

Why choose Random Forest to predict rare species distribution with few samples in large undersampled areas? Three Asian crane species models provide supporting evidence

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Species distribution models (SDMs) have become an essential tool in ecology, biogeography, evolution, and more recently, in conservation biology. How to generalize species distributions in large undersampled areas, especially with few samples, is a fundamental issue of SDMs. In order to explore this issue, we used the best available presence records for the Hooded Crane (*Grus monacha*, n=33), White-naped Crane (*Grus vipio*, n=40), and Black-necked Crane (*Grus nigricollis*, n=75) in China as three case studies, employing four powerful and commonly used machine learning algorithms to map the breeding distributions of the three species: TreeNet (Stochastic Gradient Boosting, Boosted Regression Tree Model), Random Forest, CART (Classification and Regression Tree) and Maxent (Maximum Entropy Models) Besides, we developed an ensemble forecast by averaging predicted probability of above four models results. Commonly-used model performance metrics (Area under ROC (AUC) and true skill statistic (TSS)) were employed to evaluate model accuracy. Latest satellite tracking data and compiled literature data were used as two independent testing datasets to confront model predictions. We found Random Forest demonstrated the best performance for the most assessment method, provided a better model fit to the testing data, and achieved better species range maps for each crane species in undersampled areas. Random Forest has been generally available for more than 20 years, and by now, has been known to perform extremely well in ecological predictions. However, while increasingly on the rise its potential is still widely underused in conservation, (spatial) ecological applications and for inference. Our results show that it informs ecological and biogeographical theories as well as being suitable for conservation applications, specifically when the study area is undersampled. This method helps to save model-selection time and effort, and it allows robust and rapid assessments

and decisions for efficient conservation.

1 **Why choose Random Forest to predict rare species distribution with few samples in large**
2 **undersampled areas? Three Asian crane species models provide supporting evidence**

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16 **ABSTRACT**

17 Species distribution models (SDMs) have become an essential tool in ecology, biogeography,
18 evolution, and more recently, in conservation biology. How to generalize species distributions in
19 large undersampled areas, especially with few samples, is a fundamental issue of SDMs, and
20 beyond. In order to explore this issue, we used the best available presence records for the Hooded
21 Crane (*Grus monacha*, n=33), White-naped Crane (*Grus vipio*, n=40), and Black-necked Crane
22 (*Grus nigricollis*, n=75) in China as three case studies, employing four powerful and commonly
23 used machine learning algorithms to map the breeding distributions of the three species: TreeNet
24 (Stochastic Gradient Boosting, Boosted Regression Tree Model), Random Forest , CART
25 (Classification and Regression Tree) and Maxent (Maximum Entropy Models) In addition we
26 developed an ensemble forecast by averaging predicted relative indices of occurrence for the four
27 models results. Commonly-used model performance metrics (Area under ROC (AUC) and true
28 skill statistic (TSS)) were employed to evaluate model accuracy. Latest satellite tracking data and
29 compiled literature data were used as two independent testing datasets to confront model
30 predictions. We found Random Forest demonstrated the best performance for most assessment
31 methods, provided a better model fit to the testing data, and achieved better species range maps
32 for each crane species in undersampled areas. Random Forest has been generally available for
33 more than 20 years, and by now, has been known to perform extremely well in ecological
34 predictions. However, while increasingly on the rise its potential is still widely underused in
35 conservation, in (spatial) ecological applications and for inference. Our results show that it
36 informs ecological and biogeographical theories as well as being suitable for conservation
37 applications, specifically when the study area is undersampled. This method helps to save model-
38 selection time and effort, and it allows robust and rapid assessments and decisions for efficient
39 conservation.

40 INTRODUCTION

41 Species distribution models (SDMs) are empirical ecological models that relate species
42 observations to environmental predictors (Guisan & Zimmermann, 2000; Drew et al., 2011).
43 SDMs have become an increasingly important and now essential tool in ecology, biogeography,
44 evolution and, more recently, in conservation biology (Guisan et al., 2013), management
45 (Cushman & Huettmann, 2010), impact assessments (Humphries & Huettmann, 2014) and
46 climate change research (Lei et al., 2011; Mi et al., 2016). To generalize and infer from a model,
47 or model transferability is defined as geographical or temporal cross-applicability of models
48 (Thomas & Bovee 1993; Kleyer 2002; Randin et al., 2006). It is one important feature in SDMs,
49 a base-requirement in several ecological and conservation biological applications (Heikkinen et
50 al., 2012). In this study, we used generality (transferability) as the concept of generalizing
51 distribution from sampled areas to unsampled areas (extrapolation beyond the data) in one study
52 area.

53 Detailed distribution data for rare species in large areas are rarely available in SDMs (Pearson
54 et al., 2007; Booms et al., 2010). However, they are among the most needed for their
55 conservation to be effective. Collecting and assembling distribution data for species, especially
56 for rare or endangered species in remote wilderness areas is often a very difficult task, requiring a
57 large amount of human, time and funding sources (Gwena et al., 2010; Ohse et al., 2009).

58 Recent studies have suggested that machine-learning (ML) methodology, may perform better
59 than the traditional regression-based algorithms (Elith et al., 2006). TreeNet (boosting; Friedman
60 2002), Random Forest (bagging; Breiman, 2001), CART (Breiman et al., 1984) and Maxent
61 (Phillips et al., 2004) are considered to be among the most powerful machine learning algorithms
62 and for common usages (Elith et al., 2006; Wisz et al., 2008; Williams et al., 2009; Lei et al.,

63 2011) and for obtaining powerful ensemble models (Araújo and New 2007; Hardy et al., 2011).
64 Although Heikkinen et al. (2012) compared the four SDMs techniques' transferability in their
65 study, they did not test with rare species and few samples in undersampled areas. It is important
66 to understand that the software platform of the former three algorithms (Boosted Regression
67 Trees, Random Forest and CART) applied by Heikkinen et al. (2012) from the R software
68 ("BIOMOD" framework) comes without a GUI and lacks sophisticated optimization, sample
69 balancing and fine-tuning, but as they are commonly used though by numerous SDM modelers.
70 Instead, we here run these models in the Salford Predictive Modeler (SPM version 7) by Salford
71 Systems Ltd (<https://www.salford-systems.com/>). These algorithms in SPM are further optimized
72 and improved by one of the algorithm's original co-authors (especially for TreeNet and Random
73 Forest). It runs with a convenient GUI, and produces a number of descriptive results and graphics
74 which are virtually not available in the R version. While this is a commercial software, it is
75 usually available on a 30 days trial version (which suffices for most model runs we know. As
76 well, some of the features of the randomForest R package, most notably the ability to produce
77 partial dependence plots (Herrick 2013), are not directly implemented yet in SPM7 (but they can
78 essentially be obtained by running TreeNet in a Random Forest model).

79 Model generality (transferability) testing could offer particularly powerful for model
80 evaluation (Randin et al., 2006). Independent observations from a training data set has been
81 recommended as a more proper evaluations of models (Fielding & Bell 1997; Guisan and
82 Zimmermann 2000). So the use of an independent geographically (Fielding & Haworth, 1995) or
83 temporally (Boyce et al., 2002; Araujo et al., 2005b) testing data set is encouraged to assess the
84 generality of different SDMs techniques. Data from museum specimen, published literature
85 (Graham et al., 2004) as well as tracking are good source to assess model generality
86 (transferability) performance. In addition, how the distribution map links with reality data,
87 especially in undersampled areas where modelers want to make predictions should definitely be

88 employed as a metric to assess model performance and generalization. Arguably, if model
89 predictions perform very well there, great progress is provided and usually done cost-effective
90 too. Whereas, predictions on existing knowledge and data offers less progress. The model
91 prediction and conservation frontier obviously sits in the unknown and to provide progress there
92 (Breiman 2001, Drew et al. 2011).

93 In this study, we investigated models for the best-available data for three species in East Asia
94 as test cases: Hooded Cranes (*Grus monacha*, n=33), White-naped Cranes (*Grus vipio*, n=40) and
95 Black-necked Cranes (*Grus nigricollis*, n=75). Four machine-learning model algorithms
96 (TreeNet, Random Forest, CART and Maxent) were applied to map breeding distributions for
97 these three crane species which otherwise lack empirically derived distribution information. In
98 addition, two kinds of independent testing data sets (latest satellite tracking data, and compiled
99 literature data (Threatened Birds of Asia: Collar *et al.*, 2001) were obtained to test the
100 transferability of the four model algorithms. The purpose of this investigation is to explore
101 whether there is a SDM technique among the four algorithms that could generate reliable and
102 accurate distributions with high generality for rare species using few samples but in large
103 undersampled areas? Results from this research could be useful for the detection of rare species
104 and enhance fieldwork sampling in large undersampled areas which would save money and
105 effort, as well as advance the conservation management of those species.

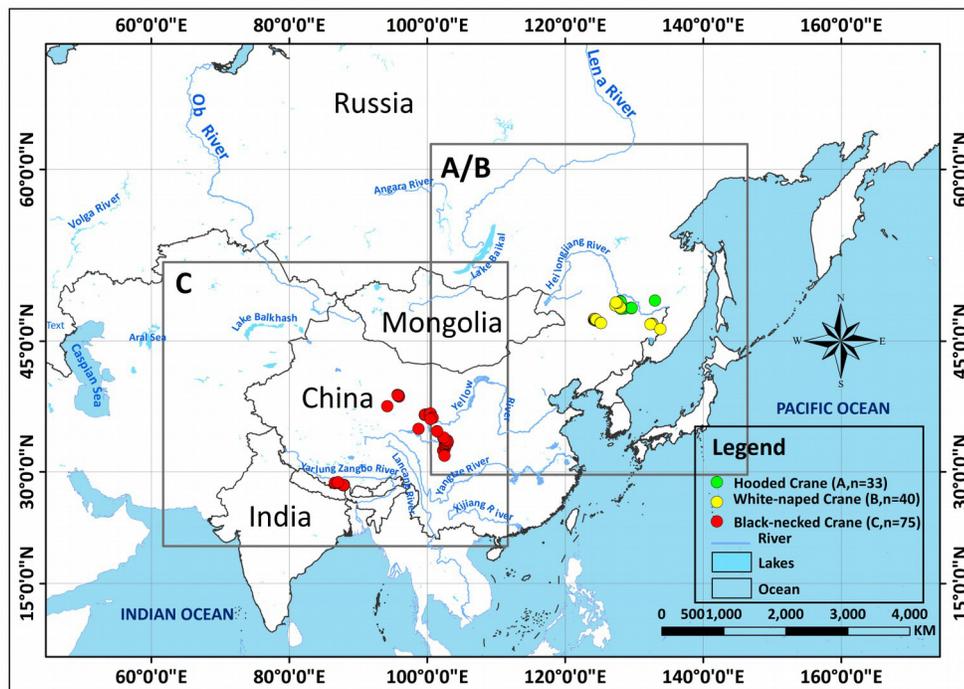
106 **MATERIALS AND METHODS**

107 **Species data**

108 In our 13 combined years of field work, we have collected 33 Hooded Crane nests (2002-2014),
109 40 White-naped Crane nests (2009-2014) , and 75 Black-necked Crane nests (2014) (see Fig. 1),
110 during breeding seasons. We used these field samples (nests) to represent species presence points
111 referenced in time and space.

112

Put Fig. 1 here



113

Figure 1 Study areas for three species cranes.

114 Environmental variables

115 We used 21 environmental layers at a 30-s spatial resolution in a GIS format and that were known
 116 to correlate with bird distribution and as proxies of habitats predictors. They included bio-
 117 climatic factors (bio_1-7, bio_12-15), topographical factors (altitude, slope, and aspect), water
 118 factors (distance to river, distance to lake, and distance to coastline), inference factors (distance to
 119 road, distance to rail road, and distance to settlements), and land cover factors (for detailed
 120 information, see Table 1). Most of these predictors were obtained from open access sources. Bio-
 121 climate factors were obtained from the WorldClim database (<http://www.worldclim.org>), while
 122 aspect and slope layer were derived from the altitude layer in ArcGIS, which was also initially
 123 obtained from the WorldClim database. Road, railroad, river, lake and coastline and settlement
 124 maps were obtained from the Natural Earth database (<http://www.naturalearthdata.com>). The land
 125 cover map was obtained from the ESA database. We also made models with all 19 bio-climate

126 variables and 10 other environmental variables, and then reduced predictors by AIC, BIC,
 127 varclust, PCA and FA analysis. When we compared the distribution maps overlaying with
 128 independent data set generated by Random Forest model, we found the model based on 21
 129 predictors have the best performance for Hooded Cranes, and the best level for White-naped
 130 Crane and Black-necked Cranes (see Supplement S1). Therefore, we decided to constructed
 131 models with 21 predictors for the all three cranes and four machine-learning techniques. All
 132 spatial layers of these environmental variables were resampled in ArcGIS to a resolution of 30-s
 133 to correspond to that of the bioclimatic variables and for a meaningful high-resolution
 134 management scale.

135

Put Table 1 here

136 Table 1 Environmental GIS layers used to predict breeding distributions of three cranes.

Environmental Description	Source	Website
Layers		
Bio_1	Annual mean Temperature (°C)	WorldClim http://www.worldclim.org/
Bio_2	Monthly mean (max temp - min temp) (°C)	WorldClim http://www.worldclim.org/
Bio_3	Isothermality (BIO2/BIO7) (*100 °C)	WorldClim http://www.worldclim.org/
Bio_4	Temperature seasonality (standard deviation *100 °C)	WorldClim http://www.worldclim.org/
Bio_5	Max temperature of warmest month (°C)	WorldClim http://www.worldclim.org/
Bio_6	Min temperature of Coldest month (°C)	WorldClim http://www.worldclim.org/
Bio_7	Annual temperature range (BIO5-BIO6) (°C)	WorldClim http://www.worldclim.org/
Bio_12	Annual precipitation (mm)	WorldClim http://www.worldclim.org/
Bio_13	Precipitation of wettest month (mm)	WorldClim http://www.worldclim.org/
Bio_14	Precipitation of driest month (mm)	WorldClim http://www.worldclim.org/

Bio_15	month (mm) Precipitation seasonality	WorldClim	http://www.worldclim.org/
Altitude	(mm) Altitude (m)	WorldClim	http://www.worldclim.org/
Aspect	Aspect (°)	Derived from	http://www.worldclim.org/
Slope	Slope	Altitude Derived from	http://www.worldclim.org/
Landcover	Land cover	Altitude ESA	http://www.esa-landcover-cci.org/
Disroad	Distance to roads (m)	Road layer	http://www.naturalearthdata.com/ from Natural
Disrard	Distance to railways (m)	Earth Railroad	http://www.naturalearthdata.com/ layer from
Disriver	Distance to rivers (m)	Natural Earth River layer	http://www.naturalearthdata.com/ from Natural
Dislake	Distance to lakes (m)	Earth Lake layer	http://www.naturalearthdata.com/ from Natural
Discoastline	Distance to coastline (m)	Earth Coastline	http://www.naturalearthdata.com/ layer from
Dissettle	Distance to settlements (m)	Natural Earth Settle layer	http://www.naturalearthdata.com/ from Natural
		Earth	

137 Model development

138 We created TreeNet, Random Forest, CART, Maxent models and ensemble models (averaged
139 value of the former four model results) for Hooded Cranes, White-naped Cranes and Black-naped
140 Cranes. These four model algorithms are considered to be among the best performing machine
141 learning methods (more information about these four models can be seen in the references by
142 Breiman et al., 1984, Breiman 2001, Friedman 2002, Phillips et al., 2004, Hegel et al., 2010). The

143 first three machine learning models are binary (presence-pseudo absence) models and were
144 handled in Salford Predictive Modeler 7.0 (SPM). For more details on TreeNet, Random Forest
145 and CART in SPM and their performances, we refer readers to the user guide document online
146 (<https://www.salford-systems.com/products/spm/userguide>). Several implementations of these
147 algorithms exist. Approximately 10,000 ‘pseudo-absence’ locations were selected by random
148 sampling across the study area for each species using the freely available Geospatial Modeling
149 Environment (GME; Hawth’s Tools; Beyer 2013; see Booms et al., 2010 and Ohse et al., 2009 for
150 examples). We extracted the habitat information from the environmental layers for presence and
151 pseudo-absence points for each crane, and then constructed models in SPM with these data. In
152 addition, we used balanced class weights, and 1000 trees were built for all models to find an
153 optimum within, others used default settings.

154 For the predictions, we created a ‘lattice’ (equally spaced points across the study area;
155 approximately 5×5 km spacing for the study area). For the lattice, we extracted information from
156 the same environmental layers (Table 1) as described above for each point and then used the
157 model to predict (‘score’) bird presence for each of the regular lattice points. For visualization,
158 we imported the dataset of spatially referenced predictions (‘score file’) into GIS as a raster file
159 and interpolated for visual purposes between the regular points using inverse distance weighting
160 (IDW) to obtain a smoothed predictive map of all pixels for the breeding distributions of the three
161 cranes (as performed in Ohse et al., 2009 and Booms et al., 2010). The fourth algorithm we
162 employed, Maxent, is commonly referred to as a presence-only model; we used Maxent 3.3.3k (it
163 can be downloaded for free from <http://www.cs.princeton.edu/~schapire/maxent/>) to construct our
164 models. To run Maxent, we followed the 3.3.3e tutorial for ArcGIS 10 (Young et al., 2011) and
165 used default settings.

166 **Testing data and model assessment**

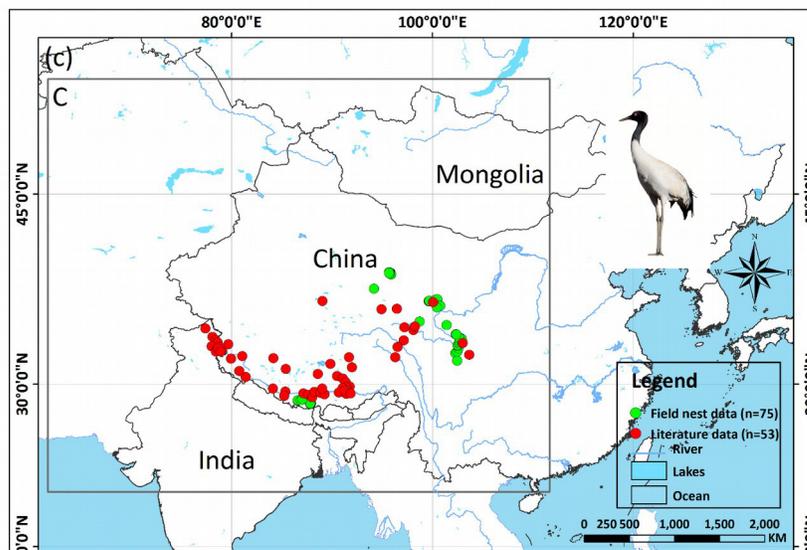
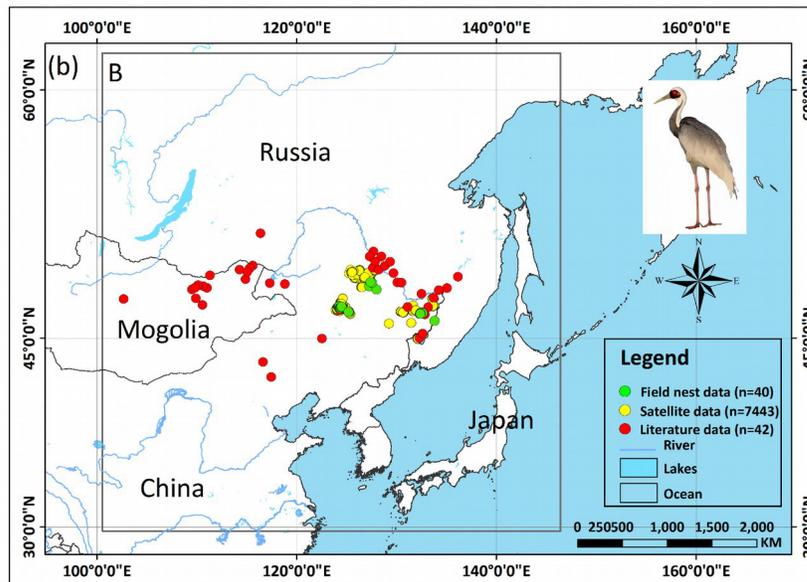
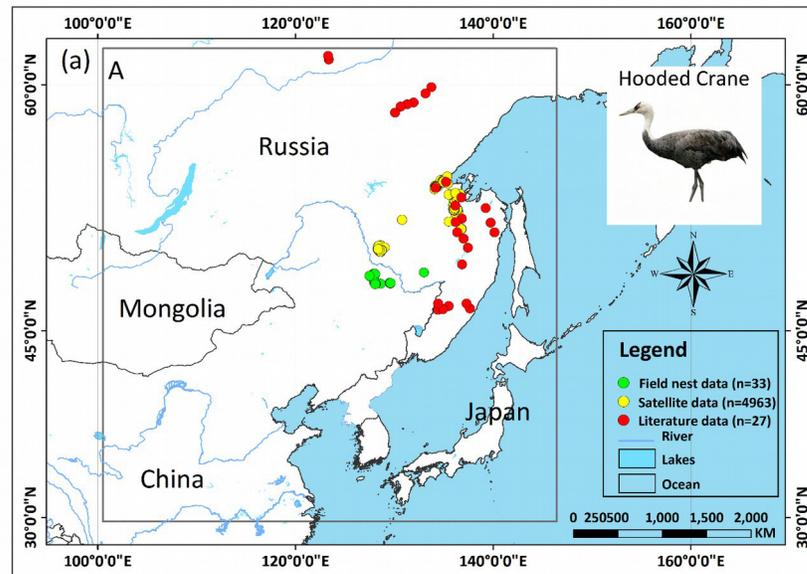
167 We applied two types of testing data in this study: one consisted of satellite tracking data, and
168 the other was represented by data from the literature. Satellite tracking data were obtained from 4
169 individual Hooded Cranes and 8 White-naped Cranes that were tracked in the breeding regions at
170 stopover sites (for more details regarding the information for tracked cranes, please see
171 Supplement S2). The satellite tracking devices could provide 24 data points per day (Databases
172 could be available upon request). Here, we chose points that had a speed of less than 5 km/h
173 during the period from 1st May to 31th June for Hooded Cranes and 15th April to 15th June for
174 White-naped Cranes as the locations of the breeding grounds for these two cranes. The total
175 numbers of tracking data points were 4,963 and 7,712 (Hooded Cranes and White-naped Crane,
176 respectively. We didn't track Black-necked Cranes, so there was no tracking testing data for this
177 species). The literature data for this study were obtained by geo-referencing the location points of
178 detections from 1980-2000 (ArcGIS 10.1) from Threatened Birds of Asia: the BirdLife
179 International Red Data Book (Collar et al., 2001). From this hardcopy data source, we were able
180 to obtain and digitize 27 breeding records for Hooded Cranes, 43 breeding records for White-
181 naped Cranes, and 53 breeding records for Black-necked Cranes (see Fig. 2a, 2b, 2c). Here we
182 digitized the only available crane data for these three species in East-Asia into a database.

183 In addition, we generated 3,000 random points for Hooded Cranes and White-naped Cranes,
184 and 5,000 random points for Black-necked Cranes as testing pseudo-absence points in their
185 respective study areas. And then, the literature locations (additional presence points for testing)
186 and random points location (testing absence points) that contrasted with the associated predictive
187 value of RIO extracted from the relative prediction map, which were used to calculate receiver
188 operating characteristic (ROC) curves and the true skill statistic (TSS) (Hijmans and Graham,
189 2006). The area under the ROC curve (AUC) is commonly used to evaluate models in species

190 distributional modeling (Manel *et al.*, 2001, McPherson *et al.*, 2004). TSS was also used to
191 evaluate model performance; we used TSS because it has been increasingly applied as a simple
192 but robust and intuitive measure of the performance of species distribution models (Allouche et
193 al., 2006).

194

Put Fig.2 here



- 195 Figure 2 Detailed study areas showing the presence of and testing data used for the three cranes.
- 196 2a) Hooded Cranes, 2b) White-naped Cranes, 2c) Black-necked Cranes.

197 To assess models transferability, we extracted the predictive value of the relative index of
198 occurrence (RIO) for testing data sets from the prediction maps using GME. We then constructed
199 resulting violin plots in R for these extracted RIOs to visualize their one-dimensional distribution.
200 This method allowed us to examine the degree of generalizability based on the local area with
201 samples to predict into undersampled areas that are otherwise unsampled in the model
202 development (=areas without training data). In addition, AUC is also commonly used to assess
203 model transferability in our study referring Randin et al. (2006).

204 **RESULTS**

205 **Model performance**

206 The results for AUC and TSS, two metrics commonly used to evaluate model accuracy, are
207 listed in Table 2. For the four SDMs technique, our results showed that the AUC values for
208 Random Forest were always highest (>0.625), ranking this model in first place, followed by
209 Maxent (>0.558), and then either CART or TreeNet (≥ 0.500). TSS showed us consistent results,
210 as was the case for AUC, and Random Forest performed the best (>0.250) followed by Maxent
211 (>0.137) for all three crane species, CART took the third place for Black-necked Cranes, and
212 TreeNet performed better than CART for White-naped Cranes. And the results showed there was
213 a trend that the value of these three metrics increased with an increase of nest site samples (33 to
214 75, Hooded Crane to Black-necked Crane, see Table. 2). Comparing the results of Random Forest
215 with ensemble models, we found their performance were close. Random Forest obtained better
216 models for Hooded Cranes and White-naped Cranes cases, the ensemble model performed better
217 for Black-necked Cranes.

218 **Put Table 2 here**

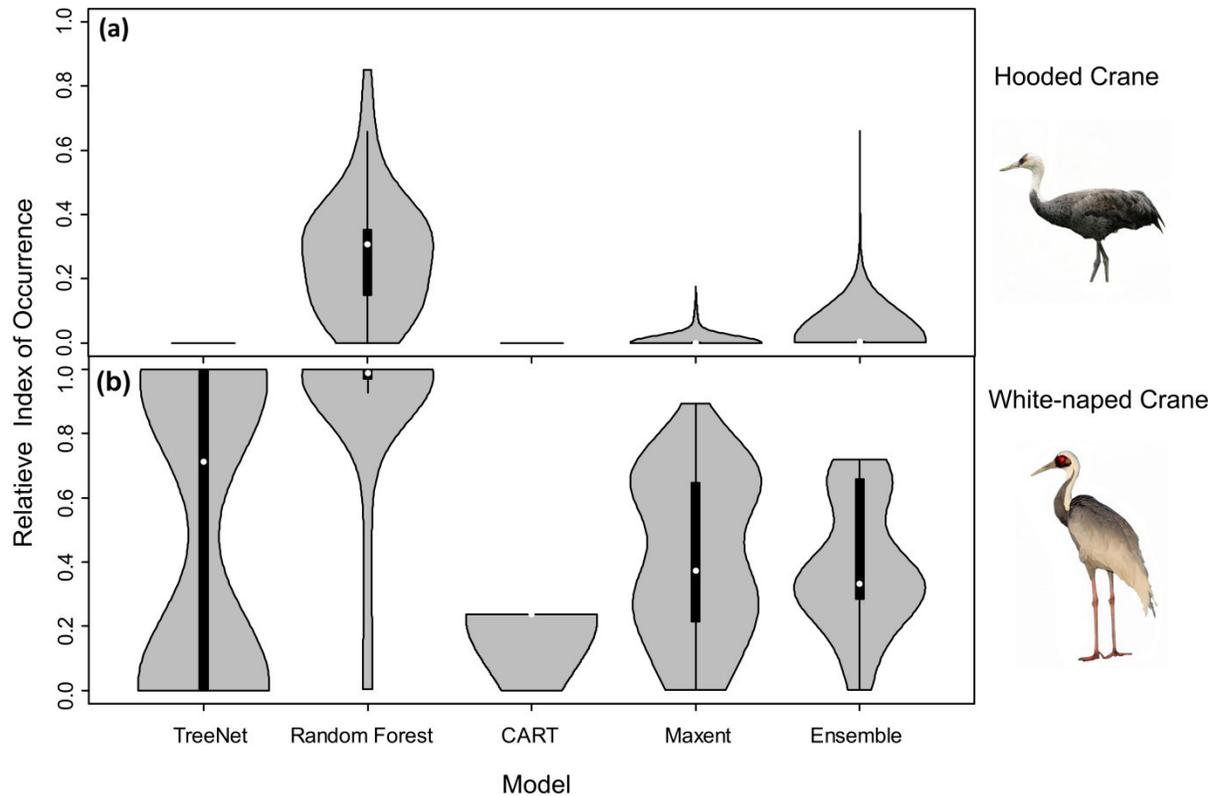
219 Table 2 AUC and TSS values for four machine learning models and their ensemble model with
220 three crane species based on literature testing data.

Accuracy metric (samples)	Species distribution model				
	TreeNet	Random	CART	Maxent	Ensemble
	Forest				
Hooded Crane (<i>Grus monacha</i> , n=33 sites)					
AUC	0.504	0.625	0.500	0.558	0.558
TSS	0.000	0.250	0.000	0.137	0.117
White-naped Crane (<i>Grus vipio</i> , n=40 sites)					
AUC	0.605	0.754	0.564	0.712	0.754
TSS	0.210	0.509	0.128	0.424	0.508
Black-necked Crane (<i>Grus nigricollis</i> , n=75 sites)					
AUC	0.528	0.830	0.672	0.805	0.843
TSS	0.055	0.660	0.345	0.611	0.686

221 Model generalization

222 Violin plots for RIOs with overlaid satellite tracking data (Fig. 3) showed that Random Forest
 223 for Hooded Cranes and White-naped Cranes performed better than the other three models. In the
 224 Hooded Crane models (Fig. 3a), the RIO for most satellite tracking data indicated that TreeNet,
 225 and CART predicted with a value around 0; Ensemble model demonstrated a slightly higher value
 226 than the other three models but was still much lower than Random Forest. Fig. 3b indicates the
 227 same situation than found in Fig. 3a: Random Forest still performed better than the other three
 228 models (median values in Random Forests were close to 1.00). TreeNet had a median RIO value
 229 of approximately 0.71, followed by Maxent (median was 0.37) and then ensemble and CART.
 230 While some tracking points had a low RIO value in TreeNet, the majority of RIO values for
 231 CART remained in the 0.20 range.

232 Put Fig. 3 here



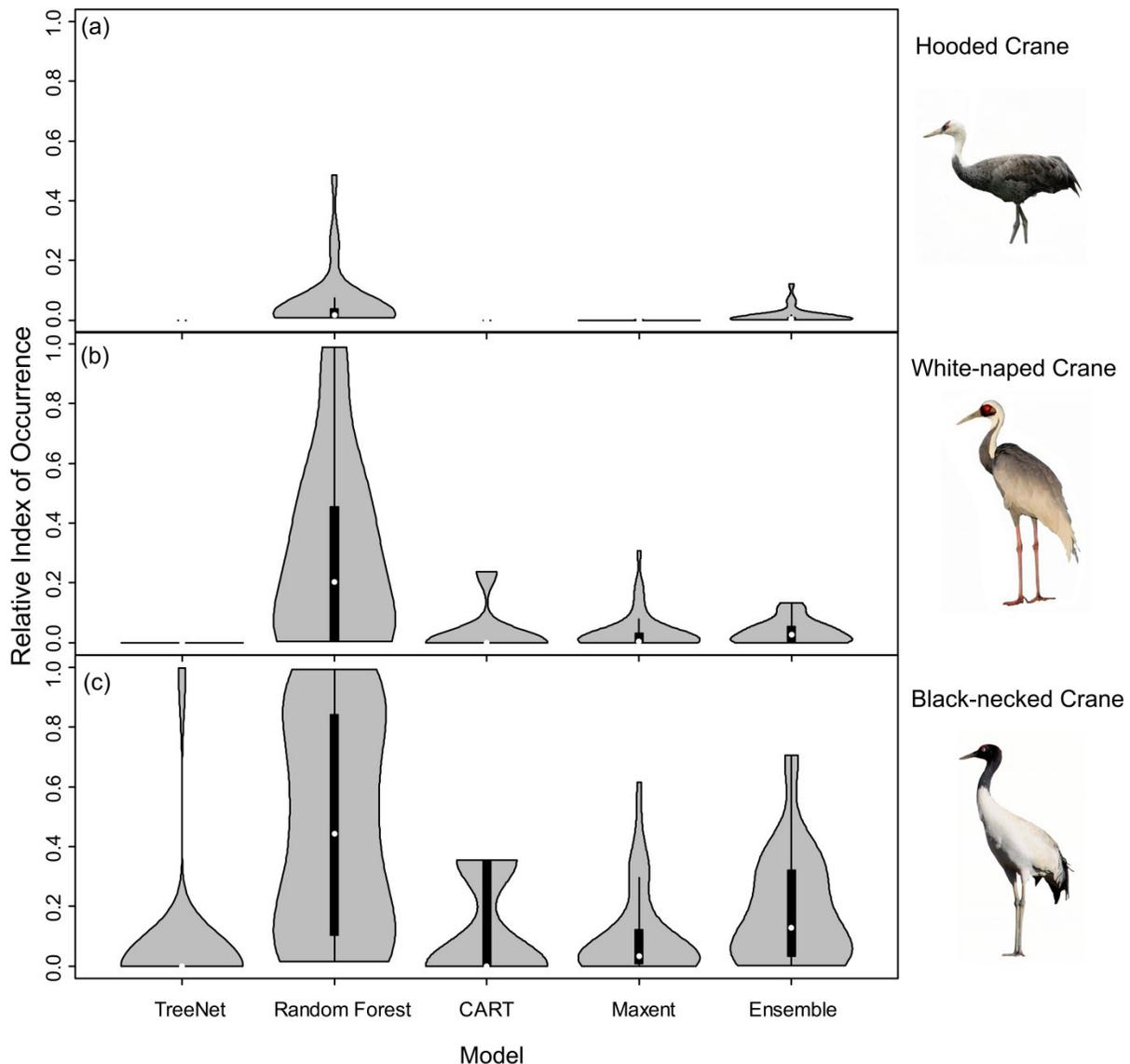
233 Figure 3 Violin plots of the Relative Index of Occurrence (RIO) for four SDMs and ensemble
 234 model for Hooded Cranes and White-naped Cranes based on satellite tracking data. 3a) violin
 235 plots of Hooded Cranes, 3b) violin plots of White-naped Cranes.

236 Violin plots of the RIOs values for the three cranes extracted for the literature data from the
 237 prediction maps (Fig. 4) demonstrated consistent trends (Fig. 3), indicating that Random Forest
 238 performed best across all models of the three species. In Fig. 4a, the RIO values for Random
 239 Forest ranged from 0 to 0.48, and most RIO values were below 0.1; the RIO values for the other
 240 three SDMs method were 0, the ensemble model performed a little bit better. As showed in Fig.
 241 4b, most RIO values for Random Forest were below 0.7, and the median value was
 242 approximately 0.20, followed by Maxent and then CART. The violin plots for Black-necked
 243 Cranes (Fig. 4c) indicated that TreeNet performed the worst, although there were some pixels that
 244 had high RIO values, followed by the ensemble model and then Maxent. The best performer was
 245 still Random Forest, and its RIOs were distributed evenly to a certain extent with a median value

246 of 0.44. The results of AUC, as mentioned in “Model performance” part (Table 2), showed
 247 consistent results with violin plots, Random Forest always get the highest value and has the best
 248 generalization.

249

Put figure 4 here

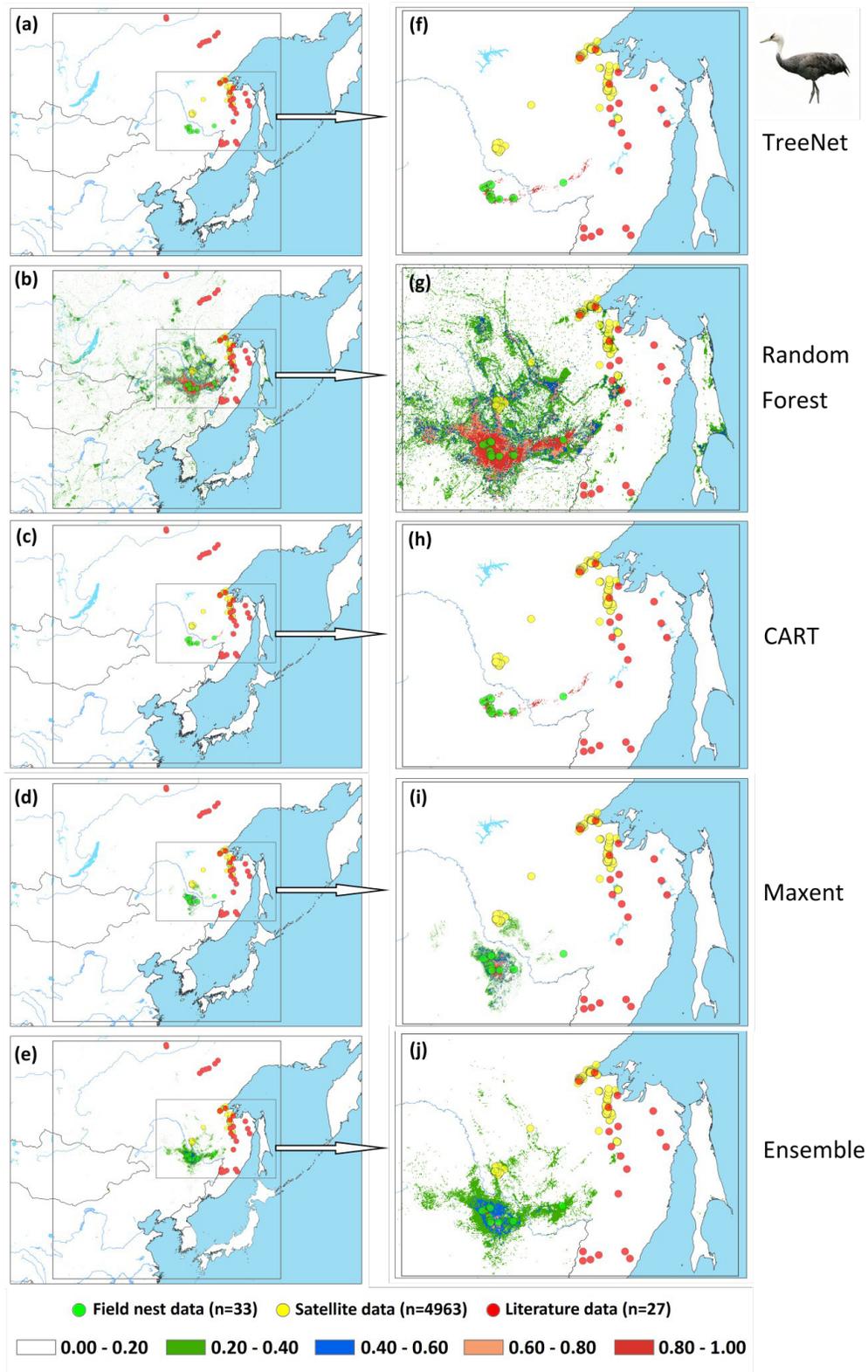


250 Figure 4 Violin plots of Relative Index of Occurrence (RIO) values for four SDMs and ensemble
 251 model for three cranes based on calibration data from Threatened Birds of Asia. 4a) Violin plots
 252 for Hooded Cranes, 4b) violin plots for White-naped Cranes, 4c) violin plots for Black-necked
 253 Cranes.

254 **Spatial assessment using a testing data overlay prediction map**

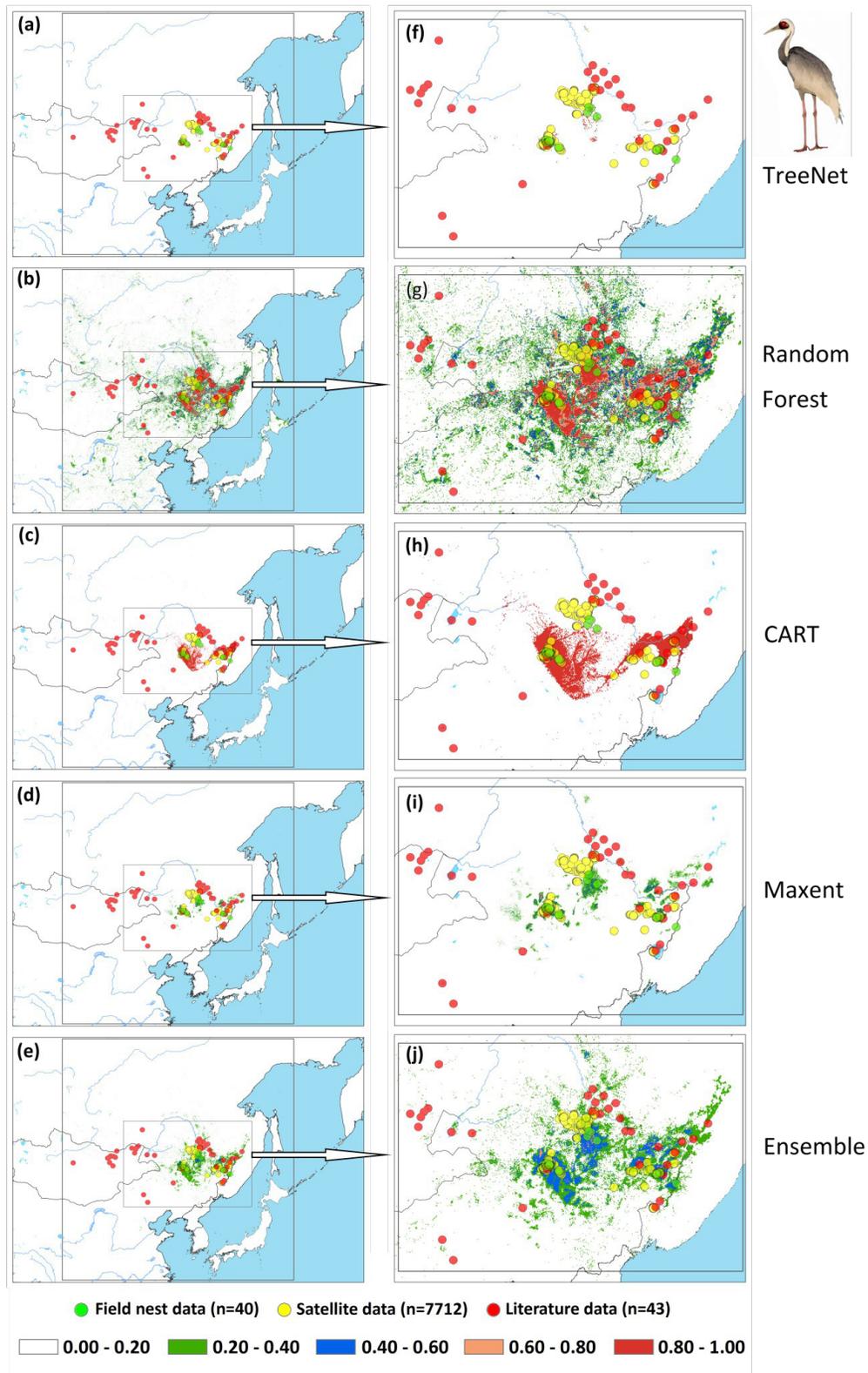
255 An assessment of niche prediction beyond the local area where samples were located
256 represents a real test of the generalizability of the model predictions in undersampled areas. This
257 approach was used to evaluate whether testing data (satellite tracking data and literature data)
258 locations matched predictions of the potential distribution area, as a spatial assessment of model
259 performance. It's a spatial and visual method to show the transferability of SDMs from sampled
260 to unsampled areas. From the results (Fig.s 5, 6 and 7. Digital version for each subgraph could be
261 available request), we found that Random Forest demonstrated the strongest performance to
262 handle generality (transferability), and a high fraction of testing data locations were predicted in
263 the distribution areas of the three cranes (Fig.s 5b, 5g, 6b, 6g, 7b, 7g). The order of the generality
264 of the remaining four models was: ensemble model followed by Maxent, CART and then
265 TreeNet. Note, however, that the capacities of these models to predict well in undersampled areas
266 were weaker than Random Forest, it holds particularly for areas that were further away from the
267 sample areas (Fig.s 5, 6 and 7). In addition, we found that the generality increased with sample
268 size (33 to 75, Hooded Crane to Black-necked Crane, see Fig.s 5, 6 and 7). This means, as
269 expected and known, that a higher sample size makes models more robust and better to
270 generalize from.

271 **Put Fig. 5 Here**



272 Figure 5 Prediction maps for Hooded Cranes and zoomed-in maps showing the four models (TreeNet,
 273 Random Forest, CART and Maxent) and ensemble model in detail. 5a-5e) prediction map for Hooded

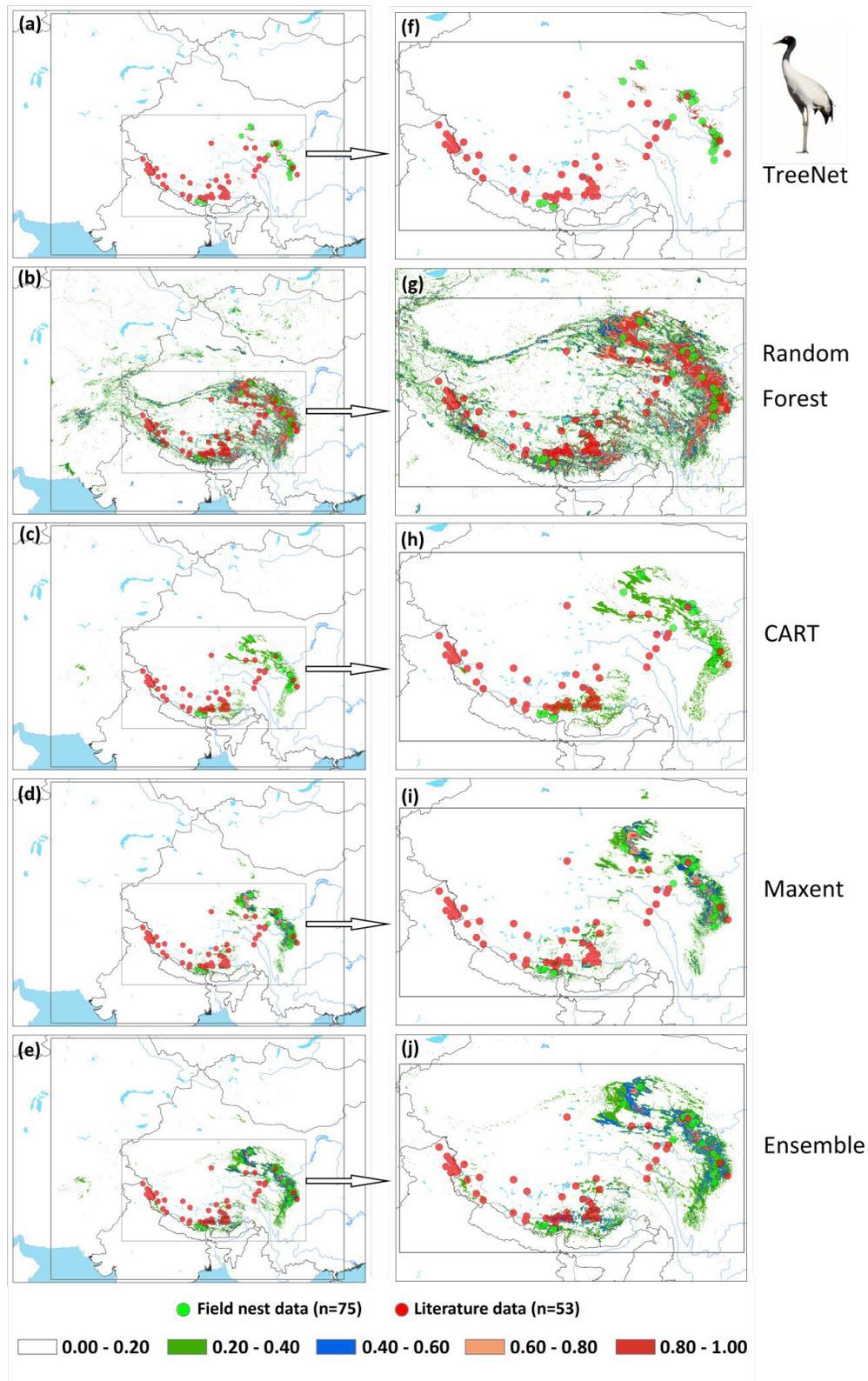
274 Cranes, 5f-5j) zoomed-in map for Hooded Cranes.



275 Figure 6 Prediction maps for White-naped Cranes and zoomed-in maps showing the four models (TreeNet,

276 Random Forest, CART and Maxent) and ensemble model in detail. 6a-6e) prediction map for White-naped
277 Cranes, 6f-6j) zoomed-in map for White-naped Cranes.

278 **Put Fig. 6 Here**



279 Figure 7 Prediction maps for Black-necked Cranes and zoomed-in maps showing the four models
 280 (TreeNet, Random Forest, CART and Maxent) and ensemble model in detail. 7a-7e) prediction map for

281 Black-necked Cranes, 7f-7j) zoomed-in map for Black-necked Cranes.

282 **DISCUSSION**

283 **Model generality (transferability)**

284 Estimating species distributions in undersampled areas is a fundamental problem in ecology,
285 biogeography, biodiversity conservation and natural resource management (Drew et al., 2011).
286 That is specifically true for rare and difficult to be detected species and which are usually high on
287 the conservation priority. The use of SDMs and with machine learning has become the method
288 for deriving such estimates (Guisan & Thuiller, 2005; Drew et al., 2011; Guisan et al., 2013) and
289 could contribute to detect new and to confirm populations of rare species. However, the
290 application of a few samples to project a distribution area widely beyond the sample range is a
291 greater challenge and has rarely been attempted in the literature until recently. And only now
292 have conservationists realized its substantial value for pro-active decision making in conservation
293 management (see work by Ohse et al., 2010; Drew et al., 2011; Kandel et al., 2015 etc.). Our
294 results based on AUC, violin plots for RIOs and spatial assessment of testing data (satellite
295 tracking data and literature data) all suggest there are difference in the generalization
296 performance of different modeling techniques (TreeNet, Random Forest , CART and Maxent).

297 Moreover, among the acknowledged four rather powerful and commonly used machine-
298 learning techniques, Random Forest (bagging) in SPM usually had the best performance in each
299 case. Our results are in agreement with those of Prasad et al. (2006), Cutler et al. (2007) and
300 Syphard and Franklin (2009) indicating a superiority of Random Forest in such applications.
301 However, initially it appears to run counter to the conclusions of recent paper (Heikkinen et al.,
302 2012) with the poor transferability of Random Forest. But we propose this is due to the fact that
303 many Random Forest implementations exist (see the 100 classifier paper Fernández-Delgado et
304 al., 2014).

305 Here we applied Random Forest in SPM which has been optimized under one of the
306 algorithm's original co-authors, while Heikkinen et al. (2012) run a basic Random Forest with
307 BIOMOD framework in the R software and which remains widely un-tuned and largely behind
308 the potential. The differences are known to be rather big (see Herrick 2013 for a comparison).

309 Furthermore, Maxent, a widely used SDM-method consequently greatly enjoyed by many
310 modelers (Phillips et al., 2006; Peterson et al. 2007; Phillips and Dudík 2008; Li et al., 2015,
311 etc.), didn't perform so good in regards to transferability in this study. This contrasts to those of
312 Elith et al. (2006) and Heikkinen et al. (2012), where Maxent and GBM perform well. We infer
313 this may be caused by sample size used as training data and due to the actual algorithms used.
314 When the sample size increased (33 to 75), the AUC and TSS value of all models rose (Table 2).
315 This indicates that higher sample sizes make models more robust and performing better. Sample
316 sizes of 33 presence points still favor by Random Forest.

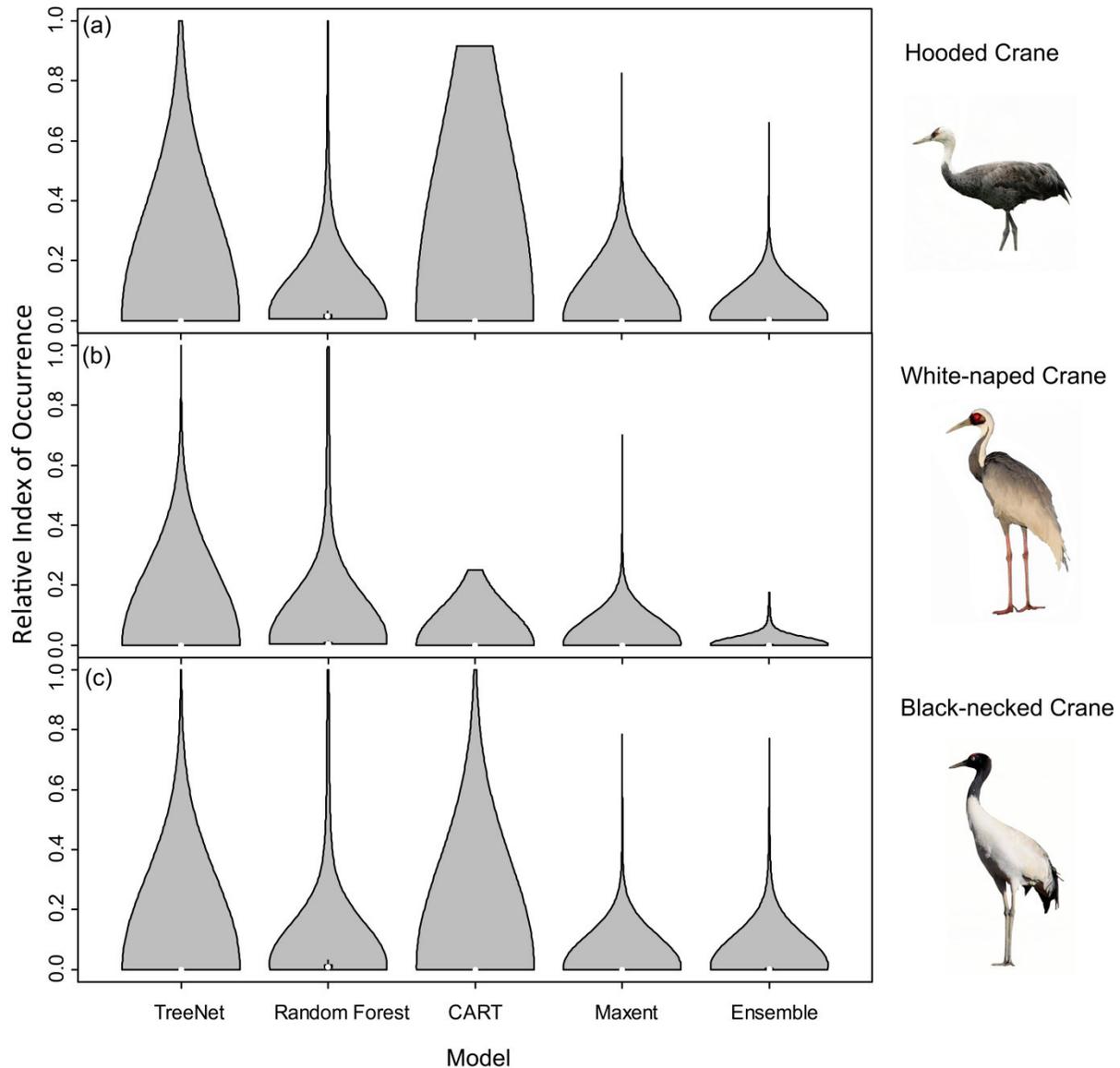
317 In Random Forest, random samples from rows and predictors are used to build hundreds of
318 trees. Each individual tree is constructed from a bootstrap sample and split at each node by the
319 best predictor from a very small, randomly chosen subset of the predictor variable pool (Herrick,
320 2013). These trees comprising the forest are each grown to maximal depth, and predictions are
321 made by averaged trees through 'voting' (Breiman et al., 2006). This algorithm avoids overfitting
322 by controlling the number of predictors randomly used at each split, using means of out-of-bag
323 (OOB) samples to calculate an unbiased error rate. And also, Random Forest in SPM utilizes
324 additional specific fine-tuning for best performance.

325 **RIOs of random points**

326 In order to explore whether Random Forest created higher RIOs for prediction maps in each grid,
327 which would result into higher RIOs of testing data, we generated 3,000 random points for
328 Hooded Cranes and White-naped Cranes, 5000 random points for Black-necked Cranes in their

329 related projected study areas. We made violin plots for RIOs of random points (Fig. 8), and we
330 found that more RIO values of random points for Maxent, Random Forest and ensemble models
331 were close to the lower value, and then followed by TreeNet. The distribution shapes of Random
332 Forest, Maxent and ensemble model are more similar to the real distribution of species in the real
333 world. The RIOs of White-naped Crane extracted from the CART model distributed in the range
334 of the low value. That means there were no points located in the high RIO areas of cranes, and
335 which is unrealistic. Consequently, we argued that Random Forest did not create higher RIOs for
336 prediction maps in each grid in our study.

337 **Put Fig. 8 here**



338 Figure 8 Violin plots of Relative Index of Occurrence (RIO) values for four SDMs and ensemble
 339 model for three cranes based on calibration data from Threatened Birds of Asia. 4a) Violin plots
 340 for Hooded Cranes, 4b) violin plots for White-naped Cranes, 4c) violin plots for Black-necked
 341 Cranes.

342 Models with small sample sizes

343 Conservation biologists are often interested in rare species and seek to improve their
 344 conservation. These species typically have limited number of available occurrence records, which

345 poses challenges for the creation of accurate species distribution models when compared with
346 models developed with greater numbers of occurrences (Stockwell & Peterson, 2002; McPherson
347 et al., 2004; Hernandez et al., 2006). In this study, we used three crane species as case studies,
348 and their occurrence records (nests) totaled 33, 40, and 75, respectively (considering the small
349 numbers of samples and given that a low fraction of the area was sampled in the large projected
350 area). In our models, we found that model fit (AUC and TSS, see Table 2) of Random Forest that
351 had the highest index, while Maxent usually ranked second. In addition, we found that models
352 with few presence samples can also generate accurate species predictive distributions (Fig. 3 to 7)
353 with the Random Forest method. Of course, models constructed with few samples underlie the
354 threat of being biased more because few samples usually had not enough information including
355 all distribution gradients conditions of a species, especially for places far away from the location
356 of training presence points. However, the potential distribution area predicted by SDMs could
357 become the place where scholars could look for the birds (additional fieldwork sampling). And
358 also, these places could be used as diffusion or reintroduction areas! It's valuable and new
359 information either way.

360 **Evaluation methods**

361 In this study, we applied two widely-used assessment methods (AUC and TSS) in SDMs (Table
362 2). For an evaluation of these three values we used the approach recommended by Fielding &
363 Bell (1997), and Allouche et al. (2006), we found our model usually didn't obtain perfect
364 performance, and some of them were 'fair' in their performance. However, for macro-ecology
365 this is more than reasonable and ranks rather high. It's good conservation progress! We identified
366 Random Forest as always the highest performing. These results are consistent with the results of
367 violin plots of the Relative Index of Occurrence (RIO) using tracking as well as literature data
368 (Figs 3 and 4), and well as matching the spatial assessment results (Figs 5-7). And we

369 recommend when modelers assess model performance they should not only depend alone on
370 some metric (such as AUC and TSS), but also should base their assessments on the combined use
371 of visualization and expert knowledge. That means modelers should also assess how the species
372 distribution map actually looks and how it links with real data (see Huettmann & Gottschalk
373 2011). Spatial assessment metrics from alternative data should matter the most. Expert experience
374 and ecological common knowledge of the species of interest could sometimes also be highly
375 effective (Drew & Perera, 2011), albeit nonstandard, evaluation methods (see Kandel et al., 2015
376 for an example). Additionally, one alternative method for rapid assessment we find is to use a
377 reliable SDM, and thus Random Forest would be a good choice in the future given our consistent
378 results (Fig.s 3 to 7, Tables 3 to 5) in this study, which involved three species, a vast landscape to
379 conserve, and only limited data. Our work certainly helps to inform conservation decisions for
380 cranes in Northeast Asia.

381 **Limitations and future work**

382 Our study is not without limitations: 1) so far, only three species of cranes are used as a test case
383 in our study. That's because nest data for rare species in remote areas are usually sparse; 2) all our
384 species study areas are rather vast and confined to East-Asia. For future work, we would apply
385 Random Forest in more species and in more geographical conditions with differently distributed
386 features for a first rapid assessment and baseline to be mandatory for better conservation e.g, by
387 governments, IUCN and any impact and court decision. Then we would apply our prediction
388 results in specifically targeted fieldwork sampling campaigns and assess the model accuracy with
389 field survey results (ground-truthing) and with new satellite tracking and drone data, for instance.
390 This is to be fed directly into the conservation management process.

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398 **REFERENCES**

- 399 Allouche OA, Tsoar, Kadmon R. 2006. Assessing the accuracy of species distribution models:
400 prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43(6):1223-
401 1232.
- 402 Araújo MB, New M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology &*
403 *Evolution* 22(1):42-47.
- 404 Araújo MB, Whittaker R, Ladle R, Erhard M. 2005. Reducing uncertainty in projections of
405 extinction risk from climate change. *Global Ecology & Biogeography* 14(6):529-538.
- 406 Ashtonw C, Perera AH. 2010. Expert Knowledge as a Basis for Landscape Ecological Predictive
407 Models. *Predictive Species & Habitat Modeling in Landscape Ecology*:229-248.
- 408 Beyer H. 2013. Hawth's Analysis Tools for ArcGIS version 3.27 (software). in.
- 409 Booms TL, Huettmann F, Schempf PF. 2010. Gyrfalcon nest distribution in Alaska based on a
410 predictive GIS model. *Polar biology* 33(3):347-358.
- 411 Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK. 2002. Evaluating resource selection
412 functions. *Ecological Modelling* 157(2-3):281-300.
- 413 Braunisch V, Coppes J, Arlettaz R, Suchant R, Schmid H, Bollmann K. 2013. Selecting from
414 correlated climate variables: a major source of uncertainty for predicting species distributions
415 under climate change. *Ecography* 36(9):971-983.
- 416 Breiman L. 2001. Random forests. *Machine learning* 45(1):5-32.
- 417 Breiman L., Friedman J, Stone CJ, Olshen RA. 1984. *Classification and regression trees*. CRC
418 press.
- 419 Bucklin DN, Basille M, Benscoter AM, Brandt LA, Mazzotti FJ, Romanach SS, Speroterra C,
420 Watling JI. 2015. Comparing species distribution models constructed with different subsets of
421 environmental predictors. *Diversity and Distributions* 21(1):23-35.

- 422 Cohen J. 1960. A Coefficient of Agreement for Nominal Scales. *Educational and Psychological*
423 *Measurement* 20(1):37-46.
- 424 Collar NJ, Crosby R, Crosby M. 2001. *Threatened birds of Asia: the BirdLife International red*
425 *data book. Volume 1.* BirdLife International Cambridge, UK.
- 426 Cushman SA, Huettmann F. 2010. *Spatial Complexity, Informatics, and Wildlife Conservation.*
427 Springer, Springer Tokyo Berlin Heidelberg New York.
- 428 Cutler DR, Edwards Jr TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random
429 forests for classification in ecology. *Ecology* 88(11):2783-2792.
- 430 Drew CA, Perera AH. 2011. Expert knowledge as a basis for landscape ecological predictive
431 models. Pages 229-248 in *Predictive Species and Habitat Modeling in Landscape Ecology.*
432 Springer.
- 433 Drew CA, Wiersma Y, Huettmann F. 2011. *Predictive species and habitat modeling in landscape*
434 *ecology.* Springer.
- 435 Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F,
436 Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura
437 M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R,
438 Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE. 2006. Novel methods
439 improve prediction of species' distributions from occurrence data. *Ecography* 29(2):129-151.
- 440 Eskildsen, A., P. C. Roux, R. K. Heikkinen, T. T. Høye, W. D. Kissling, J. Pöyry, M. S. Wisz, and
441 M. Luoto. 2013. Testing species distribution models across space and time: high latitude
442 butterflies and recent warming. *Global ecology and biogeography* 22(12):1293-1303.
- 443 Estes L, Bradley B, Beukes H, Hole D, Lau D, Oppenheimer M, Schulze R, Tadross M, Turner
444 W. 2013. Comparing mechanistic and empirical model projections of crop suitability and
445 productivity: implications for ecological forecasting. *Global ecology and biogeography*
446 22(8):1007-1018.

- 447 Fernández-Delgado M, Cernadas E, Barro S, Amorim D. 2014. Do we need hundreds of
448 classifiers to solve real world classification problems? *The Journal of Machine Learning*
449 *Research* 15(1):3133-3181.
- 450 Ferrier S, Watson G, Pearce J, Drielsma M. 2002. Extended statistical approaches to modelling
451 spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling.
452 *Biodiversity & Conservation* 11(12):2275-2307.
- 453 Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in
454 conservation presence/absence models. *Environmental conservation* 24(1):38-49.
- 455 Fielding AH, Haworth PF. 1995. Testing the Generality of Bird-Habitat Models. *Conservation*
456 *biology* 9(6):1466-1481.
- 457 Ferrier S, Watson G, Pearce J, Drielsma M. 2002. Extended statistical approaches to modelling
458 spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling.
459 *Biodiversity & Conservation* 11(12):2275-2307.
- 460 Friedman JH. 2002. Stochastic gradient boosting. *Computational Statistics & Data Analysis*
461 38(4):367-378.
- 462 Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT. 2004. New developments in museum-
463 based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*
464 19(9):497-503.
- 465 Guillera-Aroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kujala H, Lentini PE, McCarthy
466 MA, Tingley R, Wintle BA. 2015. Is my species distribution model fit for purpose? Matching
467 data and models to applications. *Global ecology and biogeography* 24(3):276-292.
- 468 Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat
469 models. *Ecology letters* 8(9):993-1009.
- 470 Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan
471 TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C. 2013. Predicting species

- 472 distributions for conservation decisions. *Ecology letters* 16(12):1424-1435.
- 473 Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological*
474 *Modelling* 135(2):147-186.
- 475 Gwena LL, Robin E, Erika F, Guisan A. 2010. Prospective sampling based on model ensembles
476 improves the detection of rare species. *Ecography* 33(6):1015-1027.
- 477 Hanley JA, McNeil BJ. 1982. The meaning and use of the area under a receiver operating
478 characteristic (ROC) curve. *Radiology* 143(1):29-36.
- 479 Hanley JA, McNeil BJ. 1983. A method of comparing the areas under receiver operating
480 characteristic curves derived from the same cases. *Radiology* 148(3):839-843.
- 481 Hardy SM, Lindgren M., Konakanchi H, Huettmann F. 2011. Predicting the distribution and
482 ecological niche of unexploited snow crab (*Chionoecetes opilio*) populations in Alaskan
483 waters: a first open-access ensemble model. *Integrative and comparative biology* 51(4):608-
484 622.
- 485 Hegel TM, SA Cushman, J Evans, Huettmann F. 2010. Current State of the Art for Statistical
486 Modelling of Species Distributions. *Spatial Complexity, Informatics, and Wildlife*
487 *Conservation*:273-311.
- 488 Heikkinen RK, Marmion M, Luoto M. 2012. Does the interpolation accuracy of species
489 distribution models come at the expense of transferability? *Ecography* 35(3):276-288.
- 490 Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species
491 characteristics on performance of different species distribution modeling methods. *Ecography*
492 29(5):773-785.
- 493 Herrick K. 2013. Predictive Modeling of Avian Influenza in Wild Birds. *Veterinary Research*.
- 494 Hijmans RJ, Graham CH. 2006. The ability of climate envelope models to predict the effect of
495 climate change on species distributions. *Global Change Biology* 12(12):2272-2281.
- 496 Huettmann F, Gottschalk T. 2011. Simplicity, Model Fit, Complexity and Uncertainty in Spatial

- 497 Prediction Models Applied Over Time: We Are Quite Sure, Aren't We? Pages 189-208 in
498 Predictive Species and Habitat Modeling in Landscape Ecology. Springer.
- 499 Humphries GRW, Huettmann F. 2014. Putting models to a good use: a rapid assessment of Arctic
500 seabird biodiversity indicates potential conflicts with shipping lanes and human activity.
501 Diversity and Distributions 20(4):478-490.
- 502 Jiguet F, Barbet-Massin M, Chevallier D. 2011. Predictive distribution models applied to satellite
503 tracks: modelling the western African winter range of European migrant Black Storks *Ciconia*
504 *nigra*. Journal of Ornithology 152(1):111-118.
- 505 Kandel K, Huettmann F, Suwal MK, Regmi GR, Nijman V, Nekaris K, Lama ST, Thapa A,
506 Sharma HP, Subedi TR. 2015. Rapid multi-nation distribution assessment of a charismatic
507 conservation species using open access ensemble model GIS predictions: Red panda (*Ailurus*
508 *fulgens*) in the Hindu-Kush Himalaya region. Biological Conservation 181:150-161.
- 509 Keith DA, Elith J, Simpson CC. 2014. Predicting distribution changes of a mire ecosystem under
510 future climates. Diversity and Distributions 20(4):440-454.
- 511 Kessler A, Batbayar N, Natsagdorj T, Batsuur D, Smith A. 2013. Satellite telemetry reveals
512 long-distance migration in the Asian great bustard *Otis tarda dybowskii*. Journal of Avian
513 Biology 44(4):311-320.
- 514 Kleyer M. 2002. Validation of plant functional types across two contrasting landscapes. Journal
515 of Vegetation Science 13(2):167-178.
- 516 Lei, Z., L. Shirong, S. Pengsen, and WangTongli. 2011. Comparative evaluation of multiple
517 models of the effects of climate change on the potential distribution of *Pinus massoniana*.
518 Chinese Journal of Plant Ecology 35(11):1091-1105.
- 519 Li, R., M. Xu, M. H. G. Wong, S. Qiu, X. Li, D. Ehrenfeld, and D. Li. 2015. Climate change
520 threatens giant panda protection in the 21st century. Biological Conservation 182:93-101.
- 521 Maggini R, Lehmann A, Zbinden N, Zimmermann NE, Bolliger J, Schröder B, Foppen R,

- 522 Schmid H, Beniston M, Jenni L. 2014. Assessing species vulnerability to climate and land use
523 change: the case of the Swiss breeding birds. *Diversity and Distributions* 20(6):708-719.
- 524 Manel S, Williams HC, Ormerod SJ. 2001. Evaluating presence–absence models in ecology: the
525 need to account for prevalence. *Journal of Applied Ecology* 38(5):921-931.
- 526 McPherson J, Jetz W, Rogers DJ. 2004. The effects of species' range sizes on the accuracy of
527 distribution models: ecological phenomenon or statistical artefact? *Journal of Applied*
528 *Ecology* 41(5):811-823.
- 529 Mi C, Huettmann. F, Guo Y. 2016. Climate envelope predictions indicate an enlarged suitable
530 wintering distribution for Great Bustards (*Otis tarda dybowskii*) in China for the 21st century.
531 *PeerJ* 4:e1630.
- 532 Mingchang C, Guangsheng Z, Ensheng W. 2005. Application and comparison of generalized
533 models and classification and regression tree in simulating trees species distribution. *ACTA*
534 *ECOLOGICA SINICA* 25(8):2031-2040.
- 535 Navarro Cerrillo R, Hernández Bermejo J, Hernández Clemente R. 2011. Evaluating models
536 to assess the distribution of *Buxus balearica* in southern Spain. *Applied Vegetation Science*
537 14(2):256-267.
- 538 Ohse B, Huettmann F, Ickert-Bond SM, Juday GP. 2009. Modeling the distribution of white
539 spruce (*Picea glauca*) for Alaska with high accuracy: an open access role-model for predicting
540 tree species in last remaining wilderness areas. *Polar biology* 32(12):1717-1729.
- 541 Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. 2007. Predicting species distributions
542 from small numbers of occurrence records: a test case using cryptic geckos in Madagascar.
543 *Journal of Biogeography* 34(1):102-117.
- 544 Peterson AT., Monica P, Muir E. 2007. Transferability and model evaluation in ecological niche
545 modeling: a comparison of GARP and Maxent. *Ecography* 30(4):550–560.
- 546 Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic

- 547 distributions. *Ecological Modelling* 190(3):231-259.
- 548 Phillips SJ, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a
549 comprehensive evaluation. *Ecography* 31(2):161-175.
- 550 Phillips SJ, Dudík M, Schapire RE. A maximum entropy approach to species distribution
551 modeling. ACM, 2004.
- 552 Prasad AM, Iverson LR, Liaw A. 2006. Newer Classification and Regression Tree Techniques:
553 Bagging and Random Forests for Ecological Prediction. *Ecosystems* 9(2):181-199.
- 554 Randin CF, Dirnböck T, Dullinger S, Zimmermann NE, Zappa M, Guisan A. 2006. Are niche-
555 based species distribution models transferable in space? *Journal of Biogeography*
556 33(10):1689-1703.
- 557 Romo H, García-Barros E, Márquez AL, Moreno JC, Real R. 2014. Effects of climate change on
558 the distribution of ecologically interacting species: butterflies and their main food plants in
559 Spain. *Ecography* 37(11):1063-1072.
- 560 Stockwell DR, Peterson AT. 2002. Effects of sample size on accuracy of species distribution
561 models. *Ecological Modelling* 148(1):1-13.
- 562 Stokes KL, Broderick AC, Canbolat AF, Candan O, Fuller WJ, Glen F, Levy Y, Rees AF, Rilov G,
563 Snape RT, Stott I, Tchernov D, Godley BJ. 2015. Migratory corridors and foraging hotspots:
564 critical habitats identified for Mediterranean green turtles. *Diversity and Distributions* 21(6):
565 665-674.
- 566 Swets JA 1988. Measuring the accuracy of diagnostic systems. *Science* 240(4857):1285-1293.
- 567 Syphard DA, Franklin J. 2009. Differences in spatial predictions among species distribution
568 modeling methods vary with species traits and environmental predictors. *Ecography*
569 32(6):907-918.
- 570 Thomas JA, Bovee KD. 1993. Application and testing of a procedure to evaluate transferability of
571 habitat suitability criteria. *Regulated rivers* 8:285-285.

- 572 Thuiller W. 2003. BIOMOD—optimizing predictions of species distributions and projecting
573 potential future shifts under global change. *Global Change Biology* 9(10):1353-1362.
- 574 Zhai T, Li X. 2012. Climate change induced potential range shift of the crested ibis based on
575 ensemble models. *ACTA ECOLOGICA SINICA* 32(8):2361-2370 (in Chinese).
- 576 Williams JN, Seo C, Thorne J, Nelson JK, Erwin S, O'Brien JM, Schwartz MW. 2009. Using
577 species distribution models to predict new occurrences for rare plants. *Diversity and*
578 *Distributions* 15(4):565-576.
- 579 Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A. 2008. Effects of sample size on
580 the performance of species distribution models. *Diversity and Distributions* 14(5):763-773.
- 581 Yen P, Huettmann F, Cooke F. 2004. A large-scale model for the at-sea distribution and
582 abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season in
583 coastal British Columbia, Canada. *Ecological Modelling* 171(4):395-413.
- 584 Young N, Carter L, Evangelista P. 2011. A MaxEnt Model v3.3.3e Tutorial.
- 585 Zhang M, Zhou Z, Chen W, Cannon CH, Raes N, Slik JWF. 2014. Major declines of woody plant
586 species ranges under climate change in Yunnan, China. *Diversity and Distributions* 20(4):405-
587 415.