Kenward, R. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, *74*(5), 1313–1325, http://doi.org/10.2307/1940062

Arlettaz, R., Maurer, M. L., Mosimann-Kampe, P., Nusslé, S., Abadi, F., Braunisch, V., et al. (2012). New vineyard cultivation practices create patchy ground vegetation, favouring woodlarks. *Journal Für Ornithologie*, *153*(1), 229–238.

Aubertot, J. N., Barbier, J. M., Carpentier, A., Gril, J. J., Guichard, L., Lucas, P., et al. (2005). *Pesticides, agriculture et environnement, Réduire l'utilisation des pesticides et limiter leurs impacts environnementaux*. pp. 64. France: INRA et Cemagref.

Barnagaud, J. Y., Devictor, V., Jiguet, F., & Archaux, F. (2011). When species become generalists: On-going large-scale changes in bird habitat specialization. *Global Ecology and Biogeography*, *20*(4), 630–640, http://doi.org/10.1111/j.1466-8238.2010.00629.x.

Baudry, J., Bunce, R., & Burel, F. (2000). Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management*, *60*(1, SI), 7–22, http://doi.org/10.1006/jema.2000.0358.

Begum, M., Gurr, G., Wratten, S., Hedberg, P., & Nicol, H. (2006). Using selective food plants to maximize biological control of vineyard pests. *Journal of Applied Ecology*, *43*(3), 547–554, http://doi.org/10.1111/j.1365-2664.2006.01168.x.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is heterogeneity the key? *Trends in Ecology and Evolution*, *18*(4), 182–188.

Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. H. (2000). *Bird census techniques* (2nd ed.). Oxford: Academic Press.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127–135, http://doi.org/10.1016/j.tree.2008.10.008.

Brotons, L., & Herrando, S. (2001). Factors affecting bird communities in fragments of secondary pine forests in the north-western Mediterranean basin. *Acta Oecologica*, *22*(1), 21–31, http://doi.org/10.1016/S1146-609X(00)01095-X.

Brugarolas, M., Martinez-Carrasco, L., Bernabeu, R., & Martinez-Poveda, A. (2010). A contingent valuation analysis to determine profitability of establishing local organic wine markets in Spain. *Renewable Agriculture and Food Systems*, *25*(1, SI), 35–44, http://doi.org/10.1017/S1742170509990202.

Bruggisser, O. T., Schmidt-Entling, M. H., & Bacher, S. (2010). Effects of vineyard management on biodiversity at three trophic levels. *Biological Conservation*, *143*(6), 1521–1528, http://doi.org/10.1016/j.biocon.2010.03.034.

Busck, A. (2003). Hedgerow planting analysed as a social system—Interaction between farmers and other actors in Denmark. *Journal of Environmental Management*, *68*(2), 161–171, http://doi.org/10.1016/S0301-4797(03)00064-1.

Calenge, C. (2005). *Des outils statistiques pour l'analyse des semis de points dans l'espace écologique*. Lyon: Université Lyon I.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519, http://doi.org/10.1016/j.ecolmodel.2006.03.017.

Calenge, C., Dufour, A., & Maillard, D. (2005). K-select analysis: A new method to analyse habitat selection in radio-tracking studies. *Ecological Modelling*, *186*(2), 143–153, http://doi.org/10.1016/j.ecolmodel.2004.12.005.

Chamberlain, D., Fuller, R., Bunce, R., Duckworth, J., & Shrubb, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, *37*(5), 771–788, http://doi.org/10.1046/j.1365-2664.2000.00548.x.

Donald, P. F., Evans, A. D., Buckingham, D. L., Muirhead, L. B., & Wilson, J. D. (2001). Factors affecting the territory distribution of Skylarks Alauda arvensis breeding on lowland farmland. *Bird Study*, *48*(3), 271–278, http://doi.org/10.1080/00063650109461227.

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B*, *268*, 25–29.

Eraud, C., Boutin, J. M., & Roux, D. (2000). Breeding habitat of the skylark (*Alauda arvensis*) in a mediterranean agrosystem. *Game and Wildlife Science*, *17*(3), 147–163.

Fiedler, A. K., Landis, D. A., & Wratten, S. D. (2008). Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biological Control*, *45*(2), 254–271, http://doi.org/10.1016/j.biocontrol.2007.12.009.

Filippi-Codaccioni, O., Devictor, V., Bas, Y., & Julliard, R. (2010). Toward more concern for specialisation and less for species diversity in conserving farmland biodiversity. *Biological Conservation*, *143*(6), 1493–1500, http://doi.org/10.1016/j.biocon.2010.03.031.

Fuller, R., Hinsley, S., & Swetnam, R. (2004). The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis*, *146*(2), 22–31, http://doi.org/10.1111/j.1474-919X.2004.00357.x.

Gillespie, M., & Wratten, S. D. (2012). The importance of viticultural landscape features and ecosystem service enhancement for native butterflies in New Zealand vineyards. *Journal of Insect Conservation*, *16*(1), 13–23, http://doi.org/10.1007/s10841-011-9390-y.

Haslem, A., & Bennett, A. F. (2008). Countryside elements and the conservation of birds in agricultural environments. *Agriculture, Ecosystems and Environment*, *125*, 191–203.

Jarrige, F. (2004). Les mutations d'une agriculture méditerranéenne face à la croissance urbaine: Dynamiques et enjeux autour de Montpellier. *Cahiers Agricultures*, *13*(1), 64–74.

Jedlicka, J. A., Greenberg, R., & Letourneau, D. K. (2011). Avian conservation practices strengthen ecosystem services in california vineyards. *PLoS ONE*, *6*(11), http://doi.org/10.1371/journal.pone.0027347.

Jiguet, F. (2010). *Les résultats nationaux du programme STOC de 1989 à 2010*. Retrieved from ⟨www2.mnhn.fr/vigie-nature⟩.

Kross, S. M., Tylianakis, J. M., & Nelson, X. J. (2012). Effects of introducing threatened falcons into vineyards on abundance of passeriformes and bird damage to grapes. *Conservation Biology*, *26*(1), 142–149, http://doi.org/10.1111/j.1523-1739.2011.01756.x.

Le Coeur, D., Baudry, J., & Burel, F. (1997). Field margins plant assemblages: Variation partitioning between local and landscape factors. *Landscape and Urban Planning*, *37*, 57–71.

Leps, J., & Smilauer, P. (2003). *Multivariate analysis of ecological data using CANOCO*. Cambridge: Cambridge University Press.

Mallord, J. W., Dolman, P. M., Brown, A. F., & Sutherland, W. J. (2007). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, *44*(1), 185–195.

Marchadour, B., & Séchet, E. (2008). *Avifaune prioritaire en Pays de la Loire*. pp. 1–221. France: Coordination régionale LPO Pays de la Loire.

Mason, C. F., & Macdonald, S. M. (2000). Influence of landscape and land-use on the distribution of breeding birds in farmland in eastern England. *Journal of Zoology*, *251*(3), 339–348.

McKinney, M., & Lockwood, J. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, *14*(11), 450–453, http://doi.org/10.1016/S0169-5347(99)01679-1.

OIV. (2012). *Statistical report on world vitiviniculture 2012*. International Organisation of Vine and Wine. Retrieved from ⟨http://www.oiv.int/oiv/info/enstatistiquessecteurvitivinicole#bilan⟩.

Petit, S., Stuart, R., Gillespie, M., & Barr, C. (2003). Field boundaries in Great Britain: Stock and change between 1984, 1990 and 1998. *Journal of Environmental Management*, *67*(3), 229–238, http://doi.org/10.1016/S0301-4797(02)00176-7.

Pithon, J. A., Fréville, M., Pain, G., & Vallet, J. (2012). L'avifaune d'un milieu viticole (AOC Saumur-Champigny): Estimations d'abondance par la méthode des plans quadrillés. *Crex—Bulletin Scientifique de la LPO Anjou*, *12*, 41–46.

Pointereau, P. (2001). Development of the space occupied by hedgerows in France over the past 40 years: The contribution and limits of statistical data. In C. Barr, & S. Petit (Eds.), *Hedgerows of the world: Their ecological functions in different landscapes* (pp. 117–122). IALE, UK: International Association of Landscape Ecology.

R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Schön, M. (2011). Long-lived sustainable microhabitat structures in arable ecosytems, and Skylarks (*Alauda arvensis*). *Journal of Nature Conservation*, *19*(3), 143–147, http://doi.org/http://dx.doi.org/10.1016/j.jnc.2010.10.003.

Sierro, A., & Arlettaz, R. (2003). L'avifaune du vignoble en Valais central: Évaluation de la diversité à l'aide de transects. *Nos Oiseaux*, *50*, 89–100.

Sigwalt, A., Pain, G., Pancher, A., & Vincent, A. (2012). Collective innovation boosts biodiversity in French vineyards. *Journal of Sustainable Agriculture*, *36*(3, SI), 337–352, http://doi.org/10.1080/10440046.2011.654008.

Sirami, C., Brotons, L., & Martin, J.-L. (2011). Woodlarks *Lullula arborea* and landscape heterogeneity created by land abandonment. *Bird Study*, *58*(1), 99–106, http://doi.org/10.1080/00063657.2010.532861.

Siriwardena, G. M., Baillie, S. R., Buckland, S. T., Fewster, R. M., Marchant, J. H., & Wilson, J. D. (1998). Trends in the abundance of farmland birds: A quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology*, *35*(1), 24–43, http://doi.org/10.1046/j.1365-2664.1998.00275.x.

Somers, C. M., & Morris, R. D. (2002). Birds and wine grapes: Foraging activity causes small-scale damage patterns in single vineyards. *Journal of Applied Ecology*, *39*, 511–523.

Svensson, S. (1979). Comparison of bird census methods. In *Bird census work and nature conservation*. pp. 13–22. Göttingen: Hans Oelke. Retrieved from ⟨http://www.luvre.org/data_o_pdf/Luvre-047,%20Svensson,%20metodjamf.pdf⟩.

Tanadini, M., Schmidt, B. R., Meier, P., Pellet, J., & Perrin, N. (2012). Maintenance of biodiversity in vineyard-dominated landscapes: A case study on larval salamanders. *Animal Conservation*, *15*(2), 136–141, http://doi.org/10.1111/j.1469-1795.2011.00492.x.

Ter Braak, C. J. F., & Smilauer, P. (2002). *CANOCO reference manual and CANODRAW for Windows user guide, Version 4.5*. Ithaca, NY: Microcomputer Power.

Thomas, D. L., & Taylor, E. J. (1990). Study designs and tests for comparing resource use with availability. *Journal of Wildlife Management*, *54*(2), 322–330.

Thomson, L. J., & Hoffmann, A. A. (2009). Vegetation increases the abundance of natural enemies in vineyards. *Biological Control*, *49*(3), 259–269, http://doi.org/10.1016/j.biocontrol.2009.01.009.

Thomson, L. J., & Hoffmann, A. A. (2013). Spatial scale of benefits from adjacent woody vegetation on natural enemies within vineyards. *Biological Control*, *64*(1), 57–65, http://doi.org/10.1016/j.biocontrol.2012.09.019.

Van Helden, M., Guenser, J., & Fulchin, E. (2012). Viticulture, landscape and functional biodiversity: Agronomy, ecology, sociology and economy. In *IOBC/WPRS bulletin*. pp. 207–211. Lleida: John Holland, Bärbel Gerowitt, Oscar Alomar, Felix Bianchi, Lisa Eggenschwiler, Maarten van Helden, Camilla Moonen, Hans-Michael Poehling and Walter Rossing.

Venables, W., & Dichmont, C. (2004). GLMs, GAMs and GLMMs: An overview of theory for applications in fisheries research. *Fisheries Research*, *70*(2–3), 319–337, http://doi.org/10.1016/j.fishres.2004.08.011.

Voříšek, P., Jiguet, F., Van Strien, A., Škorpilová, J., Klvaňová, A., & Gregory, R. D. (2010). Trends in abundance and biomass of widespread European farmland birds: How much have we lost? In *BOU proceedings—Lowland farmland birds III*.

Wilson, J. D., Evans, A. D., & Grice, P. V. (2009). *Bird conservation and agriculture*. United Kingdom: Cambridge University Press.