

Modelling the spatial distribution of White Stork *Ciconia ciconia* breeding populations in Southeast Europe

ANDREJA RADOVIĆ^{1*}, VASSILIKI KATI², MELITA PERČEC TADIĆ³, DAMIJAN DENAC⁴ and DRAŽEN KOTROŠAN⁵

¹Jelenski hrast 21, Velika Gorica 10410, Croatia; ²Department of Environmental & Natural Resources Management, University of Patras, Seferi 2, Agrinio 30100, Greece; ³Department for Climatological Research and Applied Climatology, Meteorological and Hydrological Service of Croatia, Grič 3, Zagreb 10000, Croatia; ⁴National Institute of Biology, Večna pot 111; SI-1001 Ljubljana; DOPPS – BirdLife Slovenia, Tržeška 2, p.p. 2990, Ljubljana 1001, Slovenia; ⁵Natural-History Department, National Museum of Bosnia and Herzegovina, Zmaja od Bosne 3, Sarajevo 71000, Bosnia and Herzegovina

Capsule Spatial environmental modelling well predicted nesting distribution of the White stork in Southeast Europe and can be used in conservation planning with respect to climate change.

Aims To create spatial models for predicting White Stork presence and densities in the Southeast Europe to identify areas of suitable habitat for White Storks.

Methods We quantified the habitat used by nesting White storks in Southeast Europe. Using spatial modelling, we defined a set of free and available online environmental variables that predict the breeding localities of the species. We employed pseudo-absences and the kriging of the residuals in order to create predictive models of nest presence and density.

Results The presence–absence model was found to be precise in predicting the presence of nests. Both density and presence of breeding pairs were best explained negatively by elevation, slope, minimum temperature during May, and distance to the nearest human settlement and positively by topographic wetness index, total area of human settlement and spring precipitation.

Conclusion Our robust and easily repeatable models offer a conservation tool to reveal suitable but unoccupied localities for breeding White Storks pairs which may inform our understanding of how climate change might affect the species' distribution in the future. For example, protecting White Storks on the Dalmatian coast may become even more significant in the future, because the Dalmatian coast is predicted as the only suitable breeding area in Croatia later this century.

The White Stork is a summer visitor breeding in temperate and warm areas of the Palaearctic (Hagemeijer & Blair 1997) and its breeding range covers large parts of the European continent (BirdLife International 2004). It is a flagship species indicating farmland bird diversity (Tobolka *et al.* 2012), but it has experienced a steep population decrease up until the 1980s. During last few decades the White Stork population has begun to recover, leading to its current conservation status as least concern according to International Union for Conservation of Nature criteria (BirdLife International 2013).

The ecology and breeding behaviour of the White Stork *Ciconia ciconia* have been intensively studied (Vergara *et al.* 2006, Itonaga *et al.* 2011). Overall, the population dynamics of White Storks is complex, affected by a combination of factors such as rainfall in the wintering areas in Africa (Kanyamibwa *et al.* 1993), food resource decline on the wintering grounds (Schaub *et al.* 2005), local climate conditions in the breeding areas just before arrival or in the late breeding season (Saether *et al.* 2006) or even natural disasters (Tryjanowski *et al.* 2009). Historical declines in Europe have been associated with habitat destruction and changes in agricultural practices (Carrascal *et al.* 1993), habitat alterations including drainage of wet

*Correspondence author. Email: andreja.radovic100@gmail.com

meadows (del Hoyo *et al.* 1992), prevention of flood wetland drainage (60% loss in Europe) (EEA 2010), conversion of foraging areas, development, industrialization and intensification of agricultural production (BirdLife International 2013). However, some recent research has found that local population dynamics were much less affected by the availability of suitable and stable habitats (pastures, meadows and wetlands) than expected (Tryjanowski *et al.* 2005b).

Climate is considered to be another important factor shaping the breeding distribution of the White Stork population in Europe, particularly in the light of future climate change where a significant part of current breeding areas in South-eastern Europe are predicted to become unsuitable (Huntley *et al.* 2007) and where movement of nesting habitat towards higher altitudes is expected (Tryjanowski *et al.* 2005c). Although habitat preferences of the White Stork are well-studied (Carrascal *et al.* 1993, Pleym 1995, Latus *et al.* 2000; Olson & Rogers 2009), few papers examine spatially related variation in breeding densities (Carrascal *et al.* 1993, Olson & Rogers 2009, Wickert *et al.* 2010). Such spatial information concerning habitat requirements is essential for species such as the White Stork, which have large home ranges and complex habitat needs, in order to be able to predict how population dynamics might be affected by habitat change, particularly with respect to climate change.

Here we investigate the factors determining large-scale distribution of White Storks in a region of Europe where climate change is expected to severely modify habitat availability for the species. We modelled the potential habitat distribution of the White Stork breeding population across three South-eastern European countries using nest sites and generated pseudo-absence locations. Pseudo-absence locations are necessary for using any of advanced discriminant analysis techniques such as generalized linear models (GLMs), (Guisan & Zimmermann 2000, Zaniwski *et al.* 2002, Engler *et al.* 2004). Discriminant analysis techniques are widely used in modelling habitats for diverse plant and animal species (Engler *et al.* 2004, Chefaoui & Lobo 2008). Such techniques are potentially more useful than less accurate profile modelling techniques, which only require presence data. Pseudo-absence locations are needed for large-scale predictions because presence points only reflect the realized environmental conditions of species but not their potential distribution (Lobo *et al.* 2010). Our study therefore also aimed to investigate the effect of the differences in scale of these two modelling

approaches: the distribution area of the species (presence-only density data) and when considering a larger scale (presence and pseudo-absence data). We determined the set of environmental variables that determine breeding habitat suitability (that predicted nest density and nest probability of occurrence) at two different scales so as to construct a spatially explicit model of potential White Stork breeding sites in the Southeast Europe, to identify expected changes due to global warming.

METHODS

We recorded a set of 11 environmental variables at a 1-km grid scale for the study area which included Slovenia, Croatia and Bosnia and Herzegovina (128000 km²). Variables measured were topography, climate, water presence, land use and human presence (Table 1) that are expected to influence White Stork presence (Alonso *et al.* 1991, Carrascal *et al.* 1993, Wickert *et al.* 2010). We extracted topographic and climatic variables using an open access digital elevation model of 30 m resolution (<http://www.gdem.aster.ersdac.or.jp>), and the open access global climate database, respectively (WorldClim; average values for 1950–2000) (Hijmans *et al.* 2005). We also calculated the cover of different land uses at the grid scale, using the Corine open access database (<http://www.eea.europa.eu/data-and-maps/data/>). We assigned a different weight to the different land types recorded in terms of their importance as feeding habitats for White Storks, so as to give greater weight to non-irrigated arable land and natural grassland (4), less to permanently irrigated land (3), even less to pasture (2) and none for forest types (1). We finally calculated forest cover, as well as a weighted open land type index to account for availability of suitable land types at grid scale, as a sum of the products of each land type cover with its weight (Table 1). All analysis was performed with the help of SAGA software in R ('RSAGA package': Brenning 2008).

We compiled a regional data set of White Stork breeding pairs, fully covering Slovenia and Croatia and partially Bosnia and Herzegovina. The Slovenian data set originated from a systematic national monitoring project (350 nests, survey in 2009, Denac 2010), while the Croatian data set merged data from several national and local monitoring projects (1240 nests; 2004–2009 surveys). We also collected data for Bosnia and Herzegovina, taking into consideration former known breeding sites (52 nests, 2005–2010 surveys,

Table 1. Environmental variables recorded, mean, minimum and maximum values for the study area and for the nest sites (1 km grid scale). Codes in parentheses refer to land use types (<http://www.eea.europa.eu/data-and-maps/data/>). 211: non-irrigated arable lands, 212: permanently irrigated lands, 231: pastures, 311: broad-leaved forest, 312: coniferous forest, 313: mixed forest, 321: natural grasslands, 511: permanent running water and 512: water bodies.

Type	Environmental variables		Study area		Nest sites	
	Code	Description	Mean	Min–Max	Mean	Min–Max
Topography	elev	Mean elevation (m)	491	0–2535	130	67–751
	slope	Mean slope (%)	16.7	0–69	5	0–30
Climate	precip	Total spring precipitation during the breeding season (April–July) (mm)	370	189–490	322	231–432
	temp	Minimal temperature in May (°C)	8.5	1.5–13.9	8.4	6.3–11.1
Water presence	a_water	Proportion of water cover in grid cell (%)	0.4	0–100	3	0–60
	d_water	Distance to the nearest permanent water (511, 512) (m)	19,000	0–108,260	11,541	0–48,374
	wet	Mean topographic wetness index	19.6	14.6–29	23.7	17.4–28.9
Land use	forest	Proportion of forest cover (311, 312, 313) (%)	42	0–100	7	0–100
	w_open	Weighted open land type index = [area of (211 + 321)*4] + [area of (212)*3] + [area of (231)*2]	0.36	0–4	0.58	0–4
Human presence	a_settl	Proportion of settlement area (%)	2	0–100	17	0–100
	d_settl	Distance to the nearest settlement (m)	4731	0–26,400	800	0–9849

Kotrošan 2005, 2006, Kotrošan *et al.* 2006). The accuracy of information on nesting sites differs slightly among countries. For Slovenia we have assumed that all nests were known. In Croatia, we believe that approximately 95% of nests were detected, covering the whole breeding range, while for Bosnia and Herzegovina approximately 85% of nests were detected and the same percentage area of the country covered.

Nest distribution structure

We calculated the area including all observed nests, using a convex hull procedure, in order to calculate the proportion of the study area where nesting occurred. To investigate the structure of nest distribution patterns, we first generated a simple random point pattern (rpoint function from ‘spatstat’ package: Baddeley 2008). We then calculated the nearest neighbour distance (nndist function, ‘spatstat’ package) between observed nests and distances between random points.

Pseudo-absence data set

We generated the same number of pseudo-absences as number of presences ($n = 1642$) (see Hengl 2009). First, we employed Ecological Niche Factor Analysis (ENFA) (Hirzel *et al.* 2002), in order to reduce our environmental variables into a few uncorrelated factors that pinpointed the difference of the specific environmental conditions prevailing at White Stork nests from the average conditions in the study area. To do so we used the enfa function (‘adehabitatHS’

package in R software: Calenge 2006, 2007), in order to produce a habitat suitability score for each 1 km grid, ranging from 0 to 100, from least to most suitable habitats (habitat suitability index (HSI)). We adopted a random stratified procedure for the selection of pseudo-absence localities, by applying a random algorithm (rpoint function from ‘spatstat’ package: Baddeley 2008) so that pseudo-absences had a greater probability of being (a) away from suitable habitats and (b) away from areas with highest nest density. To do so, we assigned to each grid an inadequacy probability index (range up to 64), calculated as the product of the HSI (values from 1 to 4, see below) with a nest density index from high to low nest density zones (values from 1 to 4, see below) (Fig. 1). To extract the four habitat suitability zones, we used the output of the habitat suitability map and we reclassified grids into three habitat suitability zones in decreasing order (zone 1: $HSI \geq 75.1$, zone 2: $50.1 < HSI < 75$, zone 3: $25 < HSI < 50$): no grids were left within the class of HSI under 25. To extract the nest density zones, we used the nest density database and assigned a nest density score to each grid, using the smoother intensity technique (Kernel density estimator > 75% nearest neighbour distance) (function density.ppp; package ‘Spatstat’, R). We then reclassified grids into four zones (quartiles) from the highest to the lowest nest density zone. As a result, the data set of pseudo-absences was randomly generated, but under a rule giving higher probabilities for pseudo-absence points to be generated in grids with a greater inadequacy probability index. With this procedure, our data set (presences and pseudo-absences) covered a

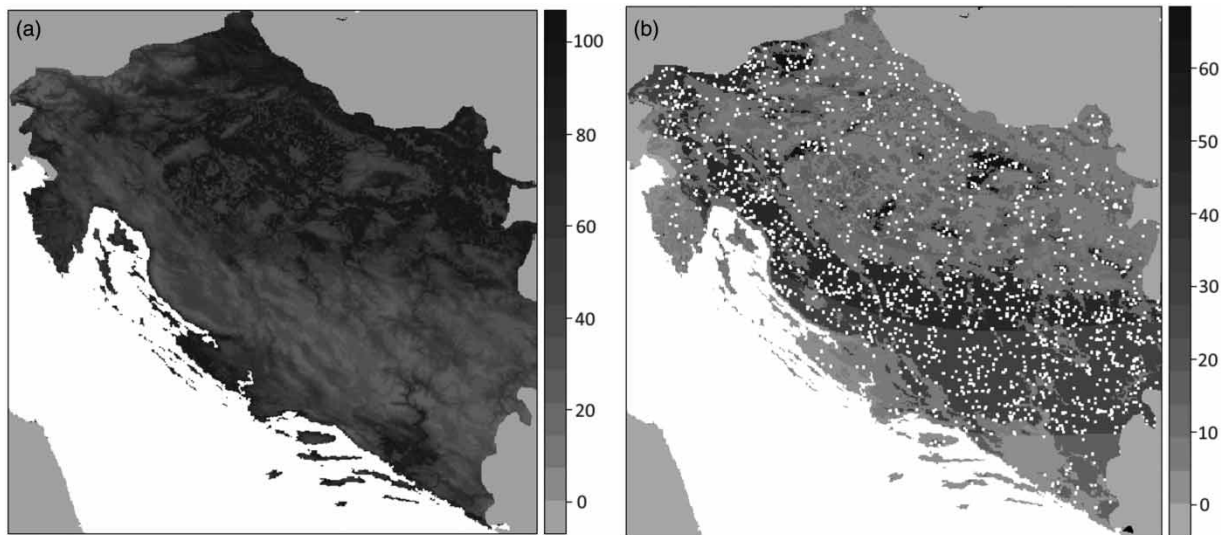


Figure 1. (a) Result of ENFA algorithm – HSI for White Stork breeding in the Southeast Europe. Darker areas stand for more suitable areas and (b) resulting grid used for generating pseudo-absence data with pseudo-absence locations superimposed.

greater spectrum of environmental conditions in the region. At the same time, pseudo-absence data are not all placed in extremely unsuitable areas, but along environmental gradients with more of them placed in less suitable areas. By covering a broader spectrum of environmental conditions than the species already uses (its realized niche) we can potentially better detect those environmental variables that limit its distribution.

Model construction

We used a data set of equal number of presences and randomly generated pseudo-absences ($n = 3284$) in the modelling procedure. First, we modelled White Stork nest density in terms of nest density score in each grid, at two scales: (a) at the scale of current distribution, including only grids with nest presence and (b) at a larger scale, including presences and pseudo-absences points in the whole study area. In both cases, we constructed the model using a backward stepwise procedure (Akaike information criterion for variable selection), using a multivariate linear model. For the model using presences and pseudo-absences, we dealt with autocorrelation in the following way. We modelled the residuals (observed densities and predicted densities), using the `fit.variogram` method ('`gstat`' package) (Pebesma 2004) and we then performed a regression kriging technique, by interpolating the residuals via kriging (`krige` from the '`gstat`' package) (Pebesma 2004, Bivand *et al.* 2008). The final model was constructed by summing the

predictions of the linear model and interpolated residuals (Hengl 2009). We assessed the performance of both nest density models as the proportion of the overall variation explained, using the normalized root mean square error (RMSEr) and model accuracy ($1 - \text{RMSEr}^2$). As a rule of thumb, an RMSEr below 40% (i.e. smaller is better) is considered to give a fairly accurate prediction assessed on the validation points (accuracy > 85%) (Hengl 2009).

Second, we modelled the presence of White Stork nests at the larger scale, considering both presences and pseudo-absences, using a GLM with a binomial link function. The optimal environmental predictor set was selected using the backward stepwise procedure (Akaike information criterion). We assessed the performance of the presence model using 70% of the data set for model construction and 30% for model validation (random selection and ten permutations). We assessed its performance in terms of the receiver operating curve (ROC) and the area under the curve (performance function in '`ROCR`' package). We considered particularly the results that validated the prediction of presence of White Stork nests (precision and positive predictive value).

RESULTS

Nest distribution structure

We recorded 52 nests in Bosnia and Herzegovina, so the total number of known breeding sites of White Storks in

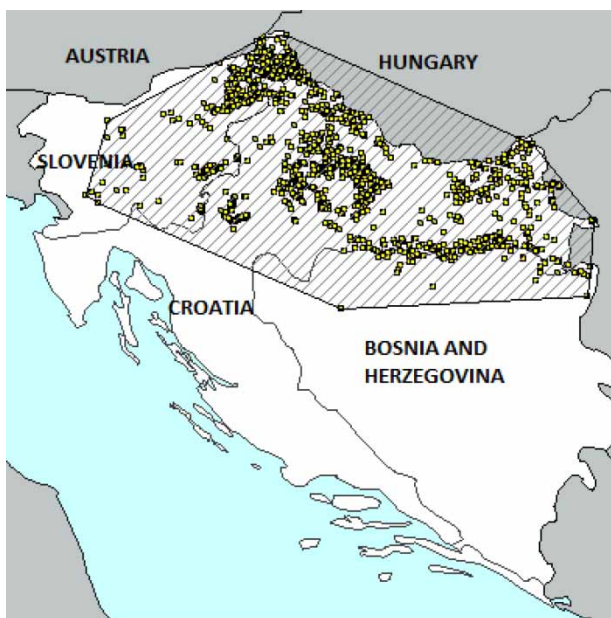


Figure 2. Nesting sites of White Stork ($n = 1642$) in Slovenia, Croatia and Bosnia and Herzegovina and minimum area of current nest distribution (convex hull procedure).

the region was 1642 nests. They were aggregated to the north and north-eastern part of the study area, covering an area of 42 049 km² (33% of the study area) (Fig. 2). The average nest density within the current distribution area was 0.04 nests/km², ranging from 1 to 25 nests/km² for grids with nest presence (mean value 3.63). We found a clustered nest distribution pattern although this included several isolated nests; distances between neighbouring nests were significantly smaller when compared with the random pattern (one-way Welch test, $F_{1,2960} = 2227.5$; $P < 0.0001$) (Fig. 3).

Nest distribution model

We found that the topographic and climatic variables were among the most important factors predicting the distribution pattern of White Stork breeding pairs, either considering the larger spatial scale (presence–absence models where all of the study area was considered) or the smaller scale (presence-only model, nest density). In all cases, the increase in minimum May temperature negatively affected nest presence and density, and nesting localities generally fell within a restricted temperature range, avoiding extremes (Table 1). The current distribution of White Storks was on relatively flat ground and with a pronounced human presence (Table 1).

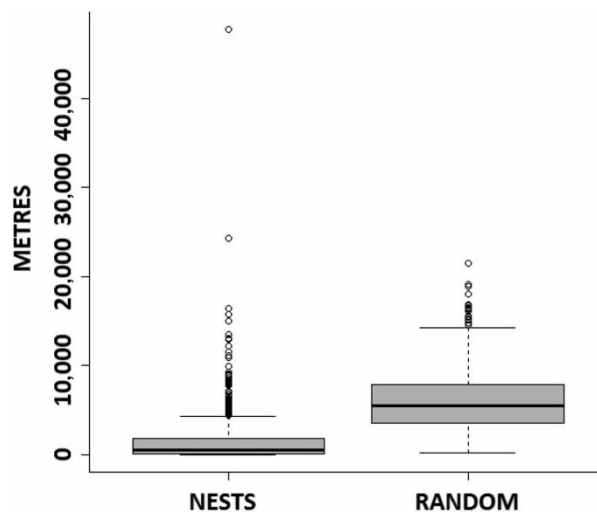


Figure 3. Box plot for the nearest neighbour distances (in metres) for White Stork nests and randomly distributed points in the study area.

When considering only the model of nest density within presence areas, the species preferred open habitat areas close to water surfaces (Table 2a). White Storks also preferred to breed in microhabitats with steeper slopes than average available conditions (Table 2a). The distance to and area of human settlements was not a significant factor in explaining local differences in breeding densities (Table 2a). When considering the two larger scale models, we found that although topographic relief was rather mild in the most parts of the study area, the species preferred even milder slopes, and preferred to nest in proximity to human settlements (Table 2b & 2c).

These results allowed us to generate a spatially explicit predictive model of nest density and nest probability of occurrence, where in both models, a gradient from the north and north-east towards the south and south-west parts of the study area was apparent (Fig. 4).

Best model method

We found that the kriging technique improved the linear regression models' fit. After preparing the linear regression model and kriging the residuals, the RMSEr improved from the initial 55.8% for the regression model to 41.4% for the regression kriging model, and accuracy also improved from 68.9% to 82.9%, respectively. We found that the presence–absence model using the binomial GLM method proved to be already very robust for predicting nesting sites of

Table 2. Predictive power of environmental variables for White Stork models: (a) nest density linear model (LM) with presence-only data, (b) nest density LM with presence and pseudo-absence data and (c) binomial GLM with presence and pseudo-absence data. Coeff.: coefficient of the regression model. For variable names see Table 1.

Environmental variables	Presence-only data			Presence and pseudo-absence data					
	(a) Nest density LM			(b) Nest density LM			(c) Nest presence GLM		
	Coeff.	z	P	Coeff.	z	P	Coeff.	z	P
(Intercept)	-0.61	11.3	***	-0.57	-6.9	***	-9.247	-6.5	***
elev (m)	-2.38e-05	-31.9	***	-0.001	-26.9	***	-0.012	-11.4	***
slope (%)	6.65e-01	9.6	***	-0.275	-4.1	***	-6.082	-3.8	***
precip (mm)	3.14e-02	45.1	***	0.007	11.3	***	0.062	4.5	***
temp (°C)	-0.114	-6.4	***	-0.018	-6.4	***	-0.163	-2.8	***
a_water (%)	-1.17e-01	-4.9	***			ns			ns
d_water (m)	1.65e-06	5.2	***			ns	-1.62e-05	-2.4	*
wet	0.046	17.2	***	0.046	17.2	***	0.195	4.5	***
forest (%)			ns			ns	-2.526	-7.7	***
w_open	8.61e-08	2.3	*			ns			ns
a_settl (%)			ns	0.163	4.2	***	4.361	5.2	***
d_settl (m)			ns	-6.26e-06	-3.5	***	-0.0002	-4.8	***

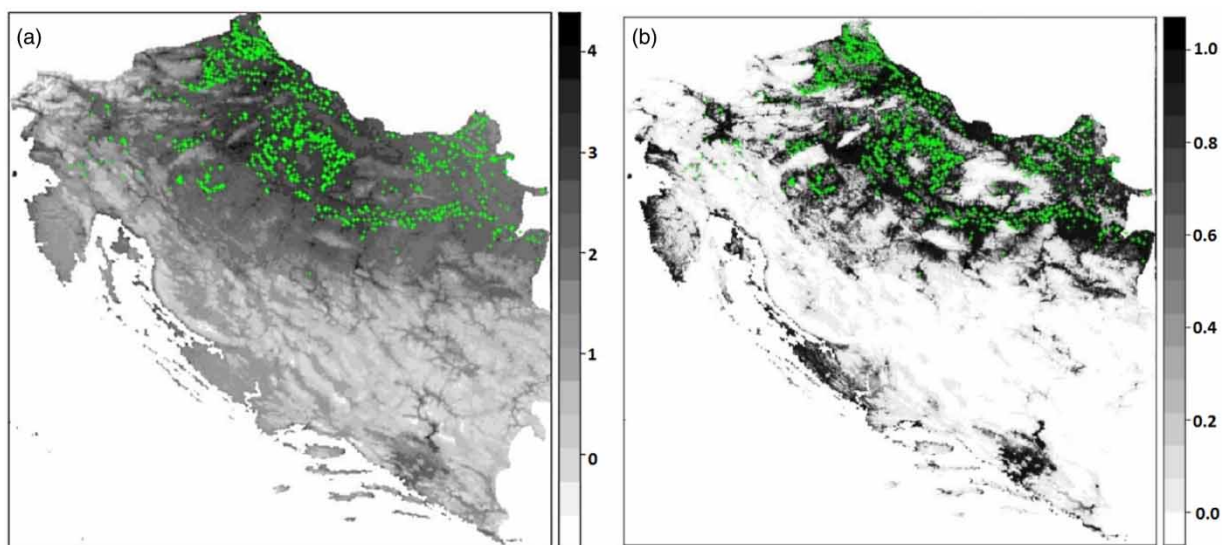


Figure 4. (a) Broad scale predictive model of White Stork nest densities (linear model with regression kriging) and (b) broad scale predictive model of White Stork nest presence (binomial GLM). Nest positions are marked in green.

White Storks in the study area (ROC area for ten repeated tests ranged from 96% to 98% and positive predictive power median 98.8%). When comparing the nest density model and the nest presence model when using presence-absence data (Table 2b & 2c), six environmental parameters (out of eight overall) were found to be in common, whereas only five variables were in common with the nest density model with presence-only data (Table 2a). In the same vein, the nest density model with presence-only data

produced conflicting results for five environmental factors compared to the nest presence model (Table 2a & 2c).

DISCUSSION

According to our results, suitable habitats for nesting sites for White Stork cover a large part of the study area (approximately 65%; HSI > 50.1). Our analysis revealed that there was good habitat quality in some

parts of the study area, especially in central parts of Croatia, where densities of known White Stork nests reached 44 nests/100 km². This is a high density, but not even close to those reported from the central part of the species' distribution in Poland (Kosicki 2010) or Lithuania (Vaitkuvienė & Dagyst 2014), although more similar to those reported for Estonia (Ots 2009).

Our models have both conservation and methodological implications. For example, within the species' distribution range, our results confirmed the importance of the availability of open habitats such as grasslands or non-irrigated arable lands in proximity to White Stork nests, and these may require a suite of management measures for their maintenance. Our results show that the presence of the White Stork nests is probably determined by a set of environmental variables with the greatest negative influence being topography (elevation) and amount of forest and the greatest positive influence being presence of human settlements. Although such findings were as expected given the known ecology of the species, we quantified and ranked the influence of the above environmental factors on a comparative basis. Thus our results allow us to identify the environmental factors that most likely regulate the probability of occurrence and nest density of White Stork in Southeast Europe, and explain the aggregated distribution pattern of the species in suitable habitats in the North Eastern part of the study area: these factors were mostly topographic and climatic in nature. Regarding topography, White Storks in Southeast Europe breed in places at lower altitudes with high values of topographic wetness index. The positive effect of wetness on White Stork potential prey is already well known (Tryjanowski *et al.* 2005a), but we show the importance of using a topographic wetness index as a good proxy for predicting White Stork presence. This index is largely dependent on topography, it can be easily extracted from freely available digital elevation models and reflects the wetness potential of a locality according to its micro-relief. Topographic wetness index was found to be a consistently significant predictor of White Stork nest occurrence at all scales of model implementation, proving that this index might be a useful proxy to detect suitable areas for White Storks, as well as for other birds dependent on humid conditions (Aguirre & Vergara 2009).

The highest altitude with a detected White Stork nest in our region was 752 m in Slovenia. Similarly, nests were reported at 890 m in Poland (Tryjanowski *et al.* 2005c) or even areas of the Tatra Mountains up to

1000 m, at 1350 m in Sierra de Gredos (Spain) and at 2500 m in Morocco (Creutz 1985, Schulz 1988). Rather than altitude per se, temperature may have been a limiting factor in our region (Table 2). Our results, similar to previous studies (Carrascal *et al.* 1993, Huntley *et al.* 2007) revealed a very good correspondence of the species' distribution in Europe with climate variables. However, the importance of climate variables should probably also be examined further using techniques that do not assume linear relationships because the species avoids extremes of the available conditions in the area in both precipitation during breeding season and minimum temperature in May. Temperatures are important for successful breeding of White Storks because young birds are sensitive to low temperatures until they develop thermoregulatory ability (Tortosa & Castro 2003). Rain and cold weather conditions can significantly reduce breeding success causing high chick mortality (Jovani & Tella 2004, Kosicki 2012, Hilgartner *et al.* 2014), but it may also have beneficial effects because of its influence on prey availability (Tryjanowski & Kuzniak 2002).

Our study also has methodological implications. Our study relied exclusively on widely available and easily accessible data sets to produce spatially explicit models of White Stork breeding sites. The kriging of the density model residuals improved the percentage of explained variance in the model of breeding densities and confirmed that hybrid techniques between point pattern analysis and geostatistics can improve model predictions. This technique is becoming more widely used in various ecological studies. Even software that is advertised that uses only presence data (e.g. Maxent) in fact uses pseudo-absence data but generates only random points in a region of interest. We also recommend using pseudo-absences spread in areas of low habitat quality for a species and geographically far from observed presence locations as has been suggested previously (Lobo *et al.* 2010, Hengl *et al.* 2009, Senay *et al.* 2013). The importance of entering pseudo-absence points into a modelling procedure is evident from our modelling of White Stork nests densities where a linear model, prepared with only presence locations, showed a non-significant influence on nest locations due to human presence in the area. However, when pseudo-absence locations were entered into our modelling procedure (the larger scale model), it was found that human presence influenced White Stork breeding densities. Possible reasons for the less satisfactory performance of the nest density models

could be because we still lack comprehensive nest counts from Croatia and Bosnia and Herzegovina (i.e. false negatives in the model) but also because we are missing important variables. Our density model should perhaps ideally have integrated both quality of foraging habitats (Tryjanowski *et al.* 2005a, Kosicki 2010) as well as potential measures of disturbance rate, but these variables are not easy to obtain for large areas.

Despite a simple methodology using only cartographic data, we constructed a robust model for breeding site prediction. As a conclusion, we suggest that modelling should consider different spatial scales, capturing on one hand the general ecological preferences of the target species at larger spatial scales, in order to identify main patterns and trends (i.e. what the species avoids or prefers), and on the other hand on smaller scales within areas of occurrence, pinpointing microhabitat preferences within its distribution range (i.e. what determines species density), so as to extract conservation recommendations at all potential spatial scales of management. In the context of the future climate change (Huntley *et al.* 2007) our results offer a conservation tool, by detecting not only the sites of high conservation value that are aggregated towards the north-eastern part of the study area, but also by pinpointing the broader area for White Stork potential breeding in the future. Models predicting presence of the species revealed highly suitable areas for White Storks in the coastal region of Croatia that are to date unoccupied (see Fig. 4b). A possible reason could be the pronounced pressure of poachers, especially in Dalmatia (Denac 2010). However, during the summer of 2011 and 2012 several non-breeding White Storks were recorded foraging on one karst field near the town of Sinj in the Croatian hinterland (I. Budinski pers. comm.), an area found to be suitable for storks with our binomial model. Protecting White Storks on the Dalmatian coast may become even more significant in the future, because the Dalmatian coast is predicted as the only suitable breeding area in Croatia during late 21st century (Huntley *et al.* 2007).

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