



Topographic wetness index predicts the occurrence of bird species in floodplains

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ABSTRACT

Aim Selecting informative variables is crucial for species distribution modelling and ecological studies in general. Proxies quantifying water accumulation may have suitable properties because hydromorphy partly determines plant and animal communities. Topographic wetness index (TWI) was developed to locate wetlands but has largely been ignored from ecological studies despite the value of these areas for biodiversity and the ecosystem services they provide. We assessed here the ability of TWI to predict the occurrence of grassland passerines and tested different settings to determine which was the best predictor for our dataset.

Location Floodplain meadows in the Loire valley, France, Western Europe.

Methods We recorded the occurrence of four grassland passerines on 64 transects in large hay meadow patches. We computed four TWIs based on digital elevation models (DEMs). TWIs compute water accumulation as a function of slope and catchment. We tested two DEM resolutions (50 m and 250 m) and four TWI algorithms to identify which combination yielded the best model fits to our dataset.

Results Results depended on the predictor settings and the species considered. TWI predicted the occurrence of the Whinchat, the most specialized species, and the combined occurrence of the others three passerines. One TWI algorithm (SWI) yielded the poorest fit, and we could not determine the best algorithm among the others three. The coarser DEM resolution (250 m pixel size) also yielded better fitting model than the finer resolution (50 m).

Main conclusions Topographic wetness index appears as an informative predictor of species occurrence, at least for the Whinchat, and a useful proxy to detect suitable areas for floodplain grassland birds. This family of indices may improve our ability to model the habitat of wetlands species. However, DEM resolution and algorithm should be selected with caution as they may impact the predictive potential of the proxy.

Keywords

Grassland, habitat, meadow, passerine, species distribution model, TWI.

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INTRODUCTION

Selecting the most informative predictors is a challenging issue for species distribution and habitat modelling and for ecological studies in general. Ideally, one chooses factors that directly influence population growth or distribution or, if these are not identified or available, proxies that reflect biotic or abiotic processes relevant to the target species (Phillips *et al.*, 2006). In addition to the usual bioclimatic variables, indices describing water flow and accumulation retention in

continental ecosystems may prove useful as vegetation largely depends on soil moisture. Although several factors, such as mineral and nitrogen content, climate, history or land management, influence vegetation, hydromorphy is often crucial (Pellissier *et al.*, 2002; Keddy, 2010). However, this factor has largely been omitted from the expanding field of habitat modelling. We tested here the ability of the topographic wetness index, common in hydrology and geography (Beven & Kirkby, 1979; Chen & Yu, 2011; Ibrahim & Huggins, 2011) to predict species occurrence of grassland birds in floodplains.

Wetlands are among the most threatened habitats in the world, and many species they host are declining (Brinson & Malvárez, 2002). By their effect on river flow regulation (Acharya, 2000) and water quality improvement (Borges *et al.*, 2008), they provide highly valuable ecosystem services. In addition, many regularly flooded areas have become local hotspots of biodiversity that sustain floodplain specialists, adapted to flood disturbance regimes (Gibbs, 2000), but also species unable to cope with intensive agriculture practices and urbanization and that find no suitable habitat elsewhere (Godreau *et al.*, 1999). Flood risk and water proximity reduce the range of activities available to agriculture, and hay meadows remain a viable economical alternative to intensive crops in floodplains (Cook, 2010). However, as in other farmland areas (Siriwardena *et al.*, 1998), floodplain biodiversity is threatened by river embanking, poplar cultivation, biological invaders (Skorka *et al.*, 2010) and the intensification of cultivation practices (Plantureux *et al.*, 2005; Britschgi *et al.*, 2006; Broyer, 2009; Zahn *et al.*, 2010). A novel threat comes from climate change (IPCC, 2007). Prospective models based on global and regional circulation models suggest that new conditions may modify flood regimes (Arora & Boer, 1999; Brinson & Malvárez, 2002) and temperature increase is expected to change plant phenology and the composition of plant communities (Thuiller *et al.*, 2005). Ultimately, novel conditions may alter the dynamics of natural habitats and allow practices less favourable to biodiversity.

In wetlands, flood regime is a major factor that structures the distribution of species (Leyer, 2005). The modelling of a flood in space and time, that is, its geographical extent and duration, is a difficult issue because it requires fine environmental data like main channel and aquifer flow models as well as continuous transversal river profiles that are rarely available and very resource-consuming if they have to be acquired over large areas. Thus, it is essential to develop proxies for flooding susceptibility and more generally water accumulation capacity in any location of an area of interest. Topographic wetness indices, hereafter referred as TWI, have been developed with this aim (Beven & Kirkby, 1979). They only require digital elevation models (DEM), which are commonly available in many parts of the world. TWI has been largely used to detect wetlands (Grabs *et al.*, 2009; Dosskey & Qiu, 2011) but have been almost entirely omitted from ecological studies. To our knowledge, only two studies have assessed these indices. The first work modelled the distribution of an Alpine plant (Parolo *et al.*, 2008). TWI proved to be a poor predictor, but the species was not associated with wetlands. The second study found correlations between TWI and forest plant communities (Kopecky & Cizkova, 2010). Thus, the informative value of TWI to predict abundance, distribution or richness for animal and plant species is still largely unknown. We believe there is a need to assess its interest in ecological studies.

Several related indices have been developed over the years from the initial index developed by Beven & Kirkby's (1979) with the objective of improving water flow modelling. We

used four versions of the TWI: the single direction algorithm D8 (O'Callaghan & Mark 1984), the multiple flow algorithm FD8 (Freeman, 1991; Quinn *et al.*, 1991), the triangular multiple flow algorithm MD ∞ (Seibert & McGlynn, 2007) and the SAGA (System for Automated Geoscientific Analyses) wetness index SWI (Böhner *et al.*, 2006). The single direction algorithm (D8) directs the flow from each grid cell to one of the eight adjacent cells following the steepest downslope. The multiple flow direction algorithm (FD8) allows a split of flow according to the slope gradient of each eight directions corresponding to the neighbouring cells. Triangular multiple flow direction algorithm (MD ∞) also allows flow splitting, but it partitions each cell in triangular facets before flow computation. Lastly, SWI is an algorithm based on a multiple flow direction method, weighing the catchment area value by a function of the slope angle and the maximum values of neighbouring pixels in the catchment area. This computation smoothes the wetness index value in flat areas.

We investigated the effect of the four TWI indices on the occurrence of four grassland bird species in a large floodplain. Birds are particularly sensitive to the structure of vegetation for reproduction (Cody, 1985; Orłowski, 2004). This sensitivity associated with a high detectability makes them informative indicators of habitat (Hvenegaard, 2010). In addition, we assessed the effect of DEM spatial resolution on model fits. There is *a priori* no reason to select one particular spatial resolution, and the optimal spatial resolution, i.e. the scale of importance for the organism, may not be the finest (De Knegt *et al.*, 2010). Thus, we calculated TWI indices at two different resolutions, consistent with the typical home range of a territorial passerine, to determine the most appropriate resolution for grassland birds.

METHODS

Study area and species sampling

The study area extends over the lower 200-km section of the Loire river drainage in Western France (Fig. 1). Grassland is the dominant habitat type encountered in the floodplain of the Loire River and some of its main tributaries. Such an ecological continuity is now unusual in Western Europe. It provides an ideal set-up to investigate the factors affecting the distribution of grassland species. The study focuses on four passerines that dominate the small grassland bird community in this area, namely the Whinchat *Saxicola rubetra*, the Yellow Wagtail *Motacilla flava*, the Corn Bunting *Emberiza calandra* and the Reed Bunting *Emberiza schoeniclus*. All four species breed in grassland, but they are more or less strictly associated with wetland (Bradbury & Bradter, 2004). The Whinchat breeds in grasslands and heathlands. It is a typical species of wet hay meadows in many floodplain areas (Yeatman-Berthelot & Jarry, 1994). The Reed Bunting breeds in the same meadows but also depends on linear structures like ditches, bushes and reed beds (Brickle & Peach, 2004). The Yellow Wagtail largely exploits grassland

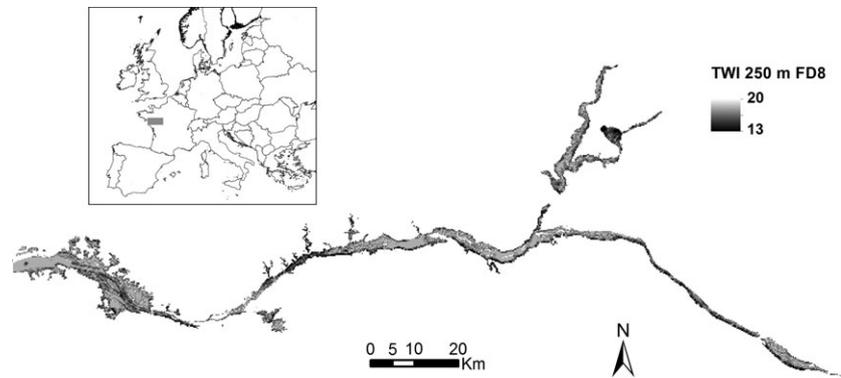


Figure 1 Map of the topographic wetness index calculated using the FD8 (multiple flow direction) algorithm. The inset shows the location of the study area in Western Europe.

but can breed in other habitats as shown by recent observations of breeding in crops (Kragten, 2011). The Corn Bunting is typically an open habitat species that is less dependent on hydromorphy (Mason & MacDonald, 2000).

We recorded the occurrence of each species in sixty-four 500-m-long transects distributed across the floodplains of the study area. A positive relationship between the size of habitat patch and presence or abundance is often observed in grassland birds (Helzer & Jelinski, 1999; Davis, 2004). To reduce the potential bias caused by patch size, we placed transects in large patches of hay meadow. We surveyed all sites in May 2009 and May 2010. Sampling was carried out between 30 min and 5 h after sunrise in low wind conditions and no precipitation. These conditions ensured optimal bird activity regarding the time of the year and the period of the day. We measured the distance of individuals to the transect using a laser telemeter (Bushnell Elite rangefinder, Bushnell Corporation, Overland Park, KS, USA). All observations were made within a 100-m radius around the transect. Given the relative homogeneity of habitat structure, we assumed that the detectability bias is constant across the study area. Thus, transect counts provided standardized estimates of occurrences. A species was considered as present when it was detected at least in one of the two sampling years.

Topographic wetness index layers

Topography remains the dominant factor that controls water flow. TWI calculates the capacity of water accumulation of each pixel in a watershed using a DEM (Beven & Kirkby, 1979). Indices other than the four selected evaluate water accumulation, but they use different data types such as pluviometry or temperature (Grabs *et al.*, 2009). Such variables are not always available at the drainage scale and require an additional step of modelling. We thus discarded these methods that may not be applicable to many users. In its original form, the D8 algorithm, TWI is computed for each pixel using slope and drainage area (Beven & Kirkby, 1979) as follows: $TWI = \ln(A_s / \tan \beta)$ where A_s is the drainage area (in m^2) and β is the local slope gradient (in%). The DEM is used to calculate A_s and β values. The three other methods are derived from the D8 index. For all algorithms, pixels with higher TWI values have higher capacity of water accumulation.

We calculated TWIs for the whole Loire catchment. We computed eight versions of this layer combining the four algorithms and two spatial resolutions with the aim of identifying the best predictor (see example Fig. 1). All indices were calculated using SAGA GIS (Böhner *et al.*, 2006) with 'Terrain Analysis – Hydrology' tools. Topographic layers were computed using two DEM (BD Alti IGN©, Institut national de l'information géographique et forestière (IGN), Saint-Mandé, France) with 50 m and 250 m pixel size and 1-m altitudinal resolution. To extract TWI values, we defined 250-m buffers around each transect and computed the mean and standard deviation of TWI for all pixels included in the buffer. Computations were carried out for the eight combinations of index and resolution. The 250-m resolution is more congruent with the home range scale of a passerine bird than the 50-m resolution. In contrast, the number of pixels used to estimate TWI around the transect is larger with the 50-m resolution and may yield more precise estimates.

Statistical analyses

We used logistic regression to test for the relationship between TWI and species occurrence with different TWI algorithms and resolutions. We used binomial generalized linear models (GLMs) with logit-link. In order to take into account the spatial autocorrelation between sampling units, we used spatial eigenvector mapping (SEVM; Griffith, 2000; Dormann *et al.*, 2007; Corkeron *et al.*, 2011). We selected this method because we could not satisfactorily fit a theoretical variogram to our dataset, which may result from the distribution of sampling units along a limited number of preferential directions in the river catchment and the heterogeneous distribution of populations in three main zones of the study area (Fig. 1). SEVM is more flexible as it does not assume a specific spatial model.

Spatial eigenvectors were computed using Spatial Analysis in Macroecology software (SAM 4.0) (Rangel *et al.*, 2010) on geographical distances. We used the broken-stick method to select eigenvectors that describe most of the spatial autocorrelation in a dataset (Jackson, 1993; Diniz-Filho *et al.*, 1998; Diniz-Filho & Bini, 2005). Three eigenvectors were selected because their observed eigenvalues exceeded the eigenvalue expected by the broken-stick distribution (Appendix S1 in

Supporting Information). Selected eigenvectors were added as covariables in models to control for spatial autocorrelation (Diniz-Filho & Bini, 2005). We checked the absence of spatial autocorrelation in model residuals using Moran's I test in the SAM software (Rangel *et al.*, 2010) (Appendix S2). GLMs were computed using R software (R Development Core Team, 2011). Null models included the three eigenvectors, that is, the spatial information about the distribution of our sampling units. They were compared with full models including eigenvectors and TWI using AICc (Akaike's information criterion corrected) and model weights (Burnham & Anderson, 2010). We used the CAR package in R software to assess multicollinearity. It was limited in all models, and statistical inferences were valid, as variance inflation factors were consistently less than 1.80 (Zuur *et al.*, 2009). We analysed the occurrence of each individual species, and all four passerines grouped together to assess whether TWI predicted the presence of at least one grassland species. However, the Whinchat was present along with at least one other species in all but one transect. Thus, we also analysed occurrence of the three remaining species (Yellow wagtail, Corn Bunting and Reed Bunting) as a group.

RESULTS

The Whinchat was the most common species (occurrence frequency 0.66, Fig. 2). The three other species were also common, but occurrence frequencies were lower (Yellow Wagtail 0.42, Corn Bunting 0.41, Reed Bunting 0.36). The combined occurrence frequency of the four species (0.67) was almost entirely accounted for by the Whinchat. The combined occurrence of the three remaining species was slightly lower (0.58).

The broken-stick method selected the first three eigenvectors that were included in all null and full models. Our data showed positive relationships between TWI and occurrence (Table 1, Fig. 3). However, model fit depended on species identity, algorithm and DEM spatial resolution. The effect of TWI varied greatly between individual species (Table 1). In the Whinchat, ΔAICc values were larger than 2 for all methods and resolutions except for the SWI algorithm with 50-m

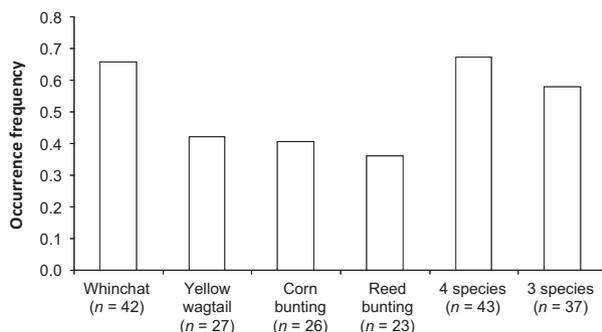


Figure 2 Occurrence frequency of the four passerine species, all species (4 species) and all species, but the Whinchat (3 species) observed in 64 transects.

DEM. We found a nearly identical result to the Whinchat model for the 4-species occurrence, which is explained by the high co-occurrence of the Whinchat with the other species. We found $\Delta\text{AICc} < 2$ for the Yellow Wagtail, the Corn Bunting and the Reed Bunting when species were considered separately. However, when we combined the occurrences of the three passerines, AICc values were lower in models with TWI than in the null models for the 250-m resolution (Table 1).

All algorithms predicted grassland species occurrence. However, SAGA Wetness Index (SWI) yielded the worst model fits (Table 1). AICc values were systematically higher for SWI than for the other algorithms regardless of DEM resolution. For example, in Whinchat data, AICc values ranged between 80.84 and 75.98 for SWI and between 73.92 and 70.03 for the three other algorithms. The three other methods consistently yielded better fitting models, but we cannot identify the best method because AICc values were too close to each other.

Finally, model fits depended on DEM spatial resolution (Table 1). For all algorithms, AICc values were systematically lower with 250-m pixel size than for 50-m pixel. We found $\Delta\text{AICc} > 2$ between the two DEM resolutions in the Whinchat and the 3-species occurrences. For the latter response variable, all 250-m DEM models were better than null model ($\Delta\text{AICc} > 2$), whereas none of 50-m DEM were. Thus, DEM with coarser resolution always yielded the best fitting model.

DISCUSSION

We found a positive relationship between TWI and both the Whinchat and the combined 3-species occurrence, which means that areas with a high potential of water accumulation have a high probability to host passerines. In our floodplain study area, topographic wetness indices are thus informative predictors of one grassland bird population. Obviously, TWI alone could erroneously predict high probability of occurrence in patches unsuitable to a species or a guild. The strength of the relationship is bound to depend on land use and agricultural practices such as drainage, land conversion to crop or poplar, grassland fertilization all of which reduce habitat suitability to grassland species. Moreover, the predictive value of TWI may depend on climatic conditions although the way in which it is affected remains unclear. In dry areas, the relationship between potential and observed wetness may be weaker. Yet, water is always expected to accumulate in low areas, and thus, water-demanding species may only survive in zones with high TWI values. Nevertheless, provided suitable habitat patches are sampled, as in the present study, TWI can be useful for predicting species occurrence. This finding is interesting because hydromorphy and water availability are environmental parameters that are difficult to estimate or access especially over large areas. TWI only requires DEM raster layers that are widely available at different resolutions across the world. It is likely to prove useful for a wide range of species, plants or animals, because water is crucial for most organisms. Furthermore, TWI was

Table 1 Corrected Akaike's information criterion (AICc) and Akaike weight (w) values for logistic regressions between the occurrence of either individual bird species or the 3-species combination (Yellow wagtail, Corn bunting and Reed bunting) and topographic wetness indices including eigenvectors. We used four algorithms (D8, FD8, MD ∞ and SAGA Wetness Index) and two resolutions (250 m and 50 m pixel). AICc₁ corresponds to the null model with spatial eigenvectors and AICc₂ to the model with spatial eigenvectors including topographic wetness index (TWI).

		AICc ₁	AICc ₂	AICc ₍₁₋₂₎	w ₁	w ₂	AUC	Coefficient \pm SE
Whinchat								
250 m	D8	81.83	70.03	11.80	0.00	1.00	0.82	1.78 \pm 0.56
	FD8	81.83	71.84	9.99	0.01	0.99	0.81	1.76 \pm 0.57
	MD ∞	81.83	70.26	11.57	0.00	1.00	0.82	1.86 \pm 0.59
	SWI	81.83	75.98	5.85	0.05	0.95	0.79	1.59 \pm 0.69
50 m	D8	81.83	72.56	9.27	0.01	0.99	0.81	1.76 \pm 0.59
	FD8	81.83	73.92	7.91	0.02	0.98	0.80	1.95 \pm 0.69
	MD ∞	81.83	72.75	9.08	0.01	0.99	0.81	1.78 \pm 0.60
	SWI	81.83	80.84	0.99	0.38	0.62		
Yellow wagtail								
250 m	D8	83.77	82.82	0.95	0.38	0.62		
	FD8	83.77	82.00	1.77	0.29	0.71		
	MD ∞	83.77	83.16	0.61	0.42	0.58		
	SWI	83.77	83.76	0.01	0.50	0.50		
50 m	D8	83.77	85.37	-1.60	0.69	0.31		
	FD8	83.77	85.73	-1.96	0.73	0.27		
	MD ∞	83.77	85.47	-1.70	0.70	0.30		
	SWI	83.77	85.63	-1.86	0.72	0.28		
Corn bunting								
250 m	D8	86.37	85.92	0.45	0.44	0.56		
	FD8	86.37	84.91	1.46	0.33	0.67		
	MD ∞	86.37	85.52	0.85	0.40	0.60		
	SWI	86.37	86.62	-0.25	0.53	0.47		
50 m	D8	86.37	86.01	0.36	0.45	0.55		
	FD8	86.37	86.74	-0.37	0.55	0.45		
	MD ∞	86.37	86.07	0.30	0.46	0.54		
	SWI	86.37	87.87	-1.50	0.68	0.32		
Reed bunting								
250 m	D8	71.38	72.50	-1.12	0.64	0.36		
	FD8	71.38	73.12	-1.74	0.71	0.29		
	MD ∞	71.38	73.01	-1.63	0.69	0.31		
	SWI	71.38	73.62	-2.24	0.75	0.25		
50 m	D8	71.38	73.35	-1.97	0.73	0.27		
	FD8	71.38	73.28	-1.90	0.72	0.28		
	MD ∞	71.38	73.31	-1.93	0.72	0.28		
	SWI	71.38	73.62	-2.25	0.75	0.25		
Three species								
250 m	D8	85.25	77.56	7.69	0.02	0.98	0.80	1.44 \pm 0.52
	FD8	85.25	75.49	9.76	0.01	0.99	0.81	1.75 \pm 0.58
	MD ∞	85.25	77.92	7.33	0.03	0.97	0.79	1.48 \pm 0.54
	SWI	85.25	80.63	4.62	0.09	0.91	0.79	1.46 \pm 0.69
50 m	D8	85.25	83.82	1.43	0.33	0.67		
	FD8	85.25	84.89	0.36	0.46	0.54		
	MD ∞	85.25	83.95	1.30	0.34	0.66		
	SWI	85.25	84.76	0.49	0.44	0.56		

Bold values are used to indicate Δ AICc larger than 2. w_1 is the weight of the null model, and w_2 the weight of the model including TWI. AUC (Area Under the Curve) and coefficient and standard error are indicated for candidate models selected by AIC.

developed as a general tool to describe spatial soil moisture patterns in wetlands. Therefore, we believe TWI could find greater applications in ecological studies as a hydrological

proxy. Its simple form and the availability of DEM data call for an assessment of its usefulness, especially in the growing research field of species distribution modelling.

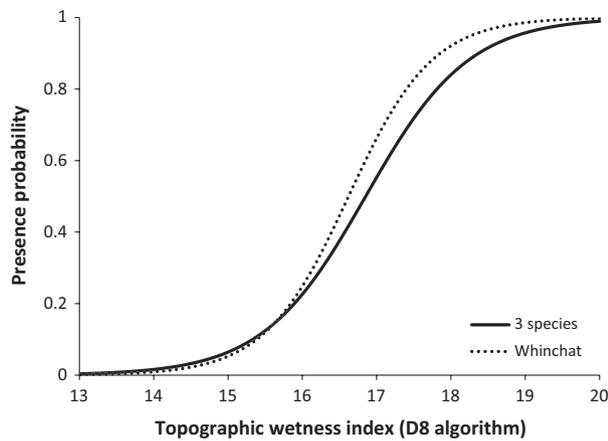


Figure 3 Probability of presence for the Whinchat and the 3 species (Yellow wagtail, Corn bunting and Reed bunting) represented as a logistic function of topographic wetness index. The topographic wetness index setting used here is D8 algorithm and 250-m digital elevation models.

Influence of algorithm, DEM resolution and species

Several factors affected the strength of the relationship between TWI and species occurrence. Algorithm and DEM resolution influenced the explanatory power of the predictor. The selection of the algorithm had the stronger influence on model fit. According to our results, model fit was worse for SWI than it was for the other three methods. SWI smooths wetness index values and thus homogenizes values between neighbouring pixels as shown by the lower standard errors for this algorithm (Appendix S4). Its use may not be recommended in floodplains with large flat areas. This index may perform better in areas with larger altitudinal variations. The three other methods, D8, FD8 and MD ∞ algorithms, are variants of the TWI algorithm created by Beven & Kirkby (1979) and were developed to model water flow in a more realistic way than the original index. They all yielded better fitting models than SWI, but we could not identify the best method among them. It is unlikely that their relative performance would change using different statistical techniques. Therefore, they seemed equally suitable to predict grassland bird distribution in our study area. The importance of algorithm choice for TWI mapping has been observed elsewhere (Kopecky & Cizkova, 2010). Multiple flow algorithm performed best in this plant ecology study. However, it did not stand out from the others in the present work. Clearly, tests on more habitats and taxonomic groups are required to determine whether any algorithm would outperform the others in different conditions.

We also found a clear effect of DEM resolution. The lower resolution (250-m pixel) provided the best model fit. Sørensen & Seibert (2007) have already highlighted that a lower DEM resolution might in some cases be more useful for landscape analyses and modelling. Landscape is important for bird habitat selection (Herkert, 1994; Naugle *et al.*, 1999; Söderström & Pärt, 2002), which may account for the effect

of DEM resolution. Grassland birds tend to select large continuous breeding patches and avoid fragmented landscapes. This process called area sensitivity has been observed in breeding grassland birds (Helzer & Jelinski, 1999; Davis, 2004). In our study site, large continuous meadows are located in the lowest areas of the floodplain, that is, have high TWI values. High-resolution DEM (50-m pixel) may thus put the emphasis on intrapatch variability rather than on landscape characteristics. Furthermore, the lower resolution may better match the scale of the breeding home ranges, whereas 50-m resolution might more closely match the scale of the territory. However, this explanation is difficult to evaluate as we did not map territories here. Finally, the 50-m resolution may be too fine relative to the altitudinal resolution (1 m). In flat areas, identical DEM and TWI values can be observed for several adjacent pixels (Appendix S5). In that case, increasing the resolution may smoothen or equalize TWI values over the area in the same way as SWI does. Thus, gain in spatial resolution may only make sense if altitudinal resolution is gained too. Unfortunately, no DEM with altitudinal resolution below 1 m is currently available at the scale of the study area.

Model fit was also influenced by the focal species too. These results are consistent with the general knowledge on species distribution modelling. The predictive ability of a model is usually better for a specialist, whose niche components can be more easily captured, than for a generalist or a species whose niche varies in space (Franklin, 2010). The Whinchat is a specialist of hay meadows. It only breeds in extensively managed grassland in most parts of its range (Broyer, 2009; Tome & Denac, 2012) and does not cope well with changes in agricultural practices (Grüebler *et al.*, 2008). As expected, its occurrence was predicted by most models. In contrast, the Yellow Wagtail can also breed in crops, although less extensively than in grasslands (Kragten, 2011). For this species, habitat selection was more variable and no models predicted an effect of TWI on its occurrence. Similar results were found for the Reed Bunting that breeds in meadows but also commonly in other wetland habitat type like ditches, ponds or streams (Brickle & Peach, 2004). The Corn Bunting is not a wetland species *per se* but rather an open habitat bird that favours large continuous patches (Mason & MacDonald, 2000) and can breed in dry open fields as well as in floodplains. However, the lack of clear relationships between each of these three species and TWI may stem from their lower occurrence that affected the statistical power. This is suggested by the positive Δ AICc observed with the 250-m spatial resolution DEM for the Yellow wagtail and the Corn bunting. We also found an effect of TWI on the combined dataset for the three species occurrence (Yellow wagtail, Corn bunting and Reed bunting) for all algorithms at the coarser resolution. Thus, TWI seems able to capture the capacity of a floodplain area to host at least some grassland bird populations and in this respect may be useful for identifying the most favourable areas for these species. The index performed well for the Whinchat here, but it was more loosely related to the least specialized

species. Transects were placed on purpose in large grassland patches to reduce the effect of area sensitivity on surveys. Our sampling design is thus not random relative to distribution of TWI in the floodplain as we sampled the higher part of the TWI range. This sampling strategy may actually underestimate the effect of TWI on the occurrence of grassland species. Adding covariables, like patch size or vegetation structure, might thus improve TWI estimates (Helzer & Jelinski, 1999; Davis, 2004).

According to our results, TWI proved to be a useful environmental predictor for modelling the distribution of at least one species. More generally, this study shows that it is potentially a valuable predictor for other plant or animal wetland species. However, several settings must be considered carefully. Algorithm choice is important because it affects model fit. High-resolution DEMs may not be ideal for bird studies as habitat selection maybe more landscape based than site based in this group. Finally, specialization level of the focal species also affects model prediction. More studies on other habitats and taxonomic groups are required to fully assess the usefulness of TWI in ecological studies, but present results suggest that its interest may lie beyond the scope of floodplain grassland birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Distribution of transects across the study area.

Appendix S2 Selection of spatial vectors using the broken-stick model.

Appendix S3 Test of spatial autocorrelations for model residuals.

Appendix S4 Standard error boxplots for the topographic wetness indices.

Appendix S5 TWI maps for all algorithms and DEM resolutions.

BIOSKETCH

Aurélien Besnard is a PhD student investigating the spatial ecology of passerines in floodplains. GECCO, Ecology and Conservation of Vertebrate Group (sites.google.com/site/geccoangers/), integrates ecology, behavioural ecology and population genetics to analyse the relationships between habitat and behavioural strategies in Vertebrates.

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