

ORIGINAL RESEARCH

Linking animal movement and remote sensing – mapping resource suitability from a remote sensing perspective

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Abstract

Optical remote sensing is an important tool in the study of animal behavior providing ecologists with the means to understand species–environment interactions in combination with animal movement data. However, differences in spatial and temporal resolution between movement and remote sensing data limit their direct assimilation. In this context, we built a data-driven framework to map resource suitability that addresses these differences as well as the limitations of satellite imagery. It combines seasonal composites of multiyear surface reflectances and optimized presence and absence samples acquired with animal movement data within a cross-validation modeling scheme. Moreover, it responds to dynamic, site-specific environmental conditions making it applicable to contrasting landscapes. We tested this framework using five populations of White Storks (*Ciconia ciconia*) to model resource suitability related to foraging achieving accuracies from 0.40 to 0.94 for presences and 0.66 to 0.93 for absences. These results were influenced by the temporal composition of the seasonal reflectances indicated by the lower accuracies associated with higher day differences in relation to the target dates. Additionally, population differences in resource selection influenced our results marked by the negative relationship between the model accuracies and the variability of the surface reflectances associated with the presence samples. Our modeling approach spatially splits presences between training and validation. As a result, when these represent different and unique resources, we face a negative bias during validation. Despite these inaccuracies, our framework offers an important basis to analyze species–environment interactions. As it standardizes site-dependent behavioral and environmental characteristics, it can be used in the comparison of intra- and interspecies environmental requirements and improves the analysis of resource selection along migratory paths. Moreover, due to its sensitivity to differences in resource selection, our approach can contribute toward a better understanding of species requirements.

Introduction

Mapping animal resource suitability, which we define as the potential attractiveness of resources within a habitat during periodic behaviors such as feeding and resting, is important for understanding a species' preference for specific habitats. Decisions such as 'where to feed?' or 'where to sleep?' are constrained by different resource

requirements (Péron et al. 2016; Abrahms et al. 2017), and the selection of a habitat is dependent on the availability and distribution of these resources (Street et al. 2017). To map resource suitability, the environmental drivers that motivate animal behavior need to be examined (Avgar et al. 2013; Dodge et al. 2014; Gibert et al. 2016) and optical remote sensing has become a popular tool to achieve this. It provides spatially and temporally explicit

information on landscape dynamics (Pereira et al. 2013; Pettorelli et al. 2014) and offers a better understanding of the environmental covariates that affect behavior.

Translating remote sensing data into indices of resource suitability requires the identification of areas of suitable and unsuitable environmental conditions in which the tracking of animal movement with GPS technologies becomes relevant. It provides data on individual and collective animal behavior (McClintock et al. 2014) and offers an insight on a species' environmental requirements (Nathan et al. 2008; Recio et al. 2013; Allen and Singh 2016). However, while satellite and movement data are used in combination extensively, the conceptual differences in scale (temporal and spatial) between these data sources have not been addressed objectively (Neumann et al. 2015) and the value of multispectral information has been ignored.

The evolution of GPS tracking technologies has allowed researchers to track animal movements on increasingly finer temporal scales (minutes, hours) motivating a demand for environmental data with high temporal resolution. In this context, sensors with a daily acquisition schedule and a broad spatial coverage such as the moderate resolution imaging spectroradiometer (MODIS) have become a cornerstone of animal movement analysis, especially through spectral indices such as the normalized difference vegetation index (NDVI). Such indices have been used extensively as proxies for foraging quantity and quality (Pettorelli et al. 2011; Borowik et al. 2013) and have been rather successful in explaining migratory movements between suitable habitats (Rubenstein and Hobson 2004; Bartlam-Brooks et al. 2013; Shamoun-Baranes et al. 2014; Van Moorter et al. 2015).

However, when looking at movements within a habitat, a daily scale of analysis is not always adequate because phenomena like land use management and land cover change, although relevant for the species, might not be perceptible at single time steps (St-Louis et al. 2014; Pasquarella et al. 2016). Moreover, the choice of an adequate spatial resolution plays an important role in accurately representing landscape dynamics and composition (Ju et al. 2005) and conditions our ability to map species–environment interactions (Sheeren et al. 2014). Very high-resolution sensors can turn out detrimental because they highlight fine-scale phenomena (e.g. single tree shadowing) which are hard to interpret and address automatically (Immitzer et al. 2012). Sensors with a moderate spatial resolution, like MODIS, on the other hand fail to describe landscapes that are highly fragmented (Saura 2004; Zhu et al. 2006). Additionally, the choice of spectral information conditions our ability to assess the composition of the landscape (Herold et al. 2003; Adam et al. 2010; Selkowitz 2010). The use of multispectral

information is often necessary, and it has been shown to overcome classification errors (Shirley et al. 2013) and preserve subtle but ecologically relevant transitions between land cover classes (St-Louis et al. 2014).

Despite the constraints imposed by satellite imagery, the status quo of remote sensing in the analysis of fine-scale movements seems to disregard them. As pointed out by Neumann (Neumann et al. 2015), many authors fail to describe the choice of spatial, temporal and spectral resolutions showing low sensibility for these issues. On the other hand, the ones that do discuss their data choices show preference for single time steps of high-resolution imagery from satellite sensors (Handcock et al. 2009; Boyle et al. 2014) and unmanned aerial vehicle (UAV) campaigns (Rodríguez et al. 2012; Mulero-Pázmány et al. 2015), existing and self-derived data products like land cover classifications based on medium resolution sensors such as Landsat (Sawyer and Brashares 2013; Bevanda et al. 2014; Zeller et al. 2017) and very high-resolution structural data acquired with Light Detection And Ranging (LiDAR) technologies (Hyde et al. 2006; Clawges et al. 2008; Potts et al. 2014). Yet, the use of multispectral imagery is limited ignoring the demonstrated value of continuity missions such as Landsat in monitoring ecological change (Wulder et al. 2012; Vogelmann et al. 2016).

The constraints imposed by satellite sensors are also relevant when linking remote sensing and movement data to model animal–environment interactions. Movement provides relevant information on revisit and avoidance patterns that can help discriminate relevant and nonrelevant resources. However, due to the coarser temporal and spatial resolutions of remote sensing data, revisits lead to the pseudo-replication of samples (Hurlbert 1984) and promotes the use of neighboring pixels for training and validation which introduces a positive model bias due to spatial autocorrelation (Dormann et al. 2007). Notwithstanding, the limitation of satellite imagery is not considered in current research and model validation with spatially independent samples is lacking. Common modeling approaches that address resource suitability mapping, such as resource selection functions (Northrup et al. 2013; Squires et al. 2013) and step selection functions (Panzacchi et al. 2015; Avgar et al. 2016), focus on continuous movements and disregard the influence of pseudo-replication and of the spatial autocorrelation of environmental predictors over model accuracies and over our ability to validate these models.

Moreover, avoidances can be driven by factors other than environmental suitability (Araújo and Peterson 2012) such as human-made barriers (Loarie et al. 2009; Northrup et al. 2016) which are not always perceptible with remote sensing. As a result, common methods to

describe unsuitable environmental conditions, such as random background sampling, can lead to a negative model bias due to the poor quality of these samples (Lobo et al. 2010; Iturbide et al. 2015).

Given the limitations of remote sensing in accompanying continuous animal movements, we propose that the analysis of movement should be disconnected from – and come second to – the analysis of the environmental conditions that guide it. However, movement data can guide the modeling of the spatial distribution of relevant environmental resources. It helps to identify patterns of occupancy from which we can derive representative samples that describe preferred environmental conditions. In practice, this implies translating movement data into a scale of analysis that is compatible with remote sensing and that supports the development of a consistent modeling and validation scheme.

Our goal was to develop a data-driven framework to map resource suitability that lays the basis for a consistent analysis of animal movement. Using high-resolution movement data, we derive representative samples of suitable (presences) and unsuitable (absences) environmental conditions collected at the pixel scale that are sensitive to local environmental conditions described through remote sensing. This is then combined with standardized remote sensing information to model the distribution of relevant resources using a spatially stratified cross-validation scheme that addresses the issue of spatial autocorrelation during validation.

As a model species, we chose the White Stork (*Ciconia ciconia*). This is a species with well-studied habitat requirements for which we can define clear assumptions on relevant resources. In particular, we focused our attention on stops during out-of-nest movements in an effort to study foraging behavior. Additionally, while wintering, this species covers different environments from the Mediterranean to Central Asia (Flack et al. 2016) allowing us to demonstrate the applicability of standardized and automatized remote sensing methodologies such as ours across contrasting environments. We looked at five populations and compared model accuracies among study sites and their relation to the choice of environmental conditions described by the spectral variability in our remote sensing data.

Materials and Methods

Study sites

We considered five study sites spread along a longitudinal gradient between Western Europe and Central Asia (Fig. 1). They are located in Donaña (Spain), Constance (Germany), Evros Delta (Greece), Ararat (Armenia) and Tashkent (Uzbekistan), and their size, defined by stork movements,

varies between 361 and 709 km². According to the MODIS MCD12Q1 land cover product (Friedl et al. 2010), the study sites are mostly covered by agriculture (>50%) with a limited urban cover (<15%). Forest cover is in general small (<20%) in all study sites but the German site (32%). Water cover varies between 1 and 10%. Topography is moderate with elevations ranging between 100 and 500 m and slope angles varying between 0 and 10°. According to the Köppen-Geiger map of climate zones (Peel et al. 2007), the study sites are located in hot-summer (Spain and Greece) and warm-summer (Armenia) Mediterranean climates, warm-summer, humid continental climates (Germany) and hot, dry-summer continental climates (Uzbekistan).

Mapping resource suitability: training and validation

We developed a modeling framework to map resource suitability (Fig. 2). Presence–absence data created from White Stork movement tracks were modeled based on seasonal composites of Landsat surface reflectances (section 1.2.1) as environmental predictors using a Random Forest (RF) classifier (Breiman 2001). Special treatment was given to the presence/absence sampling process, to ensure the use of spatially independent sample regions for training and validation (section 1.2.2) and to optimize the characterization of background environmental conditions (section 1.2.3).

In a cross-validation scheme, each sample region was kept for validation once while the remaining ones were used to fit a model using RF. At each iteration, a random set of absences was selected for training and another for validation with the same number of samples as the corresponding set of presences. The total count of true and false positives from all iterations was used to derive an F1-measure (Jäger and Benz 2000) estimated as

$$F1 = 2 \cdot \frac{P \cdot R}{P + R}$$

where P is the Precision (ratio of true positives within the number of predicted values) and R is the Recall (ratio of true positives within the number of validation samples). This process was repeated 100 times to account for model stability. We used the RF implementation of the R package randomForest (Liaw and Wiener 2002). The final output is a map of probabilities for the presence class.

Deriving environmental predictors

The White Stork is a predatory bird species that takes advantage of agricultural activities such as crop harvesting and grassland grazing to search for prey (Van den Bossche et al. 2002). Therefore, we opted for Landsat data as it provides relevant spectral information to discriminate

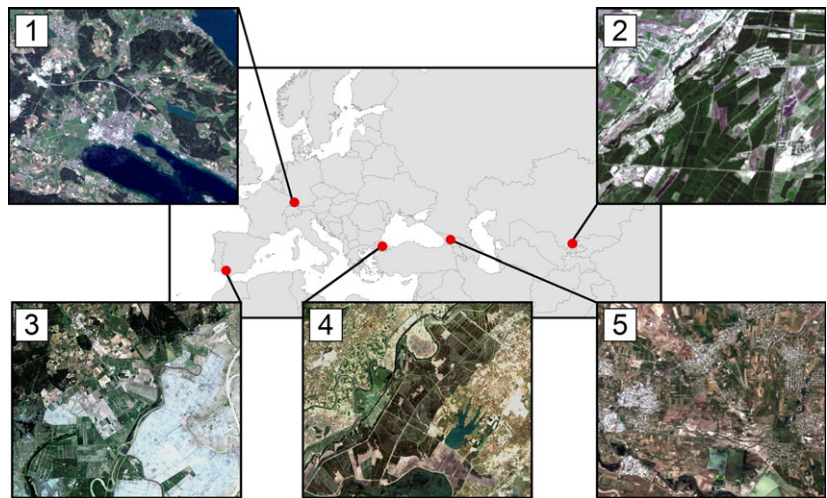


Figure 1. Spatial distribution of the study sites: (1) Constance, Germany; (2) Tashkent, Uzbekistan; (3) Donāna, Spain; (4) Evros Delta, Greece; (5) Ararat, Armenia. The background was derived with Landsat.

agricultural land (L w and Duveiller 2014) with a medium spatial resolution and a stable temporal and spatial global coverage. As a predictor, we used multitemporal Landsat 5 TM and Landsat 8 OLI surface reflectances provided through the Earth Resources Observation and Science (EROS) Center Science Processing Architecture (ESPA) (United States Geological Survey, 2010). In the context of

agriculture monitoring dense time series can be crucial to highlight phenological differences of managed land (Dong et al. 2016) and quantify management intensities (Prishchepov et al. 2012). However, the consistency of multitemporal methods within and between different environments depends on regional atmospheric conditions. Persistent cloud cover leads to an uneven temporal distribution of

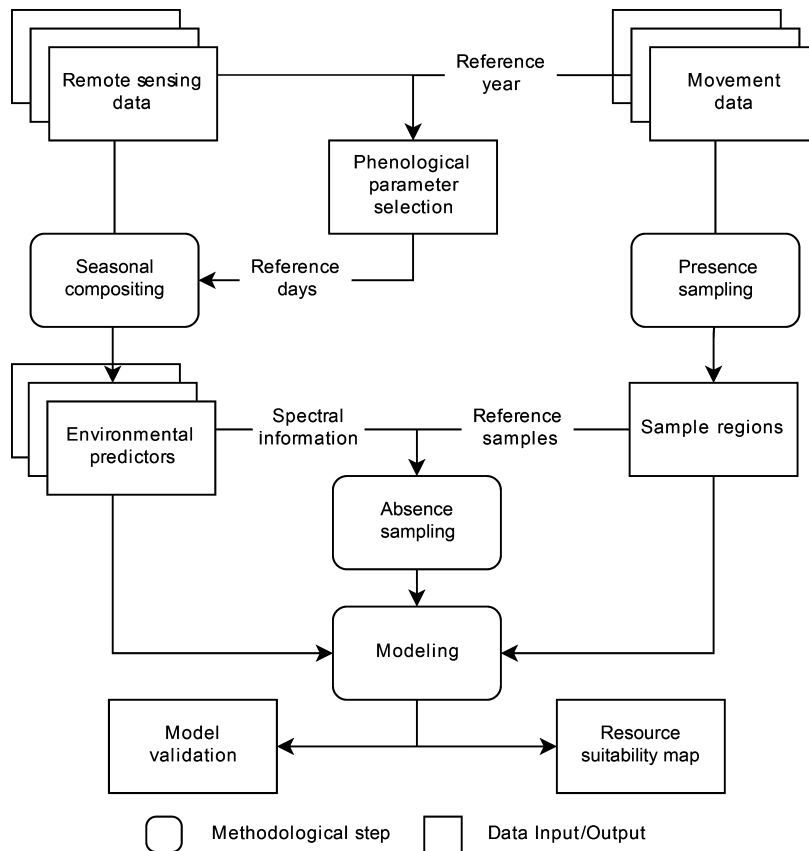


Figure 2. Framework to link animal movement with remote sensing and map resource suitability.

spectral information (Yu et al. 2015) and prompts the use of inadequate temporal information that misrepresents phenological patterns within a landscape (Zhang et al. 2009). To address this issue, we extended our approach to consider information from 2011 and 2013 while we excluded 2012 due to the degradation of Landsat 7 ETM+ and the lack of Landsat 5 TM and Landsat 8 OLI acquisitions. We searched for the best trade-off between consistent phenological information that highlight land management practices and a gap-free spatial coverage. The compromise we propose are three surface reflectance composites that limit the existence of data gaps due to atmospheric disturbances and preserve temporal information on relevant phenological stages (Tigges et al. 2013; Zhao et al. 2016). We derived seasonal composites based on the spectral bands of Landsat for the three phenological stages Start of Season (SoS), Mid of Season (MoS) and End of Season (EoS), which highlights seeding, growing and harvesting periods. This reveals differences in management practices allowing us to distinguish between land that was harvested or grazed during the observation period. As vegetation phenology changes regionally (Garonna et al. 2014; Rodriguez-Galiano et al. 2015), we based these composites on site-dependent phenological metrics. Additionally, we consider year-specific phenological information accounting for annual changes in vegetation growth cycles (Cleland et al. 2007). To derive the seasonal composites, we first built a mask of cropland pixels identified within the MODIS MCD12Q1 land cover product. Then, for each composite, we used this mask to estimate the mean and standard deviation for each of the phenology metrics provided within the MCD12Q2 product (Zhang et al. 2006) excluding pixels with multiple growing stages. Then, we calculated the temporal difference (in days) between each Landsat acquisition and the mean Day of Year (DoY) of the corresponding seasonal metric (SoS, MoS, EoS) and selected the image with the smallest day difference filling the remaining areas by subsequently using the image information from acquisitions with the next smallest day difference. We only considered acquisitions within one standard deviation from the mean DoY. The output was a stack of three gap-filled seasonal composites of surface reflectances per study site.

Deriving presence sample regions

To minimize the optimistic bias related to spatial autocorrelation, we created spatially independent sample regions of presences that prevented us from splitting nearby pixels between training and validation (Fig. 3). We based this analysis on movement data from five populations of White Storks consisting of a total of 48 juveniles tracked between 26 June 2013 and 15 September 2013 while nesting (<https://doi.org/10.5441/001/1.78152p3q>). The data were collected with solar-powered high-resolution GPS devices with a temporal resolution of 5 minutes and a standard spatial error of 3.6 m. The temporal coverage of the tracking data per individual ranged from 9 to 75 days and population sizes ranged from six individuals (Uzbekistan) to a maximum of 13 individuals (Germany).

To derive independent sample regions for training and validation, we first extracted presence samples for each individual related to potential stops during daily movements. Looking at continuous movements, we sampled when the distance between consecutive GPS points was lower than two times the standard error (7.2 m) and the time difference was greater than two times the temporal resolution (10 min). Initial tests suggested that these criteria offered a good compromise accounting for the mobility of the species while feeding and the time spent within feeding sites. The samples for each individual were translated to a 30 m resolution mask, aligned with the derived remote sensing data, to remove duplicates and thus avoid pseudo-replication effects. Groups of connected pixels which overlapped with the nests, described here by the locations that were visited every day, were masked out. Then, we aggregated the presence samples derived for each individual at the population level and filtered out groups with less than four samples to reduce the risk of including false positives related to ephemeral events such as soaring flights and GPS anomalies. Additionally, this step removes pixels representing relevant resources but which are too small to be distinguished at the Landsat scale (e.g. household crop fields). Finally, we aggregated sample regions within a radius of 500 m (~17 pixels) of each other increasing the distance between training and validation sample. The chosen minimum distance for

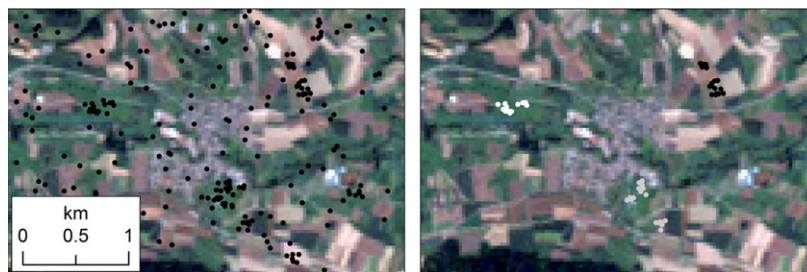


Figure 3. Population level presence samples (left) and its subsequent filtering and relabeling (right) based on the linear distance among sample regions. Points of different colors represent different regions.

aggregation aimed to maximize the distance between training and validation samples with a common threshold across study sites while preserving at least two sample regions.

Selecting absences

We developed a data-driven approach to select absences based on the environmental dissimilarity of background pixels in comparison with presences sample regions, derived in section 1.2.2. To achieve this, we first collected 4000 random background samples which were, together with the presences, used to collect surface reflectance data from the stack of seasonal composites, derived in section 1.2.1 and evaluated with a principal components analysis (PCA). We reduced the output to p principal components (PCs) where p corresponds to the number of PCs with eigenvalues greater than 1 (Kaiser 1960). For each PC, we estimated the median and median absolute deviation (MAD) of the variance for each sample region and estimated the difference from the median for each background sample. At each sample region, we selected background samples where the difference from the median was greater than the MAD. The final set of samples corresponds to the unique observations that were selected n times at each PC where n is the number of regions. These samples are adjusted to local environmental conditions through the MAD criteria which value is directly related to the higher (e.g. mixed crops) or lower (e.g. single crop) spectral variability of the reference sample regions.

Sample homogeneity

Differences in resource selection are influenced by the availability and distribution of resources and can occur within the same population (Street et al. 2017). Because our modeling approach splits spatially independent sample regions in training and validation, it becomes susceptible to this issue. Differences in resource selection can lead to the separation of contrasting environmental information between training and validation resulting in unstable models. To understand the variability of model accuracies within each study site, we supported our modeling approach with a sample homogeneity test that looks at the variability within the Landsat surface reflectance composites as a proxy for environmental complexity. For each region, we compared its distribution against the distribution of the remaining samples (as done when building a predictive model) and derived an absolute score of similarity (z -scores) based on a Z -test, calculated as

$$Z = \frac{(\bar{x}_{p_1} - \bar{x}_{p_2})}{\sqrt{\sigma_{p_1}^2 + \sigma_{p_2}^2}}$$

where p_1 corresponds to the samples of the region under evaluation and p_2 corresponds to the remaining samples. \bar{x} and σ correspond to mean and standard deviation of the sample distributions. We expected that the accuracies of our models would be higher and more stable as the choice of environmental conditions became more homogeneous. This test extends the PCA described above and used its first PC which accounts for most of the variance in our data. Finally, to compare the samples among study sites, we summarized our results by estimating the mean of all z -scores weighted by the number of samples of each sample region. We expected that study sites, where sample regions that represent a larger proportion of the total amount of samples have contrasting environmental attributes, will have lower accuracies.

Results

Seasonal compositing

The mean DoY for the reference cropland pixels used to select compositing dates varied between 57 and 154 for the SoS, 122 and 206 for the MoS and 162 and 242 for the EoS. The standard deviation varied between 23 and 30 days. The mean DoY differences were well below the recorded standard deviation (Fig. 4) with a maximum of 10 days. On average, the differences were higher for the SoS (5 days) followed by the EoS (3 days) and the MoS (2 days). Spain had the highest mean difference for the SoS (10 days) and the EoS (5 days) while Uzbekistan had the highest difference for the MoS (8 days). Among all composites, Germany had the best results with a maximum mean DoY difference of 2 days while Uzbekistan had the worst results with a minimum mean difference of 4 days.

Seasonal composites for all study sites were composed of data from 2011 and 2013 (Fig. 5). The SoS composites were fully composed of surface reflectances of 2011 while the MoS also integrated data from 2013 except for Germany. For the EoS, Armenia and Greece used 33% and 20% of data from 2011, respectively.

Sampling

The number of presence samples varied across populations. Three of the five study sites (Greece, Spain and Uzbekistan) had between 295 and 334 samples, and the two remaining ones (Armenia and Germany) had more than 1500 samples. The number of sample regions varied between 5 (Spain) and 20 (Germany) and showed a disproportional distribution of samples. The smallest sample regions represented 1–2% of the total amount of samples in each study site while the largest regions reached more than 50%. Armenia had the largest percentage of samples within a single region

Figure 4. Mean difference in days from the target day of the year for presences in each seasonal composite and within each study site. SoS, Start of Season; MoS, Mid of Season; EoS, End of Season.

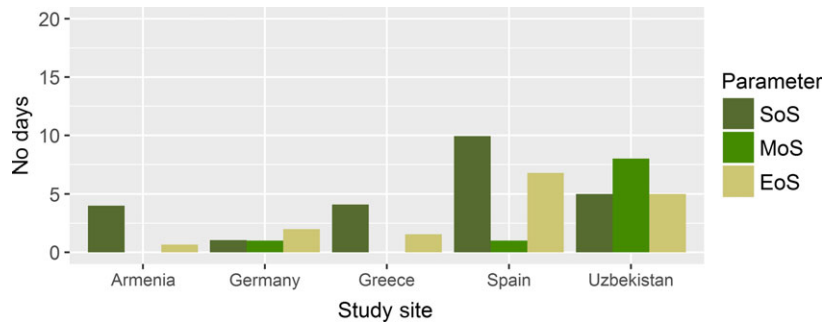
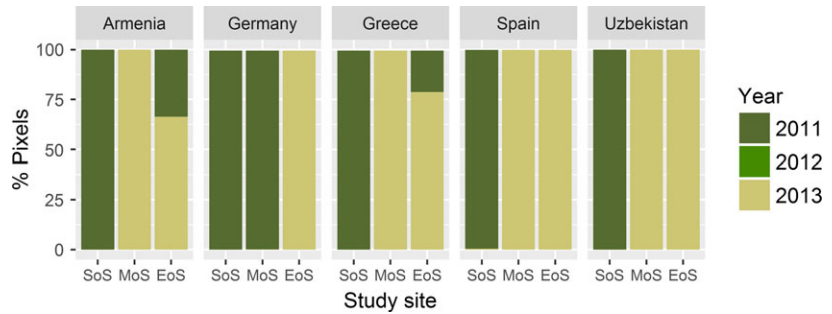


Figure 5. Distribution of presences per year for the Start of Season (SoS), Mid of Season (MoS) and End of Season (EoS) within each study site.



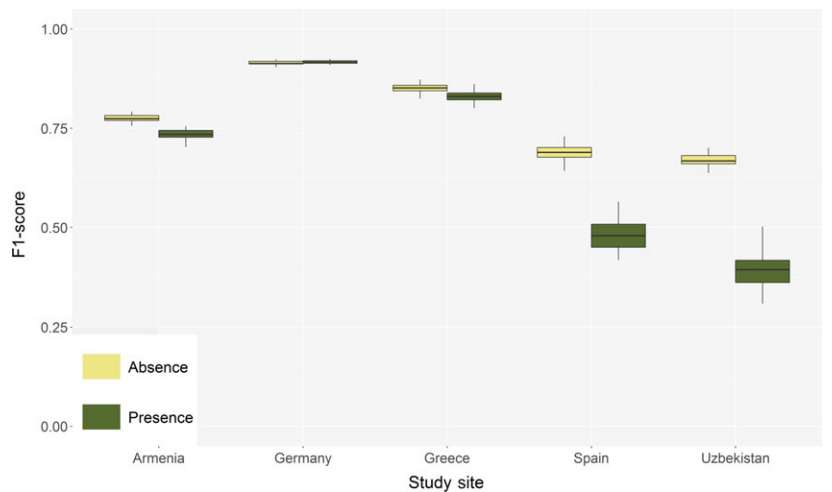
(71%) followed by Spain (64%), Germany (44%), Greece (31%) and Uzbekistan (29%). The number of absences varied between 1453 (Spain) and 3558 (Germany) and were selected using three PC for all study sites with the exception of Spain which required four.

Model validation

Mean model accuracies ranged from 0.40 to 0.91 for presences and 0.66 to 0.91 for absences (Fig. 6). The highest accuracies for both classes were found in Germany while the lowest were found in Uzbekistan. Comparably to

Uzbekistan, Spain had relatively low performances with mean values of 0.48 and 0.68 for presences and absences, respectively. In both study sites, the amplitude of the accuracies was larger than 0.2 for presences and about 0.1 for absences. For the study sites with mean accuracies above 0.7 in both classes (Armenia, Germany and Greece), the interclass amplitudes were below 0.1. Despite the differences in accuracies, a visual inspection of the resource suitability maps revealed a good compromise in distinguishing between managed and nonmanaged land while remaining sensitive to differences in agricultural practices (Fig. 7).

Figure 6. Variability of the F1-measure for presences and absences within each study site.



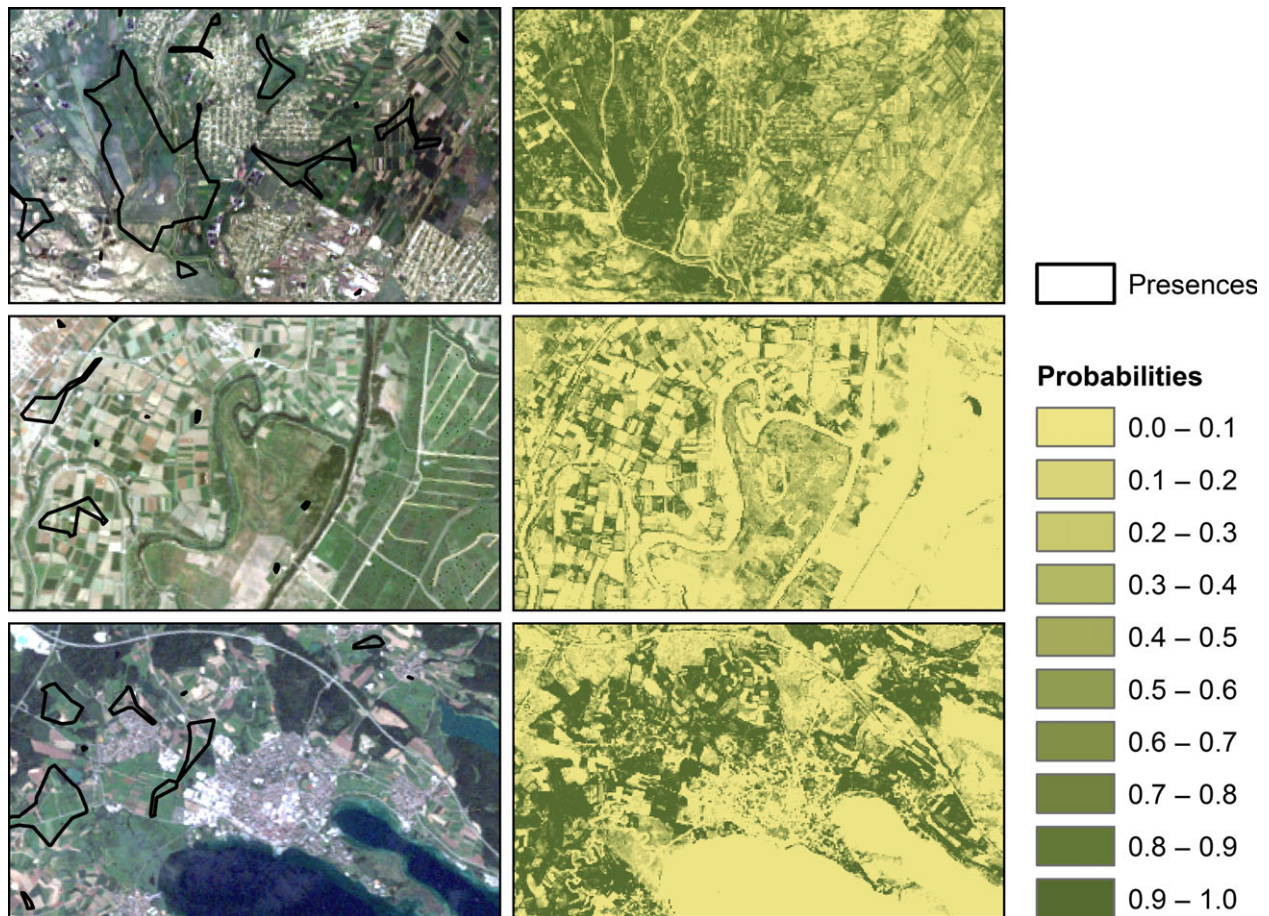


Figure 7. On the left, the distribution of presences over the MoS composite for example sites in Armenia (top), Germany (center) and Greece (bottom). On the right, the resource suitability probability maps. The maps reveal their ability to distinguish managed land as well as the differences within it.

Sample homogeneity

The mean z -scores were inversely proportional to the mean F1-scores. Germany had the lowest mean z -score (0.35) followed by Greece (0.60), Armenia (0.44), Spain (1.00) and Uzbekistan (1.10). The Z -test showed that more than 50% of presence sample regions had an absolute z -score below or equal to 1 in all test cases. In this category, Armenia, Germany and Greece were the most similar (> 90%) followed by Spain (71%) and Uzbekistan (67%). Higher percentages of samples with higher z -scores seemed to be related to an increase in the variability of model accuracies as well as to a poorer performance for presences when compared to absences and seem to suggest differences in the choice of environmental resources as described by Figure 8.

Discussion

We modeled resource suitability related to foraging for five study sites that reflect the range of occupancy of the

White Stork during breeding. For both presences and absences, we achieved high accuracies for Germany, with a F1-measure above 0.90 and relatively high accuracies (>0.75) for Greece and Armenia. However, for Spain and Uzbekistan, the performances were poor despite reasonable suitability maps. This can be explained by the spectral variability between presences. Our sample homogeneity test revealed that the mean z -scores for each study site were inversely proportional to the mean F1-measures.

This negative relationship between z -scores and mean F1 values can be owed to the temporal composition of the seasonal reflectances. The integration of multiyear information did not have an influence on the performance of the models. In fact, Germany required the most data from 2011 to fill data gaps. However, the German test site – which had the highest accuracies – showed the lowest DoY difference for the SoS followed by Greece and Armenia. On the contrary, Spain and Uzbekistan had the highest DoY differences for all temporal windows. The

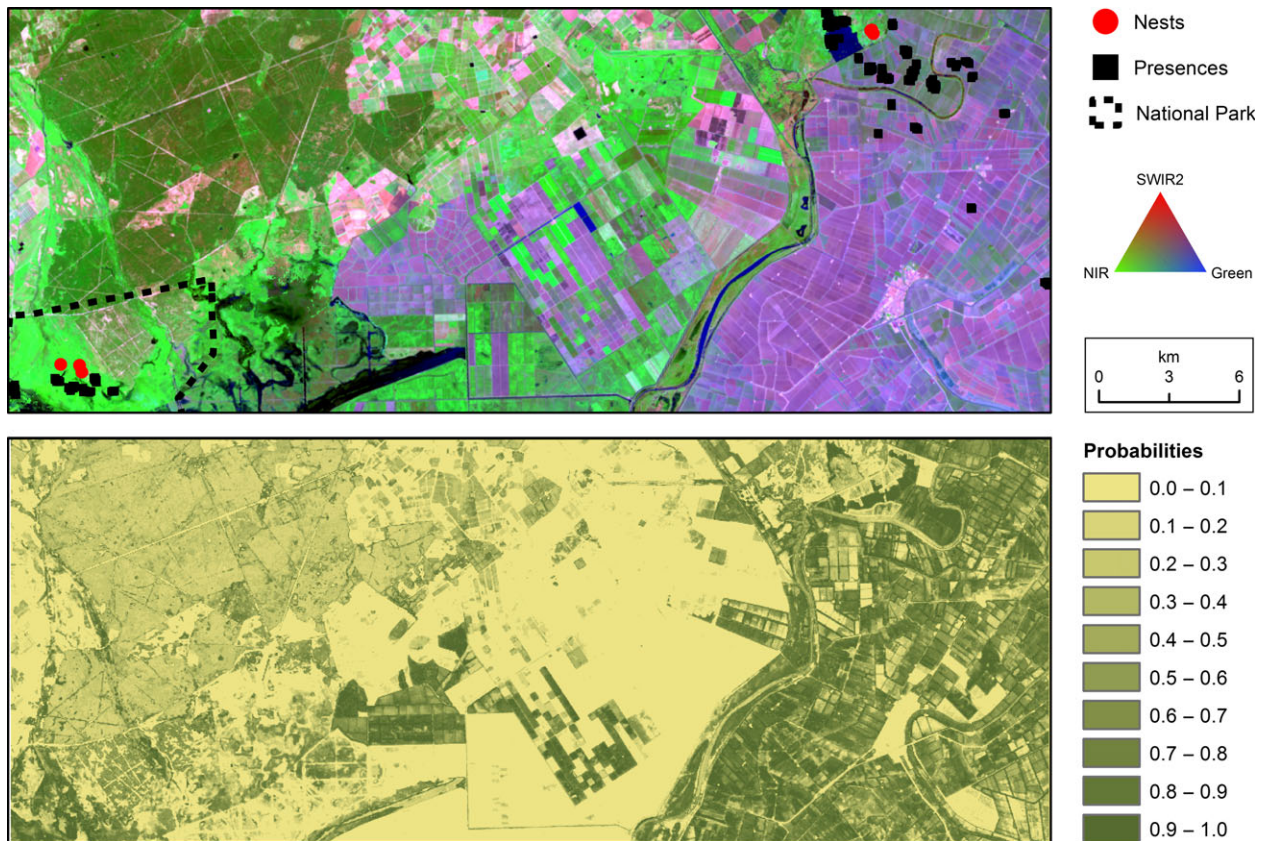


Figure 8. On top map, the relation between the location of the nests and the presence samples in Spain over a RGB composite of SWIR1, NIR and green bands for the SoS. On the bottom left, presences occur over a natural wetland (bright green) within the protected area of the Donaña national park. On the upper right, samples appear mostly over managed wetlands (purple) occupied by rice fields (Instituto Geográfico Nacional, 2005). On the bottom map, the resource suitability prediction for Spain. The results seem to accurately map the different environments visited by the individuals discriminating wetlands and rice fields with high probabilities ($P > 0.5$). Agricultural land which is not irrigated permanently, forest, urban areas and standing water received low probabilities ($P < 0.5$).

highest difference for the SoS being found in Spain which had the lowest accuracies. This supports other studies which suggested the importance of early spring acquisitions to describe differences in vegetation growth (Tigges et al. 2013) and distinguish agricultural management practices (Prishchepov et al. 2012). However, acquiring adequate temporal information is not always possible due to persistent cloud cover. To tackle this issue, recent developments in the fusion of Landsat and Sentinel-2 (Masek et al. 2015), currently provided by USGS (United States Geological Survey, 2017), should be explored.

Additionally, a visual assessment of the results suggested these differences in accuracy are related to the intrapopulation variations in resource selection, an observation highlighted in other studies (van Toor et al. 2011; Slaght et al. 2013; Federspiel et al. 2017; Street et al. 2017). On the one hand, dealing with the sampling of presences on a population scale made us more flexible. It helped us to carefully remove samples of dubious quality

and identify locations representative of the preferences of the species. On the other hand, however, differences in resource selection introduce a negative bias during the validation. Understanding these differences and their relation to the distribution and availability of resources would have supported us in better delineating our study sites by separating between subpopulations. To achieve this, knowing the land cover dependencies of the observed behavior can be useful. Due to the lack of consistent high-resolution land cover information for all study sites, we did not pursue this issue further as we could not address it consistently. However, we suggest that further research is needed and that new methods are required to derive environmental- and behavior-driven study sites based on small-scale movements extending on recent work on large-scale movement segmentation (van Toor et al. 2016). Moreover, due to the sensitivity of our methodology to this issue, we proposed it could potentially be used to track these differences.

A main weakness of our study relates to the sampling of presences as it was based on empirically derived parameters. Such parameters are species dependent making it hard to automatize this process, unlike the processing of remote sensing data. As a consequence, we believe further research is required in order to extend this sampling approach to a larger group of species. However, we highlight the importance of this development in building a consistent cross-validation scheme. While the use of independent samples for validating remote sensing-based resource suitability models is not new (Squires et al. 2013; Thurjfell et al. 2014), its current application does not consider the distance between training and validation samples ignoring the spatial autocorrelation associated with satellite data (Wulder and Boots 1998). Our sampling approach addresses this issue allowing us to derive spatially independent samples that can be split between training and validation and effectively validate predictive models.

In addition, we built a sample selection approach to describe background environmental conditions that is sensitive to the particularities of each study site. Random sampling is a common approach to achieve this, and it has been shown to lead to higher model accuracies when increasing the number of samples (Barbet-Massin et al. 2012). However, when resources are abundant – as happens within our study sites – this leads predictive models to overfit to the training data due to the spectral similarity between presences and absences. We avoid overfitting by extending this approach and removing background samples that share similar traits with the presences. Additionally, our approach preserves samples along the edges of the distribution of presences – as well as extreme values – which, as suggested by other authors (Foody 2004; Hansen 2012), are essential for a better delineation of the spectral attributes and boundaries of the target classes.

While our framework can be improved, we propose an efficient approach to link movement and remote sensing that addresses an important knowledge gap. The use of remote sensing in movement ecology is common but, as pointed by a recent review paper (Neumann et al. 2015), its application is not up to par with state-of-the-art knowledge. Current studies fail to account for the limitations of satellite data when modeling species environment interactions and disregard the spatial, temporal and spectral dependencies of the environmental processes that affect animal movement. To build this link, we sacrifice the fine temporal resolution of our movement data. But in doing so, we effectively translate it into patterns of occupancy that are compatible with the scale of analysis of remote sensing. As a consequence, this methodology does not provide a means for the direct analysis of movement but rather a basis upon which such analysis can be developed.

We suggest that studies on path and resource selection can profit from our framework. Through the consistent mapping of resource suitability, we describe the spatial distribution and aggregation of resources better and understand the influence of these factors on animal decision making. Moreover, due to its standardization, our approach can be used in regional and global applications that take full advantage of animal movement databases such as Movebank (Wikelski and Kays 2007) and continuity missions such as Landsat. Our framework provides a basis for a consistent comparison of intra- and interspecies resource requirements across different landscapes and can help improve the analysis of fine-scale resource selection along migratory paths.

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