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Habitat selection in a dynamic seasonal environment: Vegetation composition drives the choice of the breeding habitat for the community of passerines in floodplain grasslands

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ABSTRACT

The conservation of grasslands is a concern worldwide as they are threatened by climate change and the expansion of intensive agricultural practices. The management of these areas must take into account the decisional process of habitat selection by individual organisms to identify potential ecological traps or underused habitats. Organisms that live in heterogeneous environments must select their breeding habitat based on cues that reflect habitat quality. In dynamic ecosystems such as grasslands, environmental cues used by individuals should show a strong temporal autocorrelation, such that their characteristics during breeding can be predicted earlier in the season. Our objective was to test if habitat features that explain grassland birds' distribution during the nesting and chick-rearing period could be predicted from the habitat features available on territory settlement. In western France, we analysed the relationships between the occurrence, richness and abundance of four passerine species, and vegetation structure and composition during chick-rearing period. We then analysed the temporal autocorrelation of vegetation features to determine whether the cues used during the settlement period reliably predicted the vegetation features encountered at later stages of breeding. We found that birds selected habitats characterized by a low cover of grasses, but did not respond to the physical structure of vegetation. The composition of vegetation was also the only variable that exhibited temporal autocorrelation over the course of the season, suggesting that individuals may rely on this feature to select optimal breeding habitats. Our results suggest that in dynamic environments, and in the absence of breeding experience or public information, animals can choose their breeding habitat based on a simple assessment of vegetation composition. A detailed knowledge of the underlying drivers of habitat selection is essential to manage habitats, identify potential ecological traps, and enhance the attractiveness of areas especially those under agri-environmental schemes.

1. Introduction

The conservation of grasslands is a concern in many areas of the world (Brennan and Kuvlesky Jr, 2005; Donald et al., 2001). Natural grasslands are threatened by the expansion of agriculture and climate change (Ridding et al., 2015), while anthropogenic grasslands are additionally subjected to new agricultural practices that alter the communities they host (Kleijn et al., 2009). In several parts of the world, environmental schemes have been designed to halt the loss of grassland biodiversity, especially birds (Batáry et al., 2015). Because there is little alternative suitable habitats for many animal species, and because environmental schemes require substantial funding, it is important to understand which mechanisms of habitat selection prevail in order to optimize the effectiveness of these measures (Catry et al., 2017). In this regard, floodplain meadows are of particular interest. They often host habitat specialists as well as species that have declined or disappeared from neighbouring areas that do not experience floods, effectively providing shelters for grassland biodiversity (Robinson et al., 2002).

Forecasting habitat suitability for breeding may prove challenging for grassland birds though, especially in floodplains. In temperate areas,

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floodplain grasslands look relatively homogeneous when water recedes in spring, then height, density, colour, and composition of vegetation cover rapidly change. Similarly, vegetation structure can quickly change after rainfalls following a drought, offering new nesting sites. Arthropod populations, a major food resource for breeding birds, expand rapidly with vegetation growth, making abundant food resources available for nestlings (Schekkerman and Beintema, 2007). Thus, within a few weeks, the physical structure of the habitat and the availability of trophic resources have drastically changed. Moreover, flooding intensity and timing may change from year to year in such a way that the distribution and amount of suitable habitat that is available at a certain time are highly variable between years. In such environments, individuals are expected to select breeding habitats that maximize their reproductive success (Martin, 1998; Shustack et al., 2010). It implies that they must use reliable indicators to assess the future quality of the habitat (Orians and Wittenberger, 1991). Otherwise, the erroneous use of non-informative environmental cues may reduce or suppress breeding success because of low access to food or elevated predation rate (Schlaepfer et al., 2002; Battin, 2004; Arlt and Pärt, 2007). Identifying the early environmental cues selected by birds is crucial to implement practices that reconcile agricultural production and biodiversity conservation. With this information, one may ensure that areas where birds preferentially settle are not also those where nesting failure is high because of agricultural practices, i.e. ecological traps (Gilroy and Sutherland, 2007). The stakes are high as poorly designed practices increase the extinction risk of populations to be protected (Battin, 2004; Schlaepfer et al., 2002).

Nesting grassland birds have access to several sources of prior information that reflect the future quality of the breeding habitat. They can use presence cues of heterospecific individuals (Monkkonen et al., 1999) to select (intraguild attraction) or avoid (predator avoidance) a potential breeding site. Using their previous breeding experience, individuals may return to the same site when the last breeding was successful and change when it failed (Piper, 2011), so that site fidelity decreases with environmental stochasticity (Switzer, 1993). Individuals may also use cues provided by the presence (Ahlering and Faaborg, 2006) or breeding success (Doligez et al., 2002) of conspecifics to select their breeding habitat. However, experiences gained from the previous breeding season(s) can provide reliable cues of habitat quality only if this quality remains stable over time. In areas experiencing occasional, irregular, large natural disturbances, a large part of the population may fail breeding in some years. In the next year, based on their experience failed breeders may leave available territories that are otherwise of high quality in the absence of disturbance (Piper, 2011). Therefore, in environments where habitat quality and availability, and thus the reliability of social information, vary between years, it may pay off to assess directly habitat patch quality (Bollmann et al., 1997). For example, in floodplain grasslands, rare and unpredictable late floods may occasionally prevent or strongly delay breeding over large areas. Hence, in the year following such event, and especially for short-lived birds, prior breeding experience conveys no information regarding the quality of habitats in a standard year. We thus expect individuals to select their breeding habitat based on environmental cues. However, in such environment where habitat quality rapidly changes during the course of the breeding season, features selected by individuals should show a strong temporal autocorrelation, i.e. the value observed at the nesting and chick-rearing stages can be predicted from the value sampled/assessed on settlement (Orians and Wittenberger, 1991; Battin, 2004).

Many studies on habitat selection have been carried out in grassland birds but it is usually unknown whether habitat features are selected based preferentially on public information, the individuals' own breeding experience, or their direct assessment of habitat quality. We addressed this issue by analysing passerines' breeding habitat selection in a large ensemble of floodplain grasslands in western France. During two consecutive years before our study, large spring floods made the lowest sections of the area unavailable during most of the birds' breeding season. Passerines are short-lived and breed in their second year, so that most of the individuals breeding in the subsequent year have no experience of habitat quality under no-flood conditions, or of the temporal autocorrelation of habitat features, i.e. their reliability as indicators. Therefore, we predict them to rely on environmental cues based on habitat features available at territory settlement to select their breeding habitat. This is especially expected for migratory species that have a limited time budget available to make settlement decisions and prospect the area before and after breeding. As half of surveyed species are long distance migrants and half are resident, another objective was to determine whether resident species were less sensitive to environmental features measured during the settlement period. At a small scale, the local structure and composition of the vegetation affect nest site quality for chick-rearing, and the protection of eggs and nestlings against cold, rain, excess insolation, and predation (Whittingham and Evans, 2004; Wilson et al., 2005). Hence, we first analysed the relationships between bird numbers and vegetation features during the chick-rearing period. We then analysed the temporal autocorrelation of vegetation features to determine which cues available at the settlement period reliably predict the vegetation features at the incubation and chick-rearing stages. This information is crucial to optimize management at the community scale and enhance the efficiency and efficacy of environmental schemes.

2. Material and methods

2.1. Study area and sampling plots

The study area covers ca. 20,000 ha of floodplain grasslands located around the city of Angers (Lon: −0.55°, Lat: 47.48°) in western France (Fig. 1). We focused our study on hay meadows, which remain extensively managed thanks to agri-environmental schemes (AES) that consist of delayed mowing (with different dates between June and July) and a banning or reduction of fertilizers. These meadows are typically grazed after harvesting and are mainly present on the lower elevations of the area, where flood occurs annually in winter or early spring. On the other hand permanent pastures, which we did not consider here, are located in the upper reach of the valley, where flooding is less frequent or absent. The area presents a high level of environmental stochasticity regarding the timing of floods, with late spring floods occurring in some years only. In 2012, a spring flood that lasted from early April to mid-May submersed 94.4% of 36 plots we surveyed for another study in the same area. In 2013, the flood started before spring and did not recede before late June, submersing 72.2% of the same plots. Therefore, our sampling year (2014) was the first after two consecutive years of severe spring floods to be entirely spared from flooding during the birds' breeding season.

The study area is composed of two distinct zones (Fig. 1) protected as Special Protection Areas under the Bird Directive of the European Union, which is part of the NATURA 2000 network (Evans, 2012). The zones differ in their management and hydrological characteristics, and as such we investigated how vegetation characteristics and birds' response differed between them. First, south of the study area, the meadows located in the “Loire” river valley (NATURA 2000 site FR5212002) account for ca. one third of the total number of sampling points (see below). They are characterized by less frequent floods because of riverbed incision, and the allowance of low fertilization. Second, two thirds of the sampling points were located in the valleys north of Angers (NATURA 2000 site FR5210115), adjacent to the Loire's northern tributaries (Maine, Mayenne, Sarthe and Loir rivers), referred hereafter as “BVA” (standing for Basses Vallées Angevines). There, AES strictly prohibit fertilization.

To analyse the relationship between vegetation and birds, we selected sampling plots by applying a regular grid of points separated by 500 m across all the grasslands of the study area (Fig. 1). Then, the sampling grid was visually examined and slightly modified by hand to

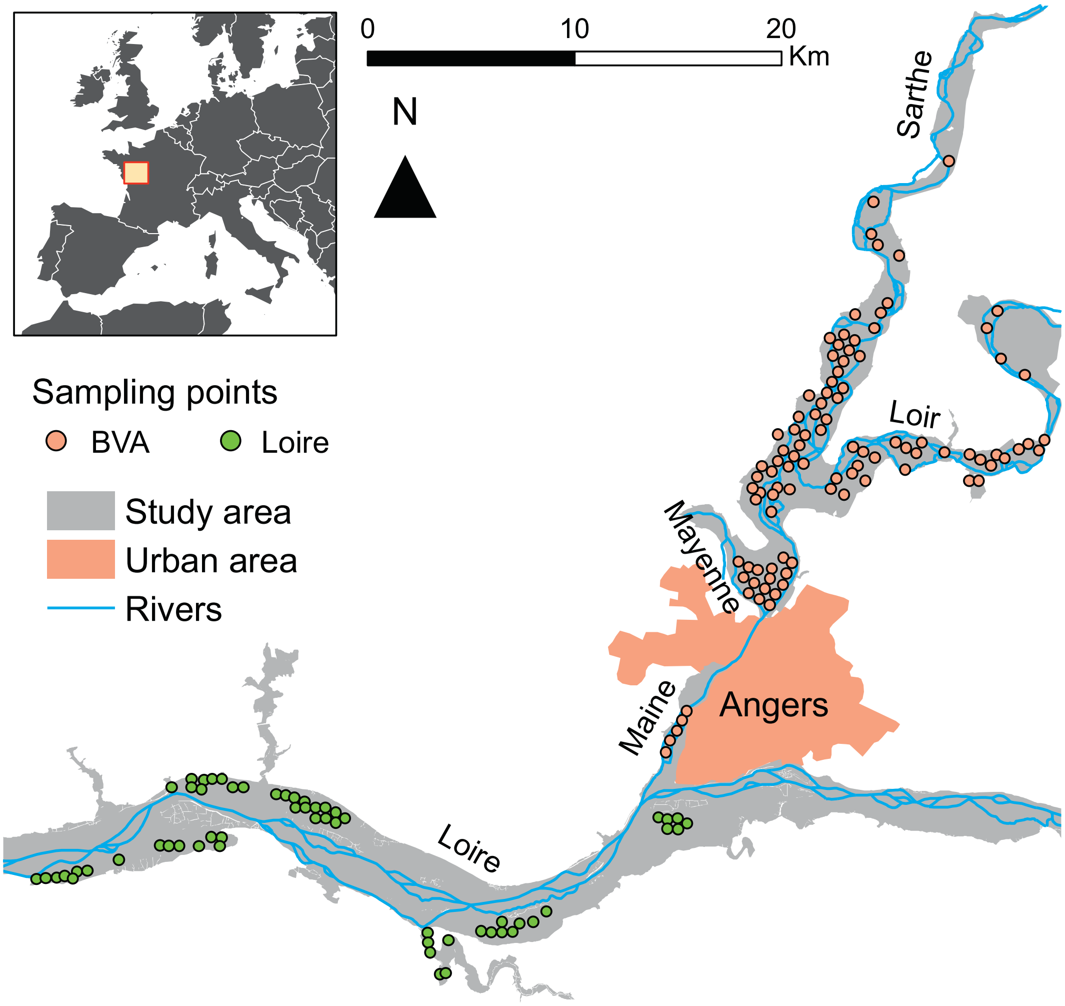

Fig. 1. Map of the 155 sampling plots in the two zones of the study area (Loire – south, main river and BVA – north, tributaries). The upper left inset shows the location of the study area in Western France.

exclude points that did not fall into hay meadows (e.g. pastures). A previous study in the study area confirmed that the bird species we sampled (see below) are sensitive to fragmenting elements of the landscape, especially hedgerows (Besnard et al., 2016). Therefore, we also shifted sampling points so that they were not within 100 m of roads, rivers or hedgerows. Additionally, the location of a few more points had to be shifted in the course of the fieldwork because they had already been mown or grazed, or because water had not entirely receded after winter flood. We recorded the coordinates of all plots using a Garmin® handheld GPS. The final set of sampling plots consisted of 155 points (Fig. 1), 57 in the "Loire" area, and 98 in the "BVA" area.

2.2. *Birds and vegetation survey*

We surveyed the four bird species that dominate the community of grassland passerines in this area (Noël, 2003). Two species are trans-Saharan migrants: the Whinchat (*Saxicola rubetra*) typically arrives in the area from mid-April, and the Yellow Wagtail (*Motacilla flava*) may arrive on its breeding grounds as early as late March. Both species lay eggs beginning in mid-May and have an incubation time of ca. 11–14 days followed by parental feeding during 13–15 days (MEEDDAT, 2012; Robinson, 2005). The two other passerines are two bunting species that are resident in the area. The Reed Bunting (*Emberiza schoeniclus*) lays eggs from mid-April to mid-May, with occasionally a second brood in June or July (MEEDDAT, 2012). Finally, the Corn Bunting (*Emberiza calandra*) lays its first clutch in late May, and some pairs may have a second clutch later in the season (Brickle and Harper, 2002).

Two large late spring floods occurred within the two years preceding our study (2012 and 2013). Given their extent and timing (see above), most of the area was unavailable during the time of territory settlement, forcing birds to nest in upper grounds, where habitat is typically of lower quality and mowing occurs earlier than in the lower areas in drier years. Alternatively, birds may have delayed their breeding until water receded, but given that grasslands are mown in June or July, we estimated that these late breeders have lost a large part of their broods because of mowing (unpublished data). Therefore, we assumed that in 2014, when the present study was conducted, a large part of the breeding population had no experience of successful breeding in the core of the study area, and had thus no information about the expected quality of meadows in a drier year. As such these individuals, and especially the ones that settled early before most of their conspecifics, had to make decisions regarding the choice of their breeding habitat based on environmental cues.

Despite some variation, all species have a relatively similar breeding phenology. Although different individuals or species may be at different stages of their nesting cycle, we assumed that most if not all males have settled on their territories in May. Bird surveys took place on the same plots used to assess vegetation structure, from the 5th to the 22nd May between sunrise and 11:00 am. After a cool-down period, we scanned for 10 min the area within a 100-m radius around the observer using binoculars (10 × 42 Ibis, Kite) and a laser telemeter (Rangefinder,

Table 1

Mean value (± standard deviation) for each of the four variables describing vegetation structure in grassland habitats in Western France: the percentage cover of grass species estimated visually as 10% classes and, based on the interpretation of photographs, the height (in cm), density (proportion of black pixels in the picture) and vertical heterogeneity of vegetation (unitless). Values are shown for the two zones of the study area (BVA and Loire, see Fig. 1) and the two time periods (April and May).

	BVA		Loire	
	April	May	April	May
% grass	60.44 ± 23.55	54.1 ± 28	74.53 ± 18.77	70.94 ± 18.66
Height	49.02 ± 12.43	93.48 ± 22.62	44.54 ± 9.04	72.42 ± 13.69
Density	0.67 ± 0.06	0.56 ± 0.08	0.65 ± 0.06	0.58 ± 0.08
Heterogeneity	0.33 ± 0.08	0.39 ± 0.12	0.35 ± 0.06	0.37 ± 0.08

Bushnell – Elite 1500), and reported all visual contacts of males or females. At the time of survey, vegetation was short enough in all sites to observe birds flying over the vegetation or standing on top of tall perches. All surveys were also carried out by in the same weather conditions, so that we have minimized as much as possible spatial and temporal variation in detection probability.

We surveyed vegetation on sampling plots in spring 2014 during the settlement period of migratory birds (21st–26th April) and during breeding (26th–31st May). We focused on vegetation features (height, density, structural heterogeneity and composition, see Table 1) that are commonly reported for the analysis of breeding habitat selection by grassland birds (see for example Herkert, 1994 and Wiens, 1973). We visually estimated the percentage cover of all grass-like plant species (graminoids), hereafter referred to as grass, in 10% bins. Grasslands in the area are composed of a well-defined assemblage of plant species, known as the phytosociological class *Agrostietea stoloniferae* (De Foucault and Catteau, 2012). It is mainly composed of a mix of graminoid species (true grasses [*Poaceae*], rushes, sedges) and various insect-pollinated forbs, including legumes. Our measure is thus equivalent to the grass-to-forb ratio that is often used in the literature. Since forbs-dominated grasslands are generally associated to a more diverse insect community (Haddad et al., 2000), we expect the proportion of grass at a sampling point to be inversely proportional to the diversity of resources for insect-feeding birds.

We then used photographs of 20-cm-wide vertical stripes of vegetation to derive three measures of vegetation structure in the sampling plot. We used a method derived from the approach implemented in the software VESTA (Zehm et al., 2003; see Supplementary material, Methods S1 for details). In each plot, we took two pictures 5–10 m apart from each other. From these pictures, we calculated vegetation density, vegetation height, and an index of vertical heterogeneity, which quantifies the presence of tall leaves and stalks above the vegetation canopy. We averaged the values of vegetation features over the two photos for analyses.

Birds and vegetation data are available from Mendeley Data Repository.

2.3. Habitat selection in response to vegetation

In order to identify the vegetation features that characterized habitat selection by grassland passerines, we used generalized linear models to assess the relationship between vegetation structure during the breeding period and birds' occurrence, richness and abundance. Specifically, we modelled the probability of presence of each species by a generalized linear model with binomial error distribution and logit link, using presence/absence as a binary response variable. Species richness was modelled with a Poisson error distribution and log link. Finally, we modelled the total abundance of passerines using a negative-binomial error distribution and log link to account for over-dispersion. We chose to model the total abundance instead of species-specific abundances because of the highly skewed distribution of abundances caused by many plots in which one single individual was recorded.

We used as explanatory variables the height, density, heterogeneity of vegetation and the cover of grass as measured in May (Table 1), the zone (BVA or Loire), as well as the two-way interactions between each vegetation variable and the zone to explore whether birds' response to vegetation structure and composition varied between zones. In the model of probability of presence, we also added species identity as explanatory variable, as well as the three-way interactions between zone and species and each vegetation variable. Therefore, we could assess whether each species exhibited a different response to vegetation variables, and whether it differed between zones. To assess explicitly whether migratory and resident species differed in their response to vegetation, we repeated this analysis replacing species identity by migratory behaviour (migratory vs. resident) in a generalized linear mixed model, adding species as a random intercept. In addition, we also included as co-variables in all models spatial eigenvectors, extracted from sampling points coordinates by a PCA on the distance matrix, to control for spatial autocorrelation (Diniz-Filho and Bini, 2005). We selected eigenvectors whose observed eigenvalue exceeded the expected eigenvalue under a broken-stick model (Diniz-Filho et al., 1998), resulting into seven spatial co-variates included in all models. Spatial eigenvectors and their associated eigenvalues were calculated with the “codep” R package (Guenard et al., 2015).

We used an information-theoretic approach (Burnham and Anderson, 2002) to infer the importance of each variable; we computed models with all possible combinations of variables (spatial eigenvectors being kept in all models), and ranked them by their second-order Akaike Information Criterion (AICc). Thereafter, we performed a multi-model inference by averaging all models whose cumulative weight was < 95%. Averaged parameter estimates, standardized by partial standard deviation, were extracted for all variables and their relative importance was estimated based on the sum of Akaike weights of all candidate models containing the variable. We also reported a coefficient of determination for the full models, based on a pseudo-R^2 calculated from a likelihood ratio test with the intercept-only model. Multi-model inferences were run using the “MuMIn” R package (Barton, 2013). All the above analysis was also repeated using vegetation variables as measured in April.

2.4. Temporal autocorrelation of vegetation

We aimed to assess whether vegetation characteristics during the breeding period could be predicted from cues obtained during territory settlement. For this purpose, we ran several complementary analyses that described the temporal autocorrelation of vegetation structure and composition.

First, we tested whether vegetation significantly changed over the course of the season by computing a Permutational Multivariate Analysis of Variance (PERMANOVA) with the Euclidian distances between sites based on vegetation measures as response variable. We included the period of measure as explanatory variable, but also the zone because we suspected that vegetation differed between the northern (BVA) and southern (Loire) zones of the study area. Significance of effects was assessed with 10,000 permutations, using the "vegan" R package (Oksanen et al., 2015).

Then, we conducted a principal component analysis (PCA), using the measures of vegetation height, density, heterogeneity and the cover of grass recorded in April and May, to assess the correlation between different variables and the temporal correlation between vegetation variables measured in April and May, and to visually identify differences between the two zones. We also reported Pearson's correlations between vegetation variables in each period. Moreover, we computed four linear regressions using each vegetation variable measured in May as response variable and the same variable measured in April as explanatory variable, to test the predictability of vegetation during the breeding season from the vegetation observed in April. We included as additional predictors the seven spatial eigenvectors described above to account for the spatial structure of sampling locations.

Finally, we aimed at testing whether the spatial heterogeneity of vegetation structure was maintained over the season. We thus tested the correlation between two distance matrices between sites calculated from vegetation variables, one based on measures in April and one based on measures in May, using partial Mantel tests. We computed 5 different tests: first using all vegetation variables together to calculate the distance matrix, and then using each of the four variables alone. We controlled for spatial autocorrelation by including the matrix of geographic distances, and ran 10,000 permutations to assess significance.

3. Results

3.1. Response of species to vegetation structure and composition

The information-theoretic procedure highlighted seven variables or interactions that had a high relative importance (> 0.9) to explain the probability of presence of passerine species (Table 2): all vegetation variables except density (grass cover, height and heterogeneity), the zone of the study area, the species identity, the interactions between vegetation height and zone, and between species and zone. However, only grass cover and the interaction species × zone had an averaged coefficient estimate whose confidence interval did not span 0 (Table 2). It revealed that the Whinchat tended to have a higher probability of presence than the other species in the BVA zone, while in the Loire zone the Yellow Wagtail and the Corn Bunting had the highest probability of presence (Fig. 2A). There was, however, no difference based on species' migratory behaviour (Table S2). We also observed that the probability of presence of all bird species decreased with increasing grass cover (Fig. 2B). Only grass cover had a relative importance > 0.7 and a coefficient that did not overlap 0, in both models explaining species richness and abundance (Table 3). As for their probability of presence, the richness and abundance of passerines declined with increasing grass cover (Fig. 2C and D). Interestingly, the response of species was also mainly affected by grass cover when vegetation features were measured in April instead of May (Supplementary material, Table S1).

3.2. Variation of vegetation structure in space and time

We found that vegetation structure significantly differed between the two periods of measures (PERMANOVA: $F_{1,307} = 140.85$, $R^2 = 29.13$, $P < 0.001$), and between the two zones of the study area (PERMANOVA: $F_{1,307} = 35.71$, $R^2 = 0.07$, $P < 0.001$). A visual inspection of the PCA revealed that the two zones mainly differed along the first PCA axis, which essentially represents grass cover (Fig. 3). It also showed weak correlations between different types of vegetation features. Pearson correlation tests confirmed that, in each time period, there was no strong correlation between variables (Supplementary material, Table S3). Although several correlations were statistically significant, only two were above 0.5: vegetation height and density in May (Pearson correlation $= -0.55$, $P < 0.001$), and vegetation density and heterogeneity in April (Pearson correlation $= -0.51$, $P < 0.001$; Supplementary material, Table S3).

In contrast, the PCA and the linear regressions between periods revealed a strong temporal autocorrelation between the grass cover recorded in April and May ($F_{8,146} = 18.904$, $R^2 = 0.482$, $P < 0.001$). Vegetation height appeared to be also significantly correlated between both periods, although only moderately ($F_{8,146} = 6.441$, $R^2 = 0.220$, $P = 0.033$). The other measures of vegetation structure did not show any temporal autocorrelation (see Fig. 3 and Table 4).

The differences between sites were significantly correlated between April and May when considering all vegetation variables together (Mantel test: $r = 0.365$, $P < 0.001$). Differences between sites were also strongly correlated across the season when they were based on grass cover alone (Mantel test: $r = 0.415$, $P < 0.001$). A weak, but significant correlation was also found when considering vegetation height (Mantel test: $r = 0.119$, $P = 0.012$). However, no significant temporal correlation was detected for vegetation density (Mantel test: $r = 0.014$, $P = 0.331$) and heterogeneity (Mantel test: $r = -0.009$, $P = 0.541$).

4. Discussion

To describe habitat selection of the grassland passerine community in our study area, we tested how vegetation structure and composition during the breeding season (May) influenced species' probability of presence, abundance and richness. Birds were primarily found during the breeding period in areas characterized by a low grass-to-forb ratio, i.e. a low proportion of grasses relative to other flowering plants, which is recognized as a main habitat feature of grassland birds (Wiens, 1969; Fisher and Davis, 2010). Forb-dominated grasslands generally host higher bird species richness than areas dominated by grasses (Blank et al., 2014, but see Fisher and Davis, 2010 and Bollinger, 1995 for examples of positive responses to grass cover). The negative effect of a high grass cover has been already identified in the Whinchat (Murray et al., 2016). This effect has generally been attributed to a negative correlation between grass cover and plant species richness (Pokorny et al., 2004). In contrast, forb-dominated grasslands provide more diverse food resources for herbivore and nectarivore insects, which results in a higher density and richness of insects and in turn more food for insectivore birds (McIntyre and Thompson, 2003; Hickman et al., 2006). A higher cover of forbs may also be associated with the presence of tall perching sites, used as singing posts by territorial males and as observation sites for foraging (Payne et al., 1998; Border et al., 2016) although in our sampling the correlation between vegetation composition and physical structure settings was weak.

It is difficult to strictly demonstrate that habitats with low grass cover are of higher quality, and preferentially selected without information about the past reproductive success and birds' decision-making process (Jones, 2001). However, our sampling design that covered the whole area without a priori assumptions allowed us to compare the used habitats with all available grassland habitats, so that results are strong indicators of positive habitat selection (Manly et al., 2002). In this regard, it is noticeable that only the percentage of grass exhibited strong predictable temporal variation between May (breeding) and April (settlement). Vegetation density and heterogeneity lacked temporal autocorrelation, while vegetation height was only weakly correlated between April and May. Here, the visual assessment of the grass-to-forbs ratio available on settlement was enough to predict vegetation composition during nesting and chick-rearing. Birds could use this information to select their territory too. In agreement with the observed temporal autocorrelation, the percentage of grass was the best predictor of species presence, abundance and richness, both when recorded in April and in May. Thus, this feature is a strong candidate for being used by birds as an early environmental cue of habitat quality later in the breeding season. It should be noted, though, that vegetation features recorded in May were better predictors – based on models'

Table 2

Model averaged coefficients (± 95% confidence intervals) and variable importance from generalized linear models explaining the probability of presence of passerines. Variables with relative importance > 0.9 are highlighted in bold font and coefficients whose confidence intervals do not overlap 0 are underlined. The interaction between species, zone and % Grass is not included in the best models selected for model averaging. Vegetation variables were measured during breeding season in May. All models also included spatial eigenvectors as co-variables. Pseudo-R^2 of full model = 0.16.

Variable		Estimate	95% CI		Importance
% grass		−0.439	−0.637	−0.240	**1.000**
Height		−0.078	−0.272	0.116	**0.973**
Heterogeneity		−0.147	−0.367	0.073	**0.891**
Density		−0.014	−0.156	0.127	0.479
Zone[a]		0.125	−0.108	0.358	**1.000**
% grass × zone		0.007	−0.098	0.112	0.263
Height × zone		−0.224	−0.458	0.009	**0.901**
Heterogeneity × zone		−0.026	−0.155	0.104	0.297
Density × zone		−0.004	−0.085	0.076	0.142
Species[b]	YW	−0.164	−0.441	0.113	**1.000**
	CB	−0.151	−0.416	0.114	
	RB	−0.238	−0.576	0.100	
% grass × species	YW	0.001	−0.037	0.039	0.038
	CB	−0.001	−0.039	0.037	
	RB	−0.002	−0.051	0.048	
Height × species	YW	−0.005	−0.075	0.066	0.102
	CB	−0.001	−0.058	0.056	
	RB	−0.014	−0.116	0.089	
Heterogeneity × species	YW	−0.021	−0.143	0.100	0.168
	CB	0.001	−0.073	0.074	
	RB	0.010	−0.083	0.103	
Density × species	YW	0.040	−0.128	0.209	0.226
	CB	−0.006	−0.094	0.082	
	RB	0.012	−0.098	0.123	
Species × zone	YW	0.270	0.088	0.451	**1.000**
	CB	0.293	0.107	0.480	
	RB	0.028	−0.244	0.300	
Density × species × zone	YW	−0.001	−0.024	0.022	0.013
	CB	0.001	−0.024	0.026	
	RB	−0.002	−0.046	0.043	
Heterogeneity × species × zone	YW	0.000	−0.010	0.010	0.003
	CB	0.000	−0.011	0.011	
	RB	0.000	−0.022	0.021	
Height × species × zone	YW	0.000	−0.005	0.005	0.001
	CB	0.000	−0.005	0.005	
	RB	0.000	−0.008	0.008	

[a] Loire taken as reference.

[b] Whinchat taken as reference (YW: yellow wagtail; CB: corn bunting; RB: reed bunting).

pseudo-R^2 – of breeding habitat than recorded in April. It suggests individuals may adjust their choice over the course of the season, perhaps based on vegetation growth or public information.

We did not find any effect of structural measures of vegetation on passerine presence, abundance or richness. By contrast, many studies found a role of vegetation height or density on grassland birds' richness, abundance or occurrence (e.g. Cody, 1981; Davis, 2004; Azpiroz and Blake, 2016), including our focal species. For instance, the occurrence of Whinchat was found to be positively associated with structural heterogeneity (Fischer et al., 2013) and vegetation density (Pearce-Higgins and Grant, 2006), and negatively associated with vegetation height (Hulme and Cresswell, 2012). Similarly, grassland structure influences predation risk and foraging efficiency in the Yellow Wagtail, the Reed Bunting and the Corn Bunting (Whittingham and Evans, 2004). Because the change in the physical structure of vegetation was largely unpredictable over the course of the breeding season, these features cannot be selected on settlement, which may explain why these variables appeared not to influence habitat selection. It remains possible that we did not observe an effect of some variables on bird distribution because all meadows of the study area were equally suitable with regard to vegetation structure, or at least within the acceptable range of variation. Alternatively, in floodplains, grass cover may be the only vegetation characteristics that remains stable within and across seasons, and may thus be the only reliable indicator of habitat quality on the long-term. In contrast, other variables like density or canopy height may exhibit high between-year variations due to flood occurrence and timing.

We also investigated the effect of the migratory behavior on habitat selection. The focal bird community is small but it includes migratory and resident species. The latter may have an extended access to information on meadow structure as they can probe earlier the breeding area. Moreover, migratory species are more likely to select non-optimal habitats because of their limited time budget available for settlement decisions at their arrival on breeding grounds (Battin, 2004). Here, we did not find any difference between species, whether they are migratory or not, in their response to vegetation structure and composition. Possibly, this is because only grass cover was temporally autocorrelated, and was thus the only possible environmental cue for habitat selection. An important aspect would be to test whether migratory and resident species select equally well the most suitable habitat to complete their reproduction, but it would require data about breeding success that were not available here.

Although the response of bird species to vegetation was similar, the probabilities of occurrence between species varied depending on the hydrological unit. These units were also characterized by different levels of grass cover, caused by two factors that favour the dominance of some grass species along the Loire river: less frequent floods and the allowance of low fertilization (prohibited in the "BVA" area). In grasslands, nitrogen fertilization decreases plant species richness (De Schrijver et al., 2011) and favours grasses at the expense of low growing forbs (Raus et al., 2012) and legumes (Mountford et al., 1993). As a consequence, fertilization reduces the richness and abundance of

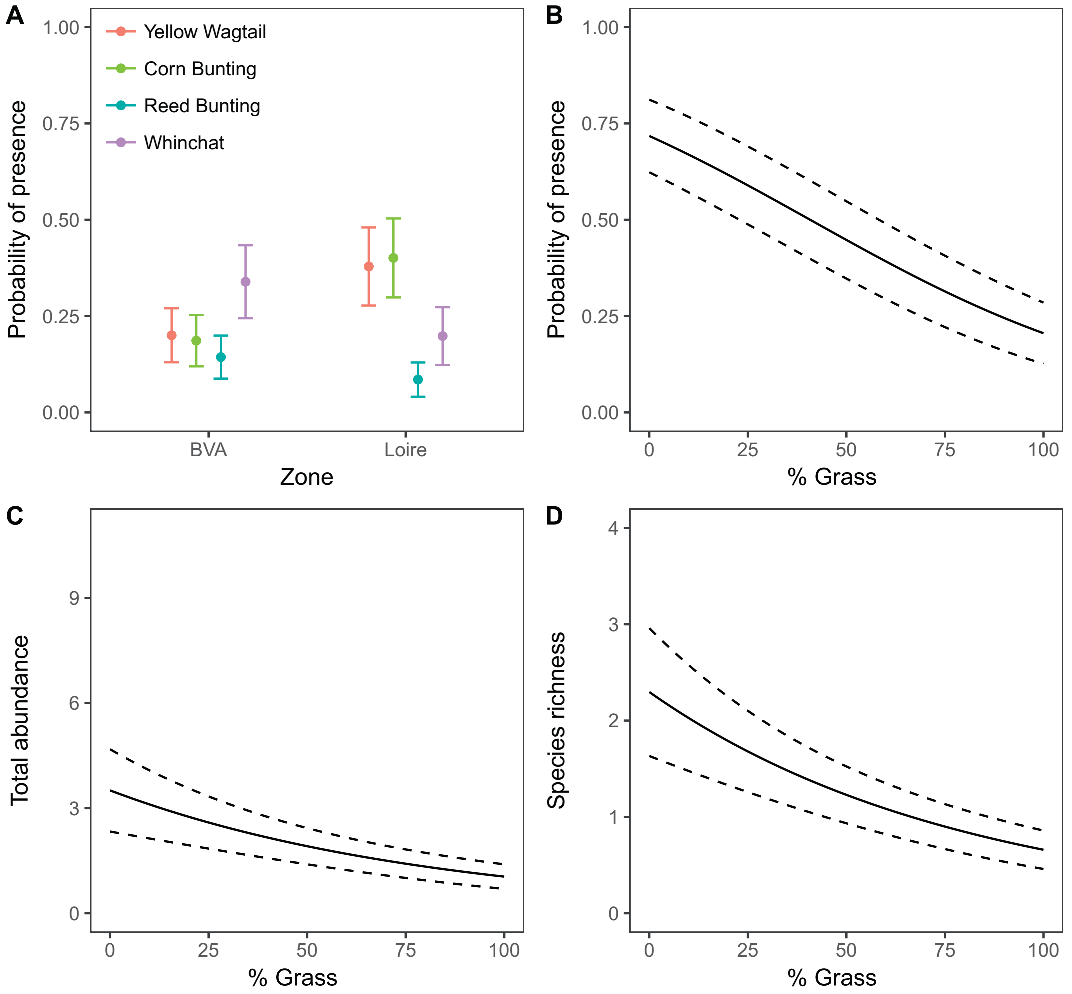

Fig. 2. Graphical representation of the effect of factors that had both a relative importance = 1 and coefficient confidence intervals that did not overlap 0 in model averaging, using all models with cumulative weight < 95%. (A) Model predictions regarding the probability of presence of each species depending on the zone of the study area. Partial regression plots showing the response of species' probability of presence (B), species richness (C) and abundance (D) to the percent cover grass species in May. All other variables (see description of models in material and methods) are kept at their mean. Standard-errors of model predictions are shown as dotted lines.

insects (Haddad et al., 2000), including prey insects for grassland passerines (Vickery et al., 2001). Moreover, grassland eutrophication also reduces plant species asynchrony (Hautier et al., 2014), which can lead to a rapid reduction of hay yield when grasslands are harvested after the peak of vegetation growth. It questions the relevance of current AES that prescribe delayed mowing and authorize fertilization at the same time when their aim is to preserve both grassland biodiversity and harvest yield.

We provided evidence that the grass-to-forb ratio in early spring contributes to the selection of breeding habitat by grassland passerines, although the actual effect of grass cover on species richness and bird's abundance remained rather low, showing that several other factors play

Table 3

Model averaged coefficients (± 95% confidence intervals) and variable importance from generalized linear models explaining the abundance and species richness of passerines. Variables with relative importance > 0.9 are highlighted in bold font and coefficients whose confidence intervals do not overlap 0 are underlined. Vegetation variables were measured during breeding season in May. All models also included spatial eigenvectors as co-variables. Pseudo-R^2 of full model = 0.16 (abundance) and 0.20 (richness).

Variable	Total abundance				Species richness			
	Estimate	95% CI		Importance	Estimate	95% CI		Importance
% grass	−0.251	−0.415	−0.088	**1.000**	−0.257	−0.397	−0.118	**1.000**
Height	−0.009	−0.153	0.135	0.660	−0.048	−0.192	0.096	**1.000**
Heterogeneity	−0.067	−0.239	0.105	0.558	−0.070	−0.231	0.091	**1.000**
Density	0.018	−0.092	0.128	0.309	0.009	−0.081	0.098	0.140
Zone[‡]	0.096	−0.132	0.323	0.668	0.061	−0.116	0.238	**1.000**
% grass × zone	−0.001	−0.069	0.067	0.144	0.004	−0.062	0.069	0.091
Height × zone	−0.121	−0.386	0.144	0.504	−0.064	−0.251	0.123	0.379
Heterogeneity × zone	−0.007	−0.077	0.062	0.106	−0.005	−0.060	0.051	0.286
Density × zone	−0.001	−0.044	0.041	0.045	0.000	−0.029	0.030	0.029

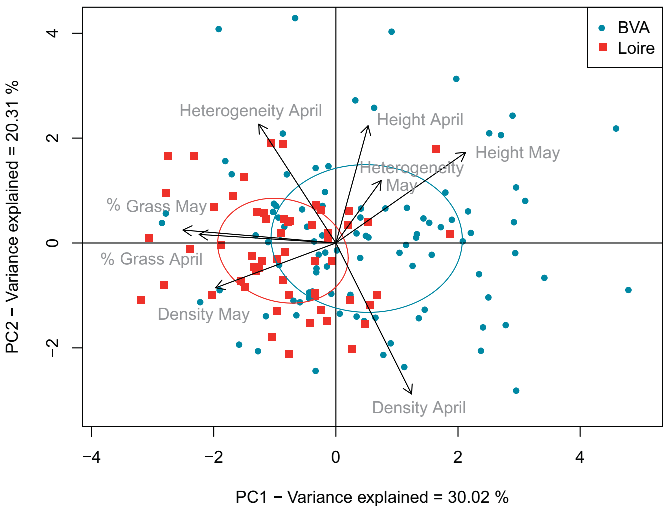

Fig. 3. Principal component analysis of sampling plots according to measures of vegetation structure recorded in April and May. Sampling points are plotted according to the two first axes of the PCA, with standard deviation ellipses showing the difference between the two zones of the study area (BVA and Loire). Variables loadings are plotted as arrows.

Table 4
Result of the four linear models describing the relationship between each vegetation variable measured in April and measured in May. All models also included spatial eigenvectors as co-variables.

Variable	$F_{8,146}$	R^2	P
% grass	18.904	0.482	< 0.001
Height	6.441	0.220	0.033
Density	1.613	0.031	0.156
Heterogeneity	1.065	0.003	0.479

a role. Previous studies also showed that the same four species have similar affinity to large patches of open habitat with high vegetation productivity (Besnard et al., 2016; Fourcade et al., 2017). The fact that all target species share ecological requirements makes it easier to design actions that would benefit all of them. In this regard, mapping the grasslands that exhibit a high forb cover may be used to target priority areas for management actions. Alternatively, the management of the vegetation cover may be an efficient method to attract individuals, and potentially to enhance breeding success, on the parcels that are under AES. Currently most of these forb-rich areas are also those that are at risk of late flooding. Attracting birds in higher grounds through vegetation management may also be a way to reduce flooding hazard for breeding passerines. This option may be selected only if the mowing date is adjusted to the breeding phenology of birds. Drier meadows, i.e. less subjected to flood, are mown earlier in our study area, which increases the risk of nest failure. It also remains to be assessed whether such management options would be friendly to biodiversity in general. For instance, carabids and spiders have been shown not to respond in the same way to early mowing (Lafage and Pétillon, 2014). Another unknown issue is whether birds use the same environmental cues to select their breeding habitats in dry and wet conditions, and how it affects habitat selection in subsequent years.

5. Conclusion

It is a challenge to mitigate the effects of agricultural practices harmful to biodiversity. Management activities must work to ensure a good match between conservation measures in agricultural areas and the ecological preferences of the species they aim to protect. One option is to prioritize the implementation of AES in habitats that are preferentially selected by individuals. Conversely, another option is to force individuals to settle where they have more chances to breed successfully, for instance in parcels under AES (Gilroy and Sutherland, 2007). Therefore, knowing the fine habitat features selected by a target bird species on settlement can help managers to enhance habitat attractiveness and more efficiently support population persistence (Ahlering and Faaborg, 2006).

In an era of global changes, two pervasive impacts of human activity affect grassland communities. First, nitrogen deposition from agriculture and industry contributes to a shift towards more grass-dominated grasslands (Southon et al., 2013). We showed here that grassland birds' preferred breeding habitat was associated with a low cover of grasses, although it remains to be demonstrated that it directly affects their breeding success. Based on this result, we recommend environmental managers to implement measures that restrict or prohibit the use of fertilization, in order to maintain a forb-rich vegetation. Second, climate change, responsible for shifts in community composition throughout all ecosystems (Parmesan and Yohe, 2003), poses an additional challenge to the conservation of grassland ecosystems. In floodplains, biodiversity conservation programs must account for flooding regime. This parameter exerts a large influence on the vegetation composition and the associated animal communities, and ultimately determines the range of possible agricultural activities. Climate change is expected to disrupt hydrological regime and flooding timing (e.g. Prudhomme et al., 2003; Moatar et al., 2010). It may increase the risk that breeding birds fail to identify high-quality habitats in dry years and avoid areas that would be otherwise suitable. On the contrary, propensity to select breeding habitat based on vegetation cues in early season may lead to an ecological trap if birds consistently select breeding habitats located in areas that become unsuitable later because of flooding. In this context, it may be essential to ensure that high quality habitats are maintained in a larger area even in years when the main breeding area is flooded. These habitats must contain the environmental cues used by breeding birds during their settlement, which then have to be assessed beforehand both during wet and dry years.

From a broader perspective, our study emphasizes the importance of identifying predictable components of the habitat in dynamic environments, a common feature of many wetlands. It also raises the question of whether the strength of short-term temporal correlations in habitat features is robust. On a larger time frame, correlations may disappear in years with unusual conditions, or gradually decay under environmental change, possibly turning a reliable cue to false cue for an ecological trap. The sensitivity and plasticity of the habitat selection process to such variation in such dynamic environment is yet to be assessed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.11.007.

References

Ahlering, M.A., Faaborg, J., 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk 123, 301–312.
Arlt, D., Pärt, T., 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology 88, 792–801.
Azpiroz, A.B., Blake, J.G., 2016. Associations of grassland birds with vegetation structure in the Northern Campos of Uruguay. Condor 118, 12–23.

Barton, K., 2013. MuMIn: multi-model inference. R package version 1.9.13. http://cran.r-project.org/package=MuMIn.
Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29, 1006–1016.
Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18, 1482–1491.
Besnard, A.G., Fourcade, Y., Secondi, J., 2016. Measuring difference in edge avoidance in grassland birds: the Corncrake is less sensitive to hedgerow proximity than passerines. J. Ornithol. 157, 515–523.
Blank, P.J., Sample, D.W., Williams, C.L., Turner, M.G., 2014. Bird communities and biomass yields in potential bioenergy grasslands. PLoS ONE 9, e109989.
Bollinger, E.K., 1995. Successional changes and habitat selection in hayfield bird communities. Auk 112, 720–730.
Bollmann, K., Reyer, H.U., Brodmann, P.A., 1997. Territory quality and reproductive success: can water pipits *Anthus spinoletta* assess the relationship reliably? Ardea 85, 83–98.
Border, J.A., Henderson, I.G., Redhead, J.W., Hartley, I.R., 2016. Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. Ibis 159, 139–151.
Brennan, L.A., Kuvlesky Jr., W.P., 2005. North American grassland birds: an unfolding conservation crisis? J. Wildl. Manag. 69, 1–13.
Brickle, N.W., Harper, D.G.C., 2002. Agricultural intensification and the timing of breeding of corn buntings *Miliaria calandra*. Bird Study 49, 219–228.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.
Catry, I., Marcelino, J., Franco, A.M.A., Moreira, F., 2017. Landscape determinants of European roller foraging habitat: implications for the definition of agri-environmental measures for species conservation. Biodivers. Conserv. 26, 553–566.
Cody, M.L., 1981. Habitat selection in birds - the roles of vegetation structure, competitors, and productivity. Bioscience 31, 107–113.
Davis, S.K., 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. Auk 121, 1130–1145.
De Foucault, B., Catteau, E., 2012. Contribution au prodrome des végétations de France : les Agrostietea stoloniferae Oberd. 1983. J. Bot. Soc. Bot. France 59, 5–131.
De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K., Verheyen, K., 2011. Cumulative nitrogen input drives species loss in terrestrial ecosystems. Glob. Ecol. Biogeogr. 20, 803–816.
Diniz-Filho, J.A.F., Bini, L.M., 2005. Modelling geographical patterns in species richness using eigenvector-based spatial filters. Glob. Ecol. Biogeogr. 14, 177–185.
Diniz-Filho, J.A.F., de Sant'Ana, C.E.R., Bini, L.M., 1998. An eigenvector method for estimating phylogenetic inertia. Evolution 52, 1247–1262.
Doligez, B., Danchin, E., Clobert, J., 2002. Public information and breeding habitat selection in a wild bird population. Science 297, 1168–1170.
Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. Lond. B Biol. Sci. 268, 25–29.
Evans, D., 2012. Building the European Union's Natura 2000 network. Nat. Conserv. 1, 11–26.
Fischer, K., Busch, R., Fahl, G., Kunz, M., Knopf, M., 2013. Habitat preferences and breeding success of Whinchats (*Saxicola rubetra*) in the Westerwald mountain range. J. Ornithol. 154, 339–349.
Fisher, R.J., Davis, S.K., 2010. From Wiens to Robel: a review of grassland-bird habitat selection. J. Wildl. Manag. 74, 265–273.
Fourcade, Y., Besnard, A.G., Secondi, J., 2017. Evaluating interspecific niche overlaps in environmental and geographic spaces to assess the value of umbrella species. J. Avian Biol. 48, 1563–1574.
Gilroy, J.J., Sutherland, W.J., 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends Ecol. Evol. 22, 351–356.
Guenard, G., Legendre, P., Pages, B., 2015. codep: multiscale codependence analysis. R package version 0.5-1. http://CRAN.R-project.org/package=codep.
Haddad, N.M., Haarstad, J., Tilman, D., 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia 124, 73–84.
Hautier, Y., Seabloom, E.W., Borer, E.T., et al., 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature 508, 521–525.
Herkert, J.R., 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecol. Appl. 4, 461–471.
Hickman, K.R., Farley, G.H., Channell, R., Steier, J.E., Lauver, C., 2006. Effects of Old World bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. Southwest. Nat. 51, 524–530.
Hulme, M.F., Cresswell, W., 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African farmland suggest that winter habitat conditions do not limit European breeding populations. Ibis 154, 680–692.
Jones, J., 2001. Habitat selection studies in avian ecology: a critical review. Auk 118, 557–562.
Kleijn, D., Kohler, F., Baldi, A., Batary, P., Conception, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. Lond. B Biol. Sci. 276, 903–909.
Lafage, D., Pétillon, J., 2014. Impact of cutting date on carabids and spiders in a wet meadow. Agric. Ecosyst. Environ. 185 (1–8).
Manly, B.F.J., McDonald, L.L., Thomas, D., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, 2nd ed. Kluwer Academic, Dordrecht, The Netherlands.
Martin, T.E., 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79, 656–670.
McIntyre, N.E., Thompson, T.R., 2003. A comparison of conservation reserve program habitat plantings with respect to arthropod prey for grassland birds. Am. Midl. Nat. 150, 291–301.
MEEDDAT, 2012. Cahiers d'habitats Natura 2000 - Tome 8 – “Oiseaux”. La Documentation Francaise, Paris.
Moatar, F., Ducharne, A., Thiéry, D., Bustillo, V., Sauquet, E., Vidal, J.-P., 2010. La Loire à l'épreuve du changement climatique. Geosciences 12, 78–87.
Monkkonen, M., Hardling, R., Forsman, J.T., Tuomi, J., 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evol. Ecol. 13, 91–104.
Mountford, J.O., Lakhani, K.H., Kirkham, F.W., 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. J. Appl. Ecol. 30, 321–332.
Murray, C., Minderman, J., Allison, J., Calladine, J., 2016. Vegetation structure influences foraging decisions in a declining grassland bird: the importance of fine-scale habitat and grazing regime. Bird Study 63, 223–232.
Noël, F., 2003. Étude de l'avifaune nicheuse des prairies inondables de fauche dans les Basses Vallées Angevines. Crex 7, 53–58.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. vegan: community ecology package. R package version 2.3-2. http://cran.r-project.org/package=vegan.
Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. Am. Nat. 137, S29–S49.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Payne, N.F., Kobal, S.N., Ludwig, D.R., 1998. Perch use by 7 grassland bird species in northern Illinois. Trans. Ill State Acad. Sci. 91, 77–83.
Pearce-Higgins, J.W., Grant, M.C., 2006. Relationships between bird abundance and the composition and structure of moorland vegetation. Bird Study 53, 112–125.
Piper, W.H., 2011. Making habitat selection more “familiar”: a review. Behav. Ecol. Sociobiol. 65, 1329–1351.
Pokorny, M.L., Sheley, R.L., Svejcar, T.J., Engel, R.E., 2004. Plant species diversity in a grassland plant community: evidence for forbs as a critical management consideration. West. N. Am. Nat. 64, 219–230.
Prudhomme, C., Jakob, D., Svensson, C., 2003. Uncertainty and climate change impact on the flood regime of small UK catchments. J. Hydrol. 277, 1–23.
Raus, J., Knot, P., Hrabě, F., 2012. Effect of fertilization and harvest frequency on floristic composition and yields of meadow stand. Acta Univ. Agric. Silvic Mendel Brun. 60, 181–186.
Ridding, L.E., Redhead, J.W., Pywell, R.F., 2015. Fate of semi-natural grassland in England between 1960 and 2013: a test of national conservation policy. Glob. Ecol. Conserv. 4, 516–525.
Robinson, R.A., 2005. BirdFacts: Profiles of Birds Occurring in Britain & Ireland (BTO Research Report 407). BTO, Thetford.
Robinson, C.T., Tockner, K., Ward, J.V., 2002. The fauna of dynamic riverine landscapes. Freshw. Biol. 47, 661–677.
Schekkerman, H., Beintema, A.J., 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. Ardea 95, 39–54.
Schlaepfer, M.A., Runge, M.A., Sherman, P.W., 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17, 474–480.
Shustack, D.P., Strong, A.M., Donovan, T.M., 2010. Habitat use patterns of bobolinks and Savannah sparrows in the northeastern United States. Avian Conserv. Ecol. 5, 11.
Southon, G.E., Field, C., Caporn, S.J.M., Britton, A.J., Power, S.A., 2013. Nitrogen deposition reduces plant diversity and alters ecosystem functioning: field-scale evidence from a nationwide survey of UK heathlands. PLoS ONE 8, e59031.
Switzer, P.V., 1993. Site fidelity in predictable and unpredictable habitats. Evol. Ecol. 7, 533–555.
Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647–664.
Whittingham, M.J., Evans, K.L., 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 146, 210–220.
Wiens, J.A., 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8, 1–93.
Wiens, J.A., 1973. Pattern and process in grassland bird communities. Ecol. Monogr. 43, 237–270.
Wilson, J.D., Whittingham, M.J., Bradbury, R.B., 2005. The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? Ibis 147, 453–463.
Zehm, A., Nobis, M., Schwabe, A., 2003. Multiparameter analysis of vertical vegetation structure based on digital image processing. Flora 198, 142–160.