BIODIVERSITY RESEARCH

Geographical generality of bird-habitat relationships depends on species traits

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Abstract

Aim: The environmental filtering process is often considered as static in ecological studies. However, growing evidence shows that species-environment relationships vary in space and time. In this study, we assessed to what extent bird responses to landscape components can be geographically generalised and whether differences in response generality can be explained by traits.

Location: France.

Methods: We collected a large bird data set (1968 point counts over two years) with a standardised protocol in three agricultural regions with different levels of intensification in France. We modelled the relationships between the distribution of 26 bird species and three landscape components (percentage of woodland, hedgerow density and landscape heterogeneity) and assessed whether differences between regions in bird responses to landscape components (i.e., landscape-region interactions) can be explained by three species traits (habitat specialisation, diet and migration strategy). We also examined the response of total species richness.

Results: We found that 16 species showed regional differences in their response at least for one of the three landscape variables. Importance of landscape-region interactions was significantly correlated with two species traits. Responses of specialist species to landscape components were geographically more constant than those of generalists. The geographical variability of responses was higher for migrants than for sedentary species. There were no significant relationships for the diet trait. Species richness responded positively to the three landscape metrics in a similar way in the three regions.

Main conclusions: The results underline the need to take into account the spatial differences between species responses to habitats according to their traits when modelling species-habitat relationships at large scales. From a conservation point of view, we suggest that conservation measures could be generalised at a large scale for specialist species which are declining in agricultural landscapes.

KEYWORDS
birds, land cover, model generality, species-habitat relationship, traits

1 | INTRODUCTION

Environmental filtering (or species sorting) is seen as a key process in structuring metacommunities (Bonthoux & Balent, 2015; Logue, Mouquet, Peter, & Hillebrand, 2011; Özkan, Svenning, & Jeppesen, 2013). Until recently, many studies have assessed correlations between species distributions and environmental factors at large scales, assuming that the environmental filtering process for a given species is constant in space. However, for a decade, several papers have shown regional variations in species-habitat relationships for several taxa (for plants Randin et al., 2006; for birds Whittingham et al., 2007; Schaub, Kéry, Birrer, Rudin, & Jenni, 2011; for mammals McAlpine et al., 2008; for amphibians Zanini, Pellet, & Schmidt, 2009). Knowing the level of generality in species-habitat relationships has a particular importance for theory by providing key information on intraspecific variability in the environmental filtering process. It can also be useful in species distribution modelling where models are usually transferred from one site to another without taking into account regional variations in environmental associations which can blur the local accuracy of predictions (Dormann et al., 2012). From a conservation point of view, it is crucial for managers and environmental policies to take into account to what extent results obtained in one region can inform decisions in another (McAlpine et al., 2008) and whether conservation actions can be generalize between regions or have to be adapted locally (Whittingham et al., 2007; Batáry, Báldi, Kleijn, & Tscharntke, 2010). However, due to the cost and the logistics of collecting large-scale data, studies assessing geographical variations in habitat selection are still rare.

Several processes may lead to shifts in habitat selection between populations of a given species. For example, a high population size can increase the importance of competition and lead certain individuals to exploit suboptimal habitats (Morris, 2003; Jensen & Cully, 2005; Beest, McLouglin, Mysterud & Brook, 2016). The regional species pool can modulate interspecific interactions and consequently local habitat uses (Sanza, Traba, Morales, Rivera, & Delgado, 2012). Preference for a habitat can change according to the habitat availability in landscapes and increase when that habitat is rare (Aarts, Fieberg, Brasseur, & Matthopoulos, 2013; Robinson, Wilson, & Crick, 2001). A few recent studies have also shown that generality of habitat selection may be linked to ecological characteristics of species (Dobrowski et al., 2011; Wasof et al., 2015). In particular, specialist species with narrow niches are likely to exploit a lower diversity of habitats between different regions than generalist species (Wasof et al., 2015). Zuckerberg, Fink, La Sorte, Hochachka, and Kelling (2016) have found in the Eastern United States that long-distance bird migrants that experience varied landscapes may show a higher seasonal plasticity (i.e., a lower generality) in habitat associations than sedentary species. Understanding how generality of species-habitat relationships is governed by species traits can provide information on which species may adapt to land cover changes and for which species conservation measures can be generalised geographically.

In agricultural landscapes, bird assemblages are strongly filtered by the amount of woody elements (i.e., woodland or hedgerow) which determines the presence or absence of species according to their nesting behaviour and their diet (Balent & Courtiade, 1992; Besnard, Fourcade, & Secondi, 2016; Bonthoux, Barnagaud, Goulard, & Balent, 2013; Fonderflick, Besnard, & Martin, 2013). A high landscape heterogeneity can be necessary for species needing complementary resources (Dunning, Danielson, & Pulliam, 1992; Pickett & Siriwardena, 2011) and can also promote bird species richness (Bonthoux et al., 2013). A few studies have assessed geographical variations in bird-habitat relationships in an agricultural system, and the results are contrasting. Whittingham et al. (2007) and Schaub et al. (2011) found a variability of habitat selection between regions for several farmland birds, while Whittingham, Wilson, and Donald (2003) showed a geographic generality of habitat response for an open habitat specialist. An approach based on species traits should help to improve understanding of the mechanisms behind these contrasting findings.

In this study, we assessed whether the responses of bird assemblages to three relevant landscape components are generalizable between three agricultural regions located along a latitudinal gradient in France. Because these regions have different levels of agricultural intensification and thus different availabilities of semi-natural and cultivated habitats, we expected to observe some changes in bird-habitat selections (Aarts et al., 2013; Robinson et al., 2001). A strong asset of our study is that it was not based on atlas data with multiple observers or a group of heterogeneous data collected in different regions, but that it used a standardized protocol applied in three regions with sampling from comparable gradients of habitat. This last point is particularly important to ensure that observed regional differences are linked to ecological processes and not to methodological bias (Menke, Holway, Fisher, & Jetz, 2009; Randin et al., 2006). We tested whether the generality level of bird-habitat relationships can be linked to three species traits: habitat specialization, diet and migration strategy. We predicted that specialists that are locally associated with a particular habitat have more constant habitat selection across regions than generalists. We also expected that diet generalist species (omnivores) which can adapt their behaviour to new food resources (Ducatez, Clavel, & Lefebvre, 2015) are more flexible to regional specificities than diet specialists (insectivorous or herbivorous). Finally, following Zuckerberg et al. (2016) who found that migrants show a high temporal plasticity in land cover associations, we explored whether populations of migratory species choose more diverse habitats between regions than residents, producing a lower spatial generality in habitat selection.

2 | METHODS

2.1 | Study area

We collected data in three Long Term Ecological Research sites 400 km apart along a north–south gradient in France (Figure 1) but subject to comparable temperate climates (see above). These three selected sites are characterized by agricultural landscapes with different levels of intensification and different availabilities of semi-natural and cultivated elements (see Fig. S1 for a visual comparison). The "Zone Atelier Armorique" (Arm) site is located in Brittany, north-western France
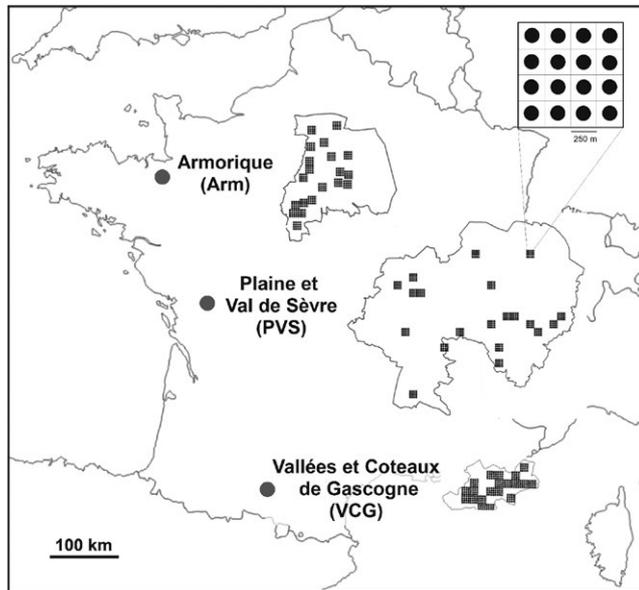
FIGURE 1 The three study sites (black dots) and spatial location of sampled landscape units within each site represented at the same scale. In each landscape unit, 16 point counts were located at the centre of 6.5 hectare cells as shown in the upper right corner of the map

(48°36′N, 1°32′W) and is characterised by "bocage" landscapes with hedgerow networks and mixed dairy farming systems. The area contains mainly annual crops (mostly winter cereals and maize), along with temporary and permanent grasslands separated by hedgerows. Hedgerows are composed of trees including oak (*Quercus robur*) or chestnut (*Castanea sativa*) planted on an earthen bank. The shrub layer is present in about 50% of hedgerows. In woodlands, dominant tree is beech (*Fagus sylvatica*). The climate is temperate oceanic (mean annual temperature 12°C; mean annual precipitation 700 mm; Joly et al., 2010).

The "Zone Atelier Plaine et Val de Sèvre" (PVS) site is located in Poitou-Charentes, western France (46°14′N, 0°24′W). This is an intensively cultivated area, with mainly winter cereals, but also oilseed rape, sunflower, maize, alfalfa and grasslands. Small woodland patches and hedgerows are present but irregularly distributed. Hedgerows are composed of a mixture of shrubs (e.g., *Prunus spinosa*, *Crataegus monogyna*) and trees (e.g., *Acer campestre*, *Quercus robur*). In woodlands, dominant trees are oaks (*Quercus robur*, *Quercus petraea*). The climate is temperate oceanic (mean annual temperature 12°C; mean annual precipitation 800 mm; Joly et al., 2010).

The "Vallées et Coteaux de Gascogne" (VCG) site is located in Midi-Pyrénées, south-western France (43°16′N, 0°51′E). The area is hilly, and the climate is suboceanic with mediterranean influences (mean annual temperature 12.5°C; mean annual precipitation 750 mm; Joly et al., 2010). Landscapes are heterogeneous and characterised by a mixed crop-livestock system, with a combination of crops (including oilseed rape, sunflower, maize and winter cereals), grasslands, hedgerows and woodlands. Hedgerows are composed of a mixture of shrubs (e.g., *Crataegus monogyna*, *Cornus mas*, *Prunus spinosa*) and trees (e.g., *Acer campestre*, *Ulmus campestris*). In woodlands, dominant trees are oaks (*Quercus robur*, *Quercus pubescens*, *Quercus petraea*).

2.2 | Site sampling and landscape metrics

In each of the three sites, we selected 20 landscape units of one square kilometre. These landscape units were distributed along a mature woodland gradient in each site as the presence of woodland is the strongest driver of bird community patterns in agricultural landscapes (Balent & Courtiade, 1992). We spatially designed our sampling to optimize the similarity of woodland gradient distributions between the three sites (Figure 2). As agricultural landscape contexts strongly differed between the three sites (see the description of the study areas), the spatial arrangement of selected landscape units of the sites also differed (Figure 1).

We recorded 16 equidistant point counts in each landscape unit. Points were separated from each other by 250 m and located in the centre of 6.25 ha cells. This area corresponded to the mean home range size of a few hectares of most of the studied species (Söderström & Pärt, 2000). We repeated point counts in 2009 and 2010 at the same locations to take into account the potential year-to-year variation in birds' habitat selection. In 2010, a further landscape unit was added in mature woodlands in the three sites to increase the sampled open-wooded gradient. A total of 1968 point counts was thus recorded ([16 points × 20 landscape units in 2009 + 16 points × 21 landscape units in 2010] × 3 sites). In each study, site point counts were performed once each year during the breeding season (May–June) under favourable weather conditions (no strong rain or wind) and during 4 hr after sunrise. In each site, point counts were spatially performed to decorrelate sampled habitat and the date of recording. At each point, the presence or absence of bird species was recorded during a period of 5 min. This duration is adequate and sufficient to obtain correct detectability of bird species and to analyse bird community distributions in our context of agricultural landscapes (Bonthoux & Balent, 2012). Once point count visit per year and a small count duration permitted us to maximize the overall sample size and to optimize the distribution of sampled points along the habitat gradients, which is important to model species distributions effectively (Brotons, Herrando, & Pla, 2007). Raptors, which have large home ranges, and human-related species (e.g., sparrows and swallows) were not considered in the analyses.

Some studies have shown the importance of landscape structure at multiple scales to explain bird distributions, but it is the effect of local landscape components that prevails in our type of context (Pelosi et al., 2014). In each 6.25 ha cell, by digitising 2008 aerial photographs and using direct field observations, we calculated six landscape components: the percentages of "Woodland," "Crop," "Permanent grassland" and "Fallow land," the length of "Hedgerow" and a landscape heterogeneity metric ("Heterogeneity") calculated with the Shannon index and based on the percentage of land covers. In models of species distribution (see above), we only used the three "Woodland," "Hedgerow" and "Heterogeneity" variables for three reasons. Firstly, gradient distributions of these variables were the most comparable between the three sites, especially for "Woodland" which was used to determine the spatial distribution of sampling (Figure 2). Secondly, these three variables were highly positively or negatively
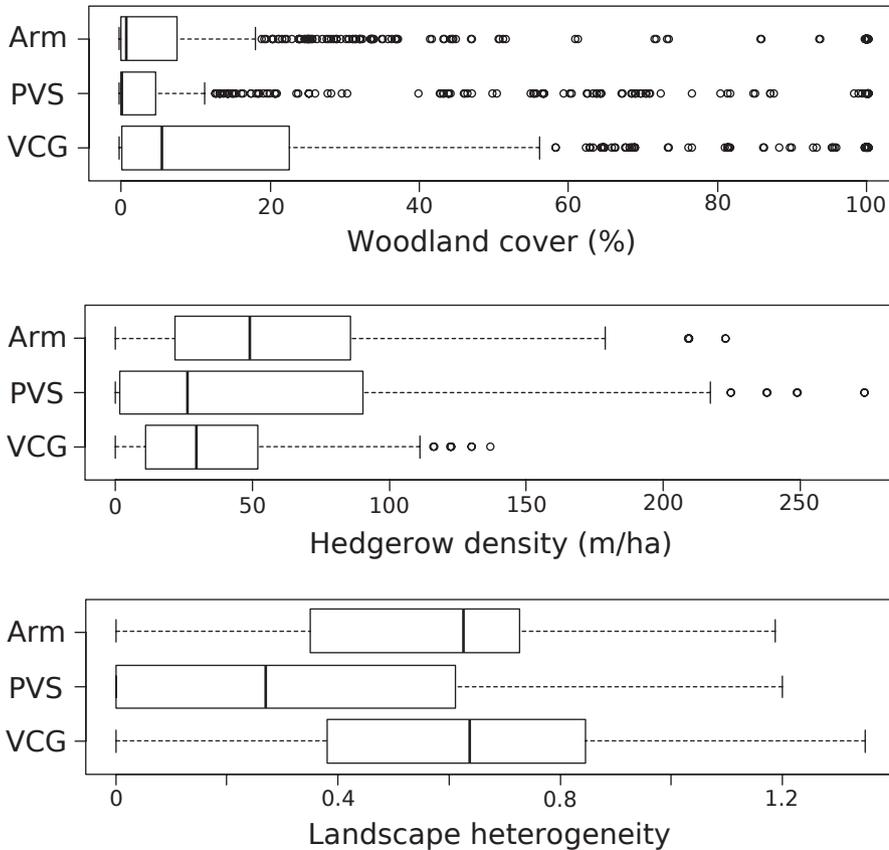
correlated with other land cover variables (i.e., with Cropland and Permanent grassland, $r > |.55|$) but were weakly correlated with each other ($r < |.26|$, see Table S1 for all correlation values). Finally, effects of these variables are the most easily interpretable. The presence of woodland and hedgerow is highly relevant to understand areas selected or avoided by bird species in agricultural landscapes (Besnard et al., 2016; Fonderflick et al., 2013) and has thus been shown to be very important to explain bird distributions and bird species richness (Berg, 2002; Bonthoux et al., 2013). Furthermore, heterogeneous landscapes with diverse habitats have been shown to be very relevant to explain the distributions of some bird species and species richness (Bonthoux et al., 2013).

2.3 | Bird trait data

Three traits were used to explain the difference of habitat generality among species (Table S2). Habitat specialization reflects the variance of distribution of species abundance between eight habitats with different vegetation structures (Barnagaud, Devictor, Jiguet, & Archaux, 2011; Bonthoux et al., 2013). This index is based on a French-scale bird survey (French Breeding Bird Survey; Jiguet, Devictor, Julliard, & Couvet, 2012) to ensure no circularity with our data. Birds were classified into three diet categories: omnivore, invertebrate or herbivore (Holland, Hutchison, Smith, & Aebischer, 2006; Gregory et al., 2007; Table S2). Migration strategy was classified as resident or long-distance migrant. Short-distance migrants were included with residents (Gregory et al., 2007).

2.4 | Analyses

Among the 57 bird species recorded in the three regions, we were able to compare habitat selection between two or three sites for 26 species (Table S2). For a given species, data from a site were considered and included in the species model (see section 2.4 below) if the species was present in more than 30 cells in cumulated 2009 and 2010 data for this site. We also calculated the total species richness as the sum of all species present in each cell.

We analysed the relationships between presence–absence of each species and the three landscape variables using generalized linear mixed models (GLMMs) with binomial distribution and Poisson distribution for the species richness. Explanatory variables were standardized to mean = 0 and SD = 1 to facilitate the interpretation of estimates (Schielzeth, 2010). We also added a fixed qualitative "Region" effect with three modalities. To assess the generality of bird-habitat relationships we added interactions between each landscape metric and the region variable. We took the temporal and spatial hierarchical structure of our sampling design into account by adding the landscape unit identity and the sampling year as random effects. Thus, the structure of our models was as follows:

Individual species, Species richness ~ Region + Woodland + Woodland: Region + Hedgerow + Hedgerow: Region + Heterogeneity + Heterogeneity: Region + (1|Landscape unit) + (1|Year).

We used a model averaging approach to take into account the uncertainty in the model selection process (Burnham & Anderson, 2003). We fitted all possible models nested within the full model and ranked them

TABLE 1 Relationships between the presence–absence of bird species and the three landscape variables and Region. These relationships were modelled with generalized mixed linear models with binomial distribution for presence–absence species data and Poisson distribution for species richness and using a model averaging approach (n = 1968 or n = 1312 when data of two or three sites were respectively included in models, see Table 1). The estimated coefficient and standard deviation (in brackets) are indicated for each variable. The significant coefficients of landscape metrics are in bold, and those of Region variable and interaction terms are indicated by 'X'. % D^2 is the explained deviance for the best model (with the smallest AICc)

	Region	Woodland		Hedgerow		Heterogeneity		Woodland: Region	Hedgerow: Region	Heterogeneity: Region	% D^2
Alauda arvensis	X	**−0.98**	**(0.18)**	**−0.91**	**(0.16)**	−0.17	(0.16)	o	o	o	0.40
Anthus trivialis	X	**0.33**	**(0.14)**	**0.68**	**(0.07)**	**0.64**	**(0.13)**	X	o	X	0.32
Certhia brachydactyla	X	**0.84**	**(0.11)**	0.29	(0.17)	**0.61**	**(0.14)**	o	o	o	0.12
Cuculus canorus	X	0.17	(0.17)	0.01	(0.15)	0.09	(0.18)	o	o	o	0.01
Carduelis carduelis	X	**−1.46**	**(0.47)**	−0.12	(0.13)	**0.58**	**(0.18)**	o	o	o	0.03
Carduelis chloris	X	**−0.90**	**(0.34)**	−0.08	(0.12)	−0.12	(0.18)	o	o	X	0.18
Corvus corone	X	−0.01	(0.08)	−0.08	(0.08)	0.20	0.10	o	o	o	0.09
Dendrocopos major	X	0.18	(0.19)	0.04	(0.13)	**0.40**	**(0.15)**	X	o	o	0.02
Emberiza calandra	X	**−2.02**	**(1.02)**	**−0.36**	**(0.14)**	**0.36**	**(0.15)**	o	o	o	0.37
Emberiza cirlus	o	−0.21	(0.18)	**0.30**	**(0.10)**	0.19	(0.13)	o	o	o	0.08
Emberiza citrinella	o	**−0.94**	**(0.52)**	−0.04	(0.15)	0.25	(0.18)	X	o	o	0.13
Erithacus rubicola	X	**0.96**	**(0.09)**	**0.45**	**(0.09)**	**0.29**	**(0.13)**	o	o	X	0.33
Fringilla coelebs	X	**0.33**	**(0.09)**	**0.60**	**(0.14)**	**0.39**	**(0.08)**	o	X	o	0.40
Garrulus glandarius	X	**0.56**	**(0.11)**	0.27	(0.16)	0.09	(0.13)	o	o	o	0.13
Hippolais polyglotta	X	**−0.73**	**(0.36)**	0.10	(0.17)	0.21	(0.18)	X	X	X	0.50
Luscinia megarhynchos	o	**0.40**	**(0.11)**	**0.77**	**(0.10)**	**0.55**	**(0.13)**	X	o	X	0.24
Cyanistes caeruleus	X	**0.46**	**(0.10)**	**0.43**	**(0.08)**	0.14	(0.10)	X	o	o	0.17
Phylloscopus collybita	X	**0.83**	**(0.08)**	**0.46**	**(0.10)**	**0.50**	**(0.12)**	o	X	o	0.35
Parus major	o	**0.34**	**(0.08)**	**0.33**	**(0.12)**	0.13	(0.12)	o	X	X	0.13
Sylvia atricapilla	X	0.12	(0.12)	**0.35**	**(0.10)**	**0.42**	**(0.11)**	X	X	o	0.21
Sylvia communis	o	−0.16	(0.16)	0.17	(0.10)	**0.27**	**(0.11)**	X	o	o	0.14
Saxicola rubicola	X	**−1.65**	**(0.45)**	**−0.41**	**(0.15)**	0.27	(0.16)	o	o	o	0.43
Streptopelia turtur	X	**0.47**	**(0.10)**	**0.39**	**(0.09)**	**0.53**	**(0.11)**	o	o	o	0.13
Turdus merula	o	**0.34**	**(0.08)**	**0.33**	**(0.12)**	0.13	(0.12)	o	X	X	0.40
Turdus philomelos	X	**0.40**	**(0.14)**	**0.24**	**(0.10)**	**0.34**	**(0.11)**	X	o	o	0.17
Troglodytes troglodytes	X	**1.15**	**(0.21)**	**0.53**	**(0.09)**	**0.35**	**(0.09)**	X	o	o	0.35
Total species richness	X	**0.17**	**(0.01)**	**0.16**	**(0.02)**	**0.15**	**(0.01)**	o	o	o	0.28

on the basis of AICc and assigned them Akaike weights (w_i). Interaction terms were included only when both pure variables of the interaction were present. We averaged the parameters of the 95% confidence set of models (sum of w_i > 0.95), weighted by w_i. We considered variables as significant when confidence intervals did not include zero. We calculated the importance of variables as the sum of the w_i over the models in which the variable appears. This approach quantifies the probability that each term is included in the best model. We then calculated the percentage of deviance explained only by the fixed factors for the model with the smallest AICc, using Nakagawa & Schielzeth's method (Nakagawa & Schielzeth, 2013). No spatial autocorrelation was found in model residuals indicating that it was not necessary to include spatial variables (data not shown).

To assess whether the spatial variability of species-habitat relationships was linked to traits, we calculated the correlations between the importance of the three interaction terms in GLMMs and trait values. We also calculated a global landscape:region interaction importance as the mean of all interaction term importance. We used Spearman correlation tests for the specialization trait and Wilcoxon tests for the two qualitative traits.

We performed all analyses using R 3.2.3 (R Development Core Team) and the lme4 (Bates, Maechler, Bolker, & Walker, 2014), MuMIn (Barton & Barton, 2015) and ncf (Bjørnstad, 2015) libraries.

3 | RESULTS

When the impact of the three landscape variables without interaction with "Region" was compared, the "Woodland" variable had the

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Diversity and
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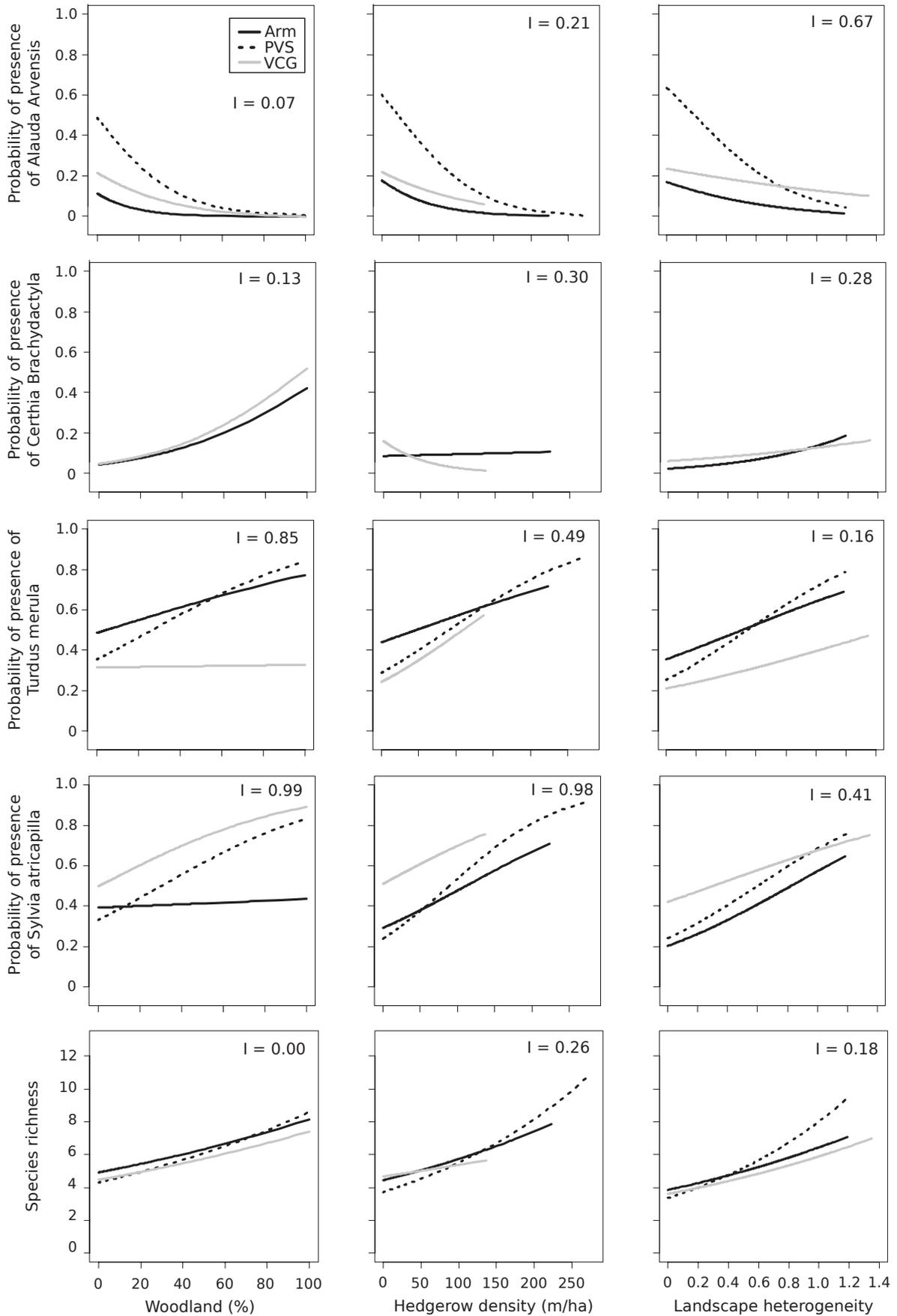Conservation
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FIGURE 3 Response curves of two habitat specialist bird species (*Alauda arvensis*, *Certhia brachydactyla*), two generalists (*Turdus merula*, *Sylvia atricapilla*) and total species richness to the three landscape variables in each site. Importance of the region interaction terms (I, ranging from 0 to 1) in the model averaging approach is added (see section 2). *Certhia brachydactyla* distribution was only modelled in Arm and VCG due to its low number of occurrences in PVS (Table S1)

highest number of significant positive or negative effects on species distributions (Table 1). Nineteen species were significantly associated with the amount of woodland and of these, 13 had a positive and six a negative effect. Regarding "Hedgerow," 13 species were positively and three species negatively associated with this variable. Fourteen species responded positively to an increase in landscape heterogeneity ("Heterogeneity"). Total species richness responded significantly and positively to the three landscape metrics (Table 1, Figure 3).

Across the 26 selected species, 16 species showed significant regional differences in their response for at least one of the three landscape variables (Table 1). For example, *Turdus merula* and *Sylvia atricapilla* showed contrasting responses to the "Woodland" variable between regions while responses of *Alauda arvensis* and *Certhia brachydactyla* to "Woodland" were similar between regions (Figure 3). The "Woodland":"Region" interaction was significant for 10 species. In four cases, the interaction was significant, while the "Woodland" effect alone was not. This is explained by the fact that for some species the "Woodland" variable had effects in some regions but not in others giving an overall non-significant effect. For instance *Sylvia atricapilla*

responded strongly and positively to "Woodland" in PVS and VCG but not in Arm (Figure 3), giving a significant "Woodland":"Region" interaction but a non-significant "Woodland" effect (Table 1). The "Hedgerow":"Region" interaction was significant for six species, and the "Heterogeneity":"Region" interaction was significant for seven species (Table 1). The three landscape:region interaction terms were not significant, and their importance in the model averaging process was low for species richness (Table 1, Figure 3).

We then assessed the relationships between the importance of landscape:interaction terms in the model averaging process and three species traits (Figure 4, see Table S3 for importance of interaction terms). There was a significant negative relationship between the importance of "Hedgerow":"Region" interaction, the mean landscape:region importance and the habitat specialization trait meaning that habitat selection for specialists was geographically more constant than for generalists. Figure 3 shows responses of two specialists (one open and one woodland species with high specialization indices, *Alauda arvensis* and *Certhia brachydactyla* respectively) and two generalists (both species with low specialization indices, *Turdus merula* and *Sylvia*
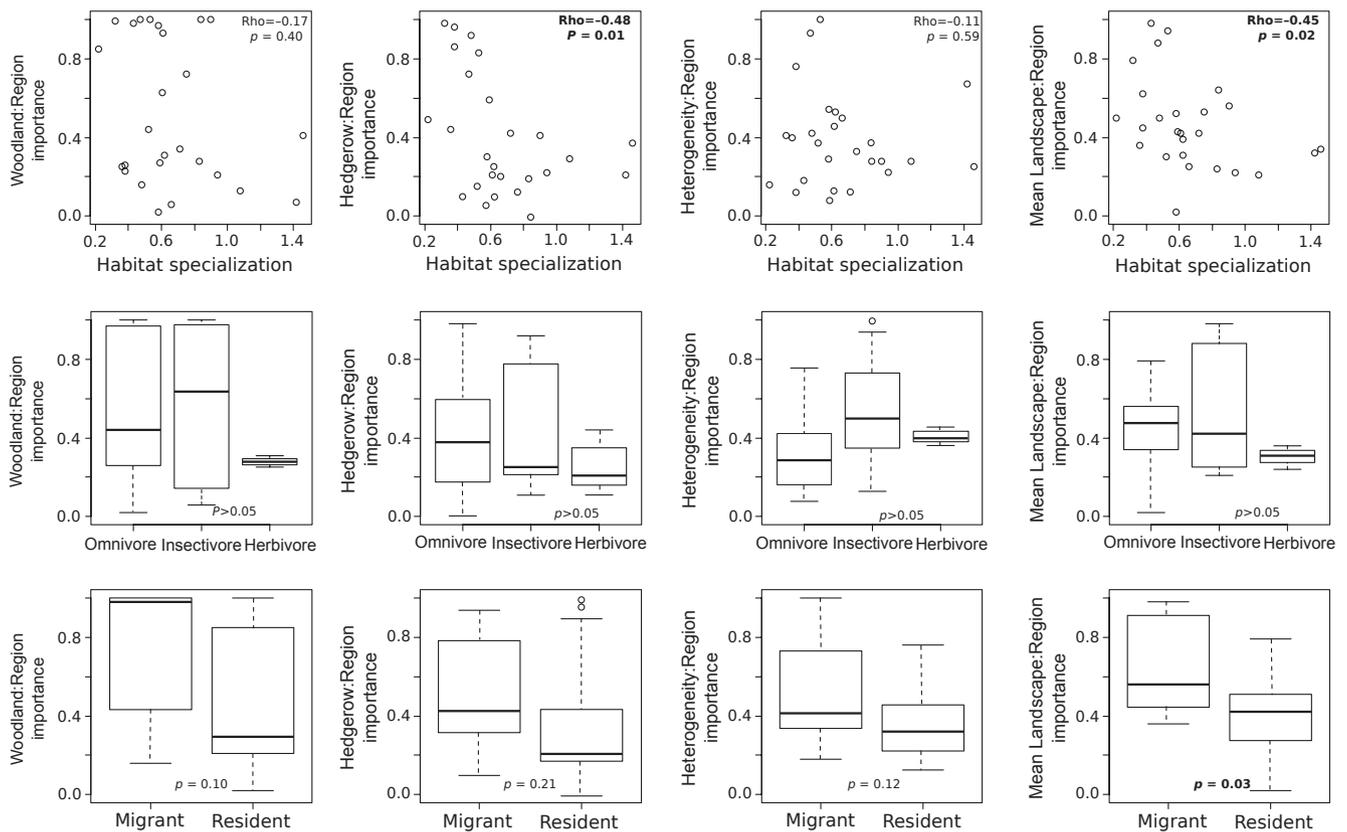

FIGURE 4 Relationships between the importance of the three landscape:region interaction terms and the three bird ecological traits. A mean landscape:region interaction term was also computed. Spearman correlation tests and Wilcoxon tests were applied for habitat specialization and the two qualitative traits, respectively

atricapilla) to the three landscape variables in each site. The importance of the three landscape:region terms tended to be greater for migrants than for residents and the mean landscape:region importance was significantly higher for migrants, meaning that habitat selection was more constant between regions for residents than for migrants (Figure 4). There were no significant relationships between the importance of interaction terms and the diet trait.

4 | DISCUSSION

Species–environment relationships are often considered as static (Dormann et al., 2012). Based on a data set collected in three regions in France, we found that habitat selection varied geographically for several bird species and that this variation was linked to their ecological traits. We showed that specialists and residents had a higher degree of generality in habitat association than generalists and long-distance migrants. We also found a high generality of relationships between bird species richness and landscape metrics.

We found many significant responses of bird species to the three landscape metrics considered. In line with other studies, the amount of woodland and hedgerow strongly discriminated bird distribution in the landscapes (Bonthoux et al., 2013). Species nesting on the ground or in low vegetation (e.g., *Alauda arvensis*, *Emberiza calandra*, *Saxicola rubicola)* selected habitats away from woodlands and hedges (Besnard et al., 2016; Fonderflick et al., 2013). On the other hand, species nesting high up in trees or bushes (e.g., *Fringilla coelebs*, *Erithacus rubecula*, *Turdus merula*) or in tree cavities (e.g., *Parus major*, *Certhia brachydactyla*, *Cyanistes caeruleus*) were strongly associated with the presence of woodland or hedgerows (Tellería & Pérez-Tris, 2004). Heterogeneity of landscape was a landscape characteristic which favoured over half the observed species (e.g., *Anthus trivialis*, *Certhia brachydactyla*, *Carduelis carduelis*).

Despite strong overall responses of species to the landscape metrics, more than half (*n* = 16) of the 26 considered species responded differently between regions for at least one landscape variable. This relatively high geographic variation in habitat selection is consistent with previous studies. Whittingham et al. (2007) found that various local habitat variables associated with agri-environment schemes (e.g., field boundary structure, surrounding land use) tended to have different effects on 11 farmland species in sites located in England and Wales. Schaub et al. (2011) observed different responses for 10 of 13 bird species to six habitats between four regions or along an altitudinal gradient in Switzerland. In contrast to the results found by these authors, the responses we found to landscape metrics between regions were not opposing (i.e., positive and negative) but were of different intensities (i.e., estimate values). In our study, the three landscape gradients considered were similar among the sites (especially for the woodland and heterogeneity gradients).We are thus confident that differences observed in species-habitat relationships were not linked to truncated responses due to insufficient gradient sampling (Menke et al., 2009; Randin et al., 2006). During sampling strategies, it was possible to control gradients of habitat quantity between regions but

not totally differences in habitat quality (e.g., plant composition, vegetation structure, management intensity; see the Method/Study area section). These differences in habitat quality are due to regional differences in landscape histories and human practices. We are aware that such differences can influence bird distributions. For example, it has been shown that some woodland birds are sensitive to growth stage of woodland, understorey structure and dominant tree species composition (Hewson, Austin, Gough, & Fuller, 2011). These differences may blur our ability to detect biological responses of birds and may lead to overestimation of the differences of habitat selection between regions. However, including more habitat descriptions in models would have led to an inability to compare similar landscape gradients between the three sites. This issue did not prevent us from finding significant relationships between generality in habitat selection and species traits and the three selected landscape metrics remain coherent because they are comparable between studies. Management guidelines are typically made considering gross classes of habitat (e.g., "hedgerows"), not with respect to regional details of vegetation composition, so it is relevant to consider relationships with such gross categories, even if they gloss over variation in habitat details. Nevertheless, more parameters on plant composition and vegetation structure should be taken into account in further similar studies, provided that habitat distributions are comparable between distant study areas.

Interestingly, we found that generality of bird-habitat relationships can be linked to certain species traits. In accordance with the theory which predicts that specialists benefit from stable habitats, whereas generalists may respond positively to habitat variability (Colles, Liow, & Prinzing, 2009), we found a higher geographical consistency in responses to landscape components for specialists than for generalists. In line with this result, Koleček, Reiff, and Weidinger (2015) found few interaction effects of the responses of *Alauda arvensis* (a farmland specialist) to several habitat characteristics (crop type, sward height and landscape structure surrounding the study site) and three European countries (Poland, Germany and the Czech Republic). From an applied perspective, this result is important and suggests that for habitat specialists, which are in decline at the European scale (Le Viol et al., 2012), conservation actions in agricultural landscapes could be applied in the same way at a large scale, particularly for the three landscape metrics considered in this study. In contrast to habitat specialization, we did not find a significant region interaction with diet specialization. We considered landscape structure through land cover metrics that did not clearly reflect diet gradients. Availability of food resources (e.g., insects and fruit) can differ between woodlands or hedgerows according to their vegetation structure or management. The approach proposed by Vanreusel, Maes, and Van Dyck (2007) of measuring the amount of food resources directly (host plants and nectar sources for two butterfly species in their study) can be useful to assess the generality of distribution models, but it is very complicated to perform for birds, which include many insectivore species.

A recent study of forest breeding birds in North America showed that Neotropical migrants have a higher seasonal variation in land cover associations than residents and temperate migrants (Zuckerberg et al., 2016). In line with this result, we found that long-distance migrants may be more

flexible in breeding habitat selection between regions than residents or partial migrants. Theoretically migration behaviour could be viewed as an ability to survive in diverse environments and to adapt to changing resources (Somveille, Rodrigues, & Manica, 2015). Further studies are needed to confirm our results, but migration strategy could thus be a useful trait for explaining the ability of species to select different habitats.

At the community level, we showed that increasing the amount of woody components (woodlands and hedgerows) and the diversity of habitats in agricultural landscapes can promote bird species richness in agricultural landscapes (Atauri & de Lucio, 2001; Batáry, Matthiesen, & Tscharntke, 2010; Bonthoux et al., 2013). This result is consistent with the fact that we found a majority of species responding positively to the three landscape metrics. The response curves of species richness to the landscape metrics were extremely similar between regions, particularly regarding the response to the amount of woodland. This result suggests that the landscape structure strongly drives bird community structures whatever the region. Pools of species associated with open and wooded habitat were very similar between the three regions, which may explain the similar species richness responses between regions.

Unlike studies or meta-analyses collecting data from different sites with different biological methods or habitat quantifications, our study was based on a large field sampling conducted across three regions using an homogeneous protocol. In an agricultural context, our findings suggest that geographic variations in bird species responses to landscape components could be partly related to species traits, particularly to habitat specialization and migration strategy. These results enhance understanding of the variability of the environmental filtering process and highlight that conservation measures could be generalized at a large scale for specialists and declining species.

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BIOSKETCH

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