Modeling bird communities using unclassified remote sensing imagery: Effects of the spatial resolution and data period

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\textbf{A B S T R A C T}

In this paper we assess the capacity of satellite images to explain and predict bird community patterns in farm-wood landscapes in southwestern France. Our goal is to examine the effect of the images’ acquisition date and spatial resolution on the models’ performance. We also seek to assess whether unclassified images provide results comparable with classified data (i.e. land-cover map). To do that we constructed species richness models (generalized additive models) based on a sample of 573 counting points and on non-classified images made up of NDVI data and digital height model (DHM), making it possible to quantify the spatial and temporal heterogeneity of habitats. To assess the acquisition date effect, we compared the performance of NDVI data acquired on four different dates (February 4th, June 24th, August 19th and October 18th, 2009) by the same sensor (SPOT-5). To assess the spatial resolution effect, we compared five NDVI images acquired over an identical period (September 2010) but by different sensors (WorldView-2, SPOT-5, SPOT-4, Landsat, MODIS) as well as two DHMs obtained from LiDAR (1 m) and radar (5 m) data. Our results show that for a constant spatial resolution (10 m) it is the NDVI data acquired at the beginning of the autumn that provide the best performance. These data better reveal the landscape requirements of birds during the breeding period. For a given period (September 2010), the higher resolution spatial data (2 m) are the highest performing. However, in view of the cost of WorldView images, we suggest that 10 m data (SPOT-5) provide a good trade-off for studying the distribution of bird communities. For the height data (DHM), the effect of the spatial resolution is not significant. The differences of performance between the spatial resolutions of NDVI data are not as great as those between the data acquisition periods. The performance of unclassified data (NDVI or DHM) is also comparable with that of land-cover maps. This suggests on the one hand that the choice of the NDVI image date is more important than that of the spatial resolution and on the other hand that the NDVI or DHM data are good alternatives to classified data when constructing a bird-habitat predictive model.

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1. Introduction

Because of its capacity to observe habitats on different spatial and temporal scales, remote sensing is now an inescapable tool for many fundamental and applied ecological issues (Boyd and Danson, 2005; Cord and Rödder, 2011; Gillespie et al., 2008).

In ecology, the landscape is usually represented discretely, as a mosaic of habitat patches, corridors and barriers within a matrix. That is why the remote-sensing usage that predominates in this area remains the production of land-cover classifications from which composition and configuration metrics can be calculated (Levin et al., 2009; Newton et al., 2009). However, despite its popularity, this discrete representation of the landscape has certain limits (Fischer and Lindemayer, 2006; Southworth et al., 2004). Choices have to be made beforehand regarding the land-cover categories to be used and their level of detail, which may have significant consequences on the ability to predict the presence or diversity of species. Indeed, the perception of the habitat by the species may be very different from the landscape perceived by man and therefore from the predefined categories (Foltête et al., 2000; Laurent et al., 2005; Manning et al., 2004). Consequently,
the species–habitat models based on the utilization of land-cover maps may be skewed by an anthropocentric vision of the landscape elements chosen and of the variables used to describe them.

Faced with these limits, the question of the most appropriate representation of the landscape for constructing ecological models has been posed (McIntyre and Barrett, 1992; Price et al., 2009). Alternative representations of the landscape integrating the notion of landscape continuum (Austin, 1985; Fischer and Lindemayer, 2006; Manning et al., 2004) or of the fuzzy membership of a category have been proposed (Arnot et al., 2004; Foody, 1996; Rocchini and Ricotta, 2007). Thus, an increasingly popular research current has emerged over the last fifteen years, based on the indirect approach to modeling biodiversity, and proposing to use unclassified images rather than land-cover maps in the models. The studies adopting this viewpoint are numerous and varied (Leyequen et al., 2007; Rocchini et al., 2010; Vierling et al., 2011).

Concerning the optical data, a great majority of the published studies have looked at using the normalized difference vegetation index (NDVI), whose relationship with the net primary productivity as well as the vegetation’s biomass has largely been established (Sellers, 1987). NDVI is calculated by dividing the difference in the near-infrared (NIR) and red (R) bands by the sum of the NIR and R bands for each pixel in the image. The spectral indicators generally derived from this measure of greenness correspond to simple statistics (min, max, average, sum, range, variance) calculated from the values of the NDVI’s pixels in a given vicinity (e.g. Bailey et al., 2004; Bino et al., 2008; Seto et al., 2004).

The optical data and associated metrics provide information on the primary productivity, with its variability, and on the landscape composition which have an impact on biodiversity. However they do not make it possible to characterize the vertical structure of the vegetation to which certain animal species are sensitive (e.g. birds, Erdelen, 1984). To achieve that it is necessary to resort to other types of data obtained from active sensors such as LiDAR or radar. LiDAR data (discrete return LiDAR or full-waveform) are the most frequent type of data used (Bergen et al., 2009; Bradbury et al., 2005; Goetz et al., 2007, 2010; Vierling et al., 2008). The radar data also offer the potential for describing the structure of the vegetation (Imhoff et al., 1997). Spaceborne radar sensors exist which make the radar data more readily available. However they have been markedly less used up until now, probably because they are more difficult to process (Bergen et al., 2009).

These previous results have opened up new perspectives for using remote sensing for monitoring biodiversity. However, when using remotely sensed data, ecologists are limited by the impact of the spatial resolution and of the date of the images on the quality of the community-habitat models.

Few studies have assessed the effect of the images’ spatial resolution to understand community patterns (Levin et al., 2009; Rocchini, 2007; Seoane et al., 2004). Furthermore, the conclusions of these studies may be limited by the fact that they were not always carried out on images taken on the same date (Chust et al., 2004; Levin et al., 2009; Rocchini, 2007). In certain cases they were based on land-cover maps, adopting a discrete representation of the landscape and not a continuous representation (Guisan et al., 2007; Seoane et al., 2004). In addition to that, some of these analyses were conducted using images that were not obtained from different sensors but, rather, images from a single sensor whose source image had been resampled at lower spatial resolutions (Gottschalk et al., 2011). From an applied viewpoint, it is necessary to assess the effect of spatial resolution based on images acquired by different sensors in order to provide useful guidance on selecting the optimal source for habitat mapping.

Concerning the choice or existence of an optimum date, no definitive answer exists in the literature. Various authors have compared the predictive performance of species–habitat models using data acquired on different dates but these works often limit themselves to comparing images on two dates and sometimes several years apart (Bino et al., 2008; Goetz et al., 2007). A study including more dates was carried out by Levin et al. (2007), but it combined images with different spatial resolutions. Other studies have sought to go beyond the bi-date comparison by using NDVI time-series summarized in a variety of phenological metrics (Foody, 2005; Hurlbert and Haskell, 2003; Oindo and Skidmore, 2002). The results obtained show a significant potential but do not indicate what date should be preferred in the case where only a few higher spatial resolution images are available in the year.

In this paper we assess the capacity of satellite images that differ in their acquisition date or in their spatial resolution, to explain and predict the bird species richness during the breeding season in an agricultural landscape. We adopt an indirect approach, using unclassified data obtained from different sensors.

First, we examine how the image acquisition date impacts our capacity to understand bird community patterns. Specifically, we assess whether different NDVI data collected at different periods in a year reflect in the same way the landscape composition and vegetation structure that affect bird distributions during the breeding period. To do that we compare four NDVI images with the same spatial resolution (10 m) acquired by the same sensor (SPOT-5) over four different periods (February, June, August, October 2009). Second, we examine whether the images’ spatial resolution impact the bird/habitat model’s performance. As many birds are sensitive to the presence of fine vegetation structures such as hedgerows, we assess whether images with fine spatial resolutions are more effective to explain bird community patterns. To achieve that we compare five NDVI images all acquired during the same period (September 2010) by different sensors (WorldView-2, SPOT-5, SPOT-4, Landsat-5, MODIS) and in a broad range of spatial resolutions (2 m, 10 m, 20 m, 30 m, 250 m respectively). We also compare two digital height models (DHM) one of which has a spatial resolution of 1 m, derived from LiDAR data, and the other with a spatial resolution of 5 m derived from a radar sensor. Finally, we assess whether the choice of landscape representation (continuous versus discrete) impact our capacity to predict bird community patterns. To examine that we compare the results obtained from continuous raw data (NDVI and LiDAR data) with those based on classified data (a land-cover map).

2. Material and methods

2.1. Study area

The study site lies between the Garonne and Touch rivers, in southwestern France (43°16’28”N, 0°51’11”E, WGS 1984) and is part of the “Coteaux de Gasconne” Long Term Ecological Research site (LTER_EU_FR_003). The area is hilly (altitude 200–400 m) and dissected by north–south valleys, within a sub-Atlantic climate subject to both Mediterranean and mountain influences. Wood cover is fragmented, and currently covers some 15% of the area. Woodlands are dominated by Quercus robur and Quercus pubescens. Dominant non-wood land-cover modalities consist of a combination of crops (including maize, oilseed rape, sorghum, and sunflower), short term grasslands (including ray grass, alfalfa), permanent grasslands, scattered trees and hedgerows. Permanent grasslands are not reseeded for at least five years or more (in accordance with the Common Agricultural Policy), and are composed of a higher floristic diversity than short term grasslands. Permanent grasslands are grazes and/or mowed. Hedgerows are mostly composed of trees and sometimes shrubs, which on average are ten meters high.
2.2. Bird data

In 2009, 573 point counts were sampled systematically on a survey grid that covers four rural municipalities (Esparron, St André, Eoux, Peyrissas) (Fig. 1). Six experienced ornithologists performed the bird survey. The point counts represent the diversity of landcover types. The point counts were separated from each other by 250 m. This distance is greater than the home range size of most of the studied species during the breeding period (usually less than 2 ha, Söderström and Párt, 2000). Point counts were visited once between May and June during the breeding period. At this period, all migrant species are present. In this survey, the choice was made to increase sample size at the expense of temporal replication (several visits per point), which is recommended by Thompson et al. (2002). The presence–absence of each bird species within a 125 m radius around each point was recorded during 20 min periods. Points were performed during the peak singing activity period (6:00–11:00 am), in favorable weather conditions only (no strong wind or rain). Counts were started 3 min after arrival at the point to limit the effect of the observer’s presence on the detection of individuals.

From these data, species richness was calculated in each point count as the sum of all species present, with the exception of raptor species excluded because their home range is larger than the point count area, and human-related species (e.g. sparrows, swallows) because they are gregarious and clustered close to human settlements. Because all bird species are not expected to respond uniformly to NDVI and LiDAR/radar data measurements, three species richness metrics were computed: woodland bird species richness (a total of 14 species) as identified in Balent and Courtiade (1992), farmland bird species richness (a total of 21 species) as identified in Filippi-Codaccioni et al. (2010), and total species richness which incorporates woodland, farmland and generalist birds (a total of 41 species). All bird species names are available in Appendix A.

2.3. Image data

Several sets of data reflecting the 2D and 3D structure of the landscapes were used to carry out the study: a series of NDVI images from 2009 with a constant resolution of 10 m acquired on different dates, a series of NDVI images with different resolutions acquired in September 2010, and two Digital Height Models (DHM) derived from LiDAR and radar data.

The 2009 NDVI images were calculated from cloud-free multispectral data (four bands) acquired by the SPOT-5 satellite. There were four dates available: February 4th, 2009; June 24th, 2009; August 19th, 2009 and October 18th, 2009. These images have the same spatial resolution (10 m).

For the year 2010, we used five NDVI images derived from cloud-free multispectral data (four bands) acquired by five different sensors: WorldView-2 (spatial resolution of 2 m), SPOT-5 (spatial resolution of 10 m), SPOT-4 (spatial resolution of 20 m), Landsat 5 (spatial resolution of 30 m) and MODIS (MOD13Q1 product, 16-day composite, spatial resolution of 250 m). All these images were acquired on approximately the same date: September 20th (WorldView), September 20th (SPOT-5), September 22nd (Landsat), September 14th–29th (16-day period for MODIS) or very nearly: September 1st (SPOT-4).

Since the characteristics of spectral bands in the red and near-infrared can vary from sensor to sensor, NDVI values are not strictly the same between the 2010 images. They are affected by differences in spectral bandwidth and location (Table 1). However, although the effect of this shifting is not insignificant (Teillet et al., 1997), we consider that the extreme NDVI differences (0.03 between WorldView-2 and MODIS) are sufficiently small to ignore them in this study.

Most of the NDVI data were taken from the OSR MiPy remote sensing reference database provided by the French Space Agency (CNES) in the framework of the Kaliedos program. All the images were geographically referenced according to the National BDOrtho database (produced by IGN, the FrenchMapping Agency) and orthorectified using a common Digital Terrain Model (DTM) with a spatial resolution of 25 m (BDTopo IGN). The raw NDVI values ranging from −1 to +1 were also rescaled from 0 to 255 (8-bit encoding).

The DHM were gathered from two sources: Airborne laser scanning (LiDAR) and interferometric synthetic aperture radar. LiDAR data were acquired over the study site using a RiegL LMS-Q560 scanner, in combination with a hyperspectral aerial survey. The imaging flight was carried out at noon, in July 2010, from an altitude of 4500–5000 ft. The digital surface model (DSM) and digital terrain model (DTM) were calculated from discrete points (~4 points/m², 15–30 cm absolute vertical accuracy) derived from the original full waveform data (100 kHz pulse repetition rate). Both models were created from a triangulated irregular network. The final DHM product was derived as the height difference between the DSM (initial canopy return) and DTM (ground return) and resulted in a raster surface of 1 m spatial resolution. The second DHM is based on the NextMap products (Intermap) derived from an airborne interferometric synthetic aperture radar (IFSAR using X–HH band). The altitude of a point on the earth’s surface is reconstructed from the phase between two SAR signals arriving at two antennae. The NextMap DSM and DTM acquired in 2010 were produced at 5 m spatial resolution with a vertical accuracy of 1–2 m. The DTM is derived from the DSM product according to an editing process and a set of rules described in the Intermap Product Handbook (Intermap, 2010). Like for the LiDAR data, the final DHM was obtained by subtracting the DTM from the DSM. Certain artifacts were then corrected by assigning a null value to the pixels with a negative height.

For each type of data, five variables were calculated within 573, 250 × 250 m cells (i.e. surface area of 6.25 ha) on the point count grid: the average (Avg), variance (Var), minimum (Min), maximum (Max) and the range of the values.

2.4. Land-cover map

A land-cover map was produced by computer assisted photo-interpretation using the BDOrtho orthorectified digital database dating from 2006 (IGN). Land-cover categories were digitized using the ArcGIS 9.2 software (Environmental Systems Research Institute) and the interpretation of aerial photographs was completely checked with field observations made during the bird censuses. Eight land-cover categories were considered relevant for describing the landscape composition in order to explain bird distributions: percentage of crop, short term grassland, permanent grassland, hedge, woodland, road, water and built-up area. Landscape heterogeneity was also calculated through Shannon’s diversity index. These variables were calculated within the 573 point counts.

2.5. Analysis

The three species richness metrics were linked to the different data groups (i.e. 3 richness variables X 12 groups environmental data = 36 models) using generalized additive models (GAMs) with the R 2.15.1 software (R Development Core Team, 2012) and the ‘gam’ package (Hastie, 2011). Being completely data-driven, GAMs avoid making untested assumptions on the relationship between the dependent and independent variables (Hastie and Tibshirani, 1990).

High correlation between the explanatory variables can inflate the variance of regression parameters and potentially lead to the
wrong identification of relevant predictors (Dormann et al., 2013). For NDVI and DHM data, the Min and Range variables were not included in the models because they were highly correlated with other variables beyond a threshold of $r = 0.7$ (Dormann et al., 2013). For each richness variable and for each image data type, the model took the form: species richness $\sim$ average + variance + maximum. For the land-cover map, the landscape variables were not highly correlated and the model took the form: species richness $\sim$ % crop + % short term grassland + % permanent grassland + % hedge + % woodland + % road + % water + % built-up area + Shannon index. The Poisson family distribution was used to fit the species richness models. A stepwise backward and forward selection was used on the basis of the Akaike Information Criterion (AIC) (Burnham and Anderson, 1998; Johnson and Omland, 2004). AIC is a parsimonious approach that covers both model fit and parameter number. The smallest AIC value identifies the most parsimonious model. In addition to selecting the variables, the procedure was allowed to choose between one and four degrees of smoothing (1 = no smoothing) for each explanatory variable. For each species richness variable, we also constructed a model using the NDVI image and the DHM providing the best performance individually to assess the complementarity of the 2D and 3D data.

The goodness of fit of the models was quantified by examining the amount of the explained deviance ($\% D^2$) based on the total datasets. The predictive performance (i.e. the capacity of the model to predict species richness on new data) was quantified using a three-fold cross-validation repeated 100 times. In cross-validation, the dataset is split randomly into a number of groups ($k$) of equal size, here $k = 3$ is used. A training set is then formed by combining all except one of these groups, with the last group forming the test set to derive performance measures. Predictions and observations of the test set derived by cross-validation were compared using Spearman rank correlations (Rho). This method provides an indication of similarity between the ranks of the observed and predicted values which can differ from the values computed using the total dataset. It varies from $-1$ to $+1$. The correlation is considered to be weak for $0 < \text{Rho} < 0.25$, fair for $0.25 < \text{Rho} < 0.5$, moderate for $0.50 < \text{Rho} < 0.75$ and strong $\text{Rho} > 0.75$ (Colton, 1974). The root mean square error (RMSE) between observations and predictions was also calculated. The predictive performances between each dataset were compared using t-tests. Finally, the response curves of the species richness variables against NDVI Avg and Var variables and DHM Avg and Var variables for the best datasets were plotted.

3. Results

3.1. Comparison of the goodness of fit and predictive performance of the different types of satellite data

Based on non-parametric spline correlograms (“ncf” R package; Bjørnstad, 2012), no evidence of spatial autocorrelation was found
between the models’ residuals of GAMs, indicating that non-spatial statistical models were appropriate (Dormann et al., 2007). Correlograms are provided in Appendix B.

Given that the Rho values and the RMSE values lead to similar results, we decided only to present the Rho values that are easier to interpret. Generally speaking, the three species richness variables are fairly explained (Table 2) and predicted by the satellite data (Fig. 2). The best models predict the woodland bird richness well (maximum mean Rho = 0.76) and predict the farmland birds richness fairly (maximum mean Rho = 0.48) and the total richness moderately well (maximum mean Rho = 0.59) (Fig. 2).

For a constant spatial resolution (10 m), the date of October 18th, 2009 best explains and predicts the three richness variables (Table 2, Fig. 2). For farmland species richness, the predictive performance of the data from October 18th is not, however, significantly better than that of August 19th.

This effect of the period on the performance is linked to NDVI’s seasonal variations in agricultural landscapes. NDVI is sensitive to change in vegetation cover and structure. The NDVI Avg variable is lower for October 18th than it is for June 24th or August 19th in the most cultivated areas and precisely in the wheat and summer crop (sunflower and maize) areas, respectively (Fig. 3). The NDVI Avg variable is higher for October 18th than it is for February 4th in the wooded areas (Fig. 3).

For a constant period (September 2010), the 2 m spatial resolution data have the best goodness of fit and predictive performance (Table 2, Fig. 2). However the differences of prediction performance between resolutions are slight, above all for the finest resolutions (NDVI 2 m Rho=NDVI 10 m Rho=0.08 for the woodland richness, 0.02 for the farmland richness and 0.06 for the total richness). These performance differences between spatial resolutions are smaller than between the different dates (Rho October 18th, 2010–Rho February 4th, 2010 = 0.37 for the woodland richness).

The effect of the height data’s spatial resolution is not significant for the three species richness variables. The model that includes the best data (September 20, 2010 with 2 m resolution) and the DHM LiDAR performs slightly better than the NDVI or LiDAR data alone, except for the total richness.

The performance of the discrete data obtained from the landcover map is very similar to that with NDVI data. The mean value of Rho is slightly better for farmland richness and not
significantly different for woodland richness and total richness (respectively land-cover map \( Rho - NDVI \) 2 m \( Rho = 0.04, -0.01 \) and 0).

### 3.2. Species richness responses to the satellite variables

We constructed response curves for the three species richness variables using the NDVI 2010 data with 2 m spatial resolution and the LiDAR DHM data with 1 m spatial resolution which, as seen above, have the best goodness of fit and predictive capability. The three species richness variables give different responses to the Average and Variance variables (Figs. 4 and 5). Average and Variance were the most important variables to explain the richness distribution (see \( SD^2 \) in Fig. 4). In comparison, the importance of the Max variable was low (\( SD^2 = 7 \) for the woodland, 0 for the farmland and 7, for the total richness) in univariate models.

According to the response curves, woodland richness increases as the average value of NDVI increases to reach a threshold beyond
Table 2
Comparison of the goodness of fit ($D^2$) of GAMs for each species richness linked to each type of satellite data. For the temporal effect, the NDVI 2009 data was provided by the same sensor (SPOT-5, 10 m). For the effect of the spatial resolution, the NDVI 2010 data were acquired during the same period (September 2010). The GAMs were constructed with 573 points counts collected in 2009. For each data type (e.g. NDVI February 4th or DHM radar 5 m), three explanatory variables were used: average, variance, and maximum. For the land-cover map, nine landscape variables were used.

<table>
<thead>
<tr>
<th>NDVI temporal effect</th>
<th>NDVI spatial resolution effect</th>
<th>DHM spatial resolution effect</th>
<th>Complete model</th>
<th>Land cover map</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4-Feb</td>
<td>24-Jun</td>
<td>19-Aug</td>
<td>18-Oct</td>
</tr>
<tr>
<td>SR woodland</td>
<td>14</td>
<td>28</td>
<td>30</td>
<td>49</td>
</tr>
<tr>
<td>SR farmland</td>
<td>5</td>
<td>24</td>
<td>36</td>
<td>31</td>
</tr>
<tr>
<td>SR total</td>
<td>10</td>
<td>17</td>
<td>17</td>
<td>32</td>
</tr>
</tbody>
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150 DN (digital number, i.e. the intensity value). A similar trend is obtained with the variance of NDVI (Fig. 4). The woodland richness also increases as the average height of the vegetation increases, stabilizing above 10 m (Fig. 5). It responds in quite a similar way with the height variance.

Farmland bird richness reaches its maximum for an average NDVI value of 85 DN. The relationship is not so strong with the NDVI variance. This richness decreases quickly as the average height and its variance increase.

The total species richness increases until it reaches a threshold beyond an NDVI of 120 DN. It increases in the same way with the NDVI variance. Concerning the height, the total species richness increases up to a threshold value of about 3 m. The response curve of this total richness with respect to the height variance is very similar.

4. Discussion

4.1. Temporal effect of the NDVI data

In this study we show a significant effect of the date of the NDVI satellite data to explain and predict bird community patterns. Other
authors have shown an asynchronous agreement between bird and NDVI data (Bino et al., 2008). The October period is best for revealing the requirements of the woodland bird and farmland bird communities and of the total community. The asynchrony between the biological data (collected in May and June) and the environmental data (October) is clearly explained by the fact that the NDVI data acquired at different dates reveal in different ways the landscape composition and structure relevant to explain community patterns.

A major factor to explain the bird richness during the breeding period in European agricultural landscapes is the distinction between the woody structures (woodlands, hedgerows) and open components (Berg, 2002; Bonthoux et al., 2012). NDVI variable discriminates differently woody and open components of the landscape between the different periods of the year. In our data, NDVI values are high for June and August in areas with wheat and with summer crops (maize and sunflower), respectively (mean DN = 130 for wheat in June, mean DN = 250 for maize in August). In contrast, in October these crops have been harvested and the NDVI values are lower (mean DN = 30 for wheat and for summer crops). For woods and grasslands, the NDVI values are more stable from spring to autumn. Consequently, the NDVI data in October allow a better discrimination between crop areas, grasslands and woody structures, and thus better explain community patterns. In June and August, the high NDVI values for crops cause an overestimation of the woodland species richness and, consequently, of the total richness in the crop areas (Appendix C).

In February the NDVI values are lower in deciduous-tree wood formations with respect to the other periods (Fig. 3) because the trees do not have their leaves at that time. Using these data leads to an underestimation of the woodland species richness and of the total richness in wooded areas and to an overestimation of the farmland bird richness associated with open landscapes (Appendix C).

We therefore recommend that NDVI data should be used that reveals the landscape composition and structure best, as that is an important parameter for explaining the community patterns, rather than data that are contemporaneous with the bird counts. In an agricultural landscape context with summer crops we have shown that the beginning of autumn is the best period for NDVI data acquisition (i.e. when the various crops have been harvested and agricultural parcels have been ploughed up, which distinguishes them from the permanent grasslands and the wooded areas in the NDVI data). In highly wooded landscapes, the spring, summer and autumn would probably be the best-suited periods. In drier areas with other crops and a strong seasonality (hot summers), the results could be different. In urban areas, for a Mediterranean region, Bino et al. (2008) have shown that spring NDVI data are better correlated with the species richness than summer data characterized by lower values (disappearance of annual plants, slowing down of the activity of shrubs). Additional works should be extended to provide findings for other regions and other systems.

4.2. Effect of the spatial resolution of NDVI and DHM data

Our results show that spatial resolution has an effect on the models’ performance. For the three species richness variables, the data at 2 m resolution have the best performance, even though the 10 m data have values that are very close. These results are in line with the works of Gottschalk et al. (2011) who found that...
the finest environmental data (1 m resolution) are on average better for predicting the distribution of bird species in Germany. Their approach, however, is different from ours as, on the one hand, they used classified data and, on the other hand, they do not compare data from different sensors but images with different spatial resolutions obtained by resampling the initial image.

The lowering of the models’ performance when the spatial resolution is reduced can be explained by the fact the coarser resolutions tend to homogenize the landscape toward the nature of the landscape’s dominant landscape patches (Saura, 2002). So, fine objects such as hedges or isolated trees whose presence plays an important role for farmland birds (Hinsley and Bellamy, 2000) tend to disappear as the size of the pixel increases. This increase is therefore accompanied by a decrease in the spectral heterogeneity, which affects the quality of the models (Rocchini, 2007).

In order to quantify the effect of the spatial resolution, we used data acquired in September. The choice of this period takes account of our previous conclusions indicating that the end of the summer, after the crops have been harvested, is the best period for revealing the requirements of birds on our study site. For the 20 m spatial resolution we used data from September 1st (the only data available), in advance with respect to the other images. On that date not all the crops had been harvested which probably explains the fact that the performance of the 20 m data is not as good as with coarser, 30 m data (see the discussion on the period effect). This once again highlights the importance of the data’s date for constructing reliable models.

We used 2010 data to study the effect of the spatial resolution, whereas the avifauna data were collected in 2009. This may have introduced noise in models and caused a lowering of the explanatory and predictive performances. Nevertheless, we think that this impact is limited. Although some land cover changes occurred, these changes were low with regard to the strong correlations between the NDVI 10 m data on October 18th, 2009 and the 10 m data on September 20th, 2010 (Pearson correlation of $r=0.90$, Var $=0.78$, Max $=0.78$). There is also variability in bird detection from one year to another but we noticed only slight difference of goodness of fit between the two dates (e.g. $\Delta \%D^2 = 4$ for woodland richness and $-1$ for farmland richness). From a practical viewpoint it is necessary to find the best trade-off between the costs of the data and their predictive capability. The very high spatial resolution data, such as the WorldView data, are very expensive whereas the SPOT-5 and SPOT-4 data are much more affordable (see Section 4.5 for the price details). Landsat-5 and MODIS data are even free of charge. We do not think that the gains of performance obtained with 2 m data justify the price differential (which can vary by a factor of between 5 and 20 depending on the type of product ordered and the surface area covered) with the 10 m data. That is why we suggest that the 10 m data (such as SPOT-5) are a good trade-off for the study of bird community distributions in farm-wood type landscapes.

Concerning the height data (DHM), we did not find any effect of spatial resolution on the models’ performance when passing from 1 m (LiDAR data) to 5 m (radar data). The difference of resolution is probably too slight, which limits the difference of height heterogeneity within each point count (the DHM Avg variable is 97.5%-correlated between the two sources). Consequently, we consider it is preferable to acquire radar data with 5 m spatial resolution rather than LiDAR 1 m data if the landscape’s 3D structure is only represented by height data (DHM). The radar data are easier to access, as well as being less costly. On the contrary, in forest landscapes with few agricultural parcels, a finer description of the physiognomy of the vegetation is required. In this case, LiDAR data should be preferred in order to take account of additional variables describing the vertical structure of the habitats (Goetz et al., 2010; Lesak et al., 2011; Müller et al., 2010). The use of such LiDAR-derived metrics is very promising but was out of the scope of this study.

4.3. Comparison and complementarity of the NDVI and DHM data

Our results show that the performance differences between the finest resolutions of NDVI data are not as great as the performance differences between the data acquisition periods. This suggests that the choice of NDVI image date is more important (or at least, equally) when it comes to explaining the bird community patterns than the effect of the spatial resolution.

Our results also show that the best-performing NDVI data, which characterize the landscape’s spatial heterogeneity, have predictive capabilities equivalent to the height data, which characterize the vertical heterogeneity. Combining the two sources only improves the model’s performance very slightly (with the optimum date and spatial resolution). This means that if the NDVI data are available for the right period (in the autumn in our case) with sufficient spatial resolution ($\geq 10$ m), it is preferable to acquire those data (more easily available and less costly) than height data.

4.4. Bird responses to NDVI and DHM

We find different responses from the three richness variables to the NDVI and vegetation height variables. As is the case in other studies (Lee et al., 2004; Seto et al., 2004), we find that the total species richness increases with the NDVI which represents a good substitute for primary productivity. There is an NDVI threshold beyond which the richness no longer increases.

Farmland bird richness reaches a maximum for an average NDVI of 85 DN. This average value represents varied landscapes made up of ploughed land with a low NDVI, permanent grasslands with an intermediate NDVI and hedges with a high NDVI. This habitat heterogeneity provides additional resources for nesting and feeding a large number of farmland bird species (Benton et al., 2003).

Farmland bird richness decreases when the height of the vegetation increases, because the majority of these species nest on the ground or in the lower parts of hedges and therefore avoid high-vegetation structures (Chamberlain et al., 1999).

Lastly, we found that the total richness increases as the NDVI and DHM variances increase. This result is in agreement with the habitat heterogeneity hypothesis whereby complex habitat mosaics make it possible to have a variety of ecological niches and, as a consequence, allow a greater number of species to coexist (Tews et al., 2004).

4.5. Unclassified remotely sensed data or land cover map?

Bird-habitat models are usually constructed from classified data (Gottschalk et al., 2005). These data require, on the one hand, a human perception of the landscape’s spatial heterogeneity and, on the other hand, the implementation of an automated classification procedure or of a field survey. In our context, we show that by choosing the optimum date and spatial resolution, the unclassified data (NDVI or DHM) have a performance comparable with that of land-cover maps. This finding is in line with that of Bino et al. (2008) who showed that the NDVI data represent a good and less labor-intensive alternative to land-cover map for predicting bird community patterns in an urban habitat.

In terms of benefit–cost, the use of satellite images is not less attractive than the land-cover maps. Indeed, detailed land-cover maps produced by the mapping agencies are generally expensive. For instance, the more detailed French topographical database BDTopo® (1:25 K) produced by IGN costs €24 per km$^2$ (≈500€ of fixed cost) for a minimum order between 0 and 100 km$^2$ (IGN, 2009). In comparison, the more detailed satellite images used in
this study are less expensive: 16€ per km² for WorldView-2 (minimum order of 25 km²), from 0.75 to 2.55€ per km² for SPOT-5 (minimum order of 400 km²) and 0.53€ per km² for SPOT-4 (full scene of 60 × 60 km). Free land-cover maps such as CORINE data from the European Union exist. However, the minimum mapping unit of 25 ha is inadequate to construct reliable bird-habitat models because of class mixing. Collaborative mapping projects such as OpenStreetMap could be a good alternative to CORINE data. Nevertheless, the current thematic resolution is too coarse with no distinction between crops, permanent and short-term grasslands.

With a view to making predictions, the utilization of unclassified data can be more judicious to identify quickly the landscapes that have potentially high species richness on which conservation measures should be put in place. From an operational viewpoint, land-cover maps remain the best-suited for the concrete implementation of actions in the field and the prescription of management practices that are favorable to biodiversity because they provide a direct representation of the landscape elements on which it is possible to act.

5. Conclusion

In this paper we have assessed the effect of the acquisition date and of the spatial resolution of NDVI data and of height data (DHM) on the explanatory and predictive performances of bird-habitat models. The effect of the date was measured on NDVI data provided by the same sensor (SPOT-5), whereas that of the spatial resolution was estimated using images acquired from the same period (September 2010). To our knowledge, this comparison at a constant date or spatial resolution has never been examined in this way.

First, we have shown that the choice of date has a significant impact on the models’ responses. The optimum date is the one that best reveals the land cover and the structure of the landscapes’ vegetation, and not the one contemporaneous with the bird counts, nor the one corresponding to maximum plant productivity. We have also shown that the spatial resolution had an effect on the models’ performance. However the differences of performance between the spatial resolutions of the NDVI data are not as great as the differences between the data acquisition periods. Furthermore, the effect of the spatial resolution is not significant on the height data used (LiDAR at 1 m and radar at 5 m).

Our results also reveal that for predictive purposes, the unclassified data (NDVI or DHM) constitute a good alternative to land-cover maps because they provide comparable levels of performance. This approach offers the opportunity to estimate species distributions over large scales in a cost-effective way. It should also facilitate or increase the use of remote sensing in ecological studies.

Further investigations are needed on other systems to corroborate the findings of our study related to farm-wood landscapes. Shirley et al. (2013) demonstrated recently the relevance of the unclassified data-based approach in forest landscapes of western Oregon, USA. For tropical systems where seasonality is little pronounced, high-resolution hyperspectral raw data might be better adapted to the production of accurate prediction models, even if some experiments using raw multispectral imagery were already applied with success (Foody and Cutler, 2006).

Acknowledgments

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Appendix A.

Names of the species chosen to calculate the three species richness variables.

<table>
<thead>
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<th>Latin names</th>
<th>Common names</th>
<th>SR woodland</th>
<th>SR farmland</th>
<th>SR total</th>
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<td></td>
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Appendix B.

Spline correlograms, with 95% pointwise bootstrap confidence intervals of the Pearson residuals from GAMs, based on NDVI data (2 m, September 20th). 500 resamples were done for the bootstrap.  
Fig. B.1.
Appendix C.

Fig. C.1

**Fig. C.1.** Relationships between the prediction accuracy of woodland species richness (predicted species richness–observed species richness) and the land-cover types for NDVI at the different dates.
Appendix D. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.02.023.

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