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# Towards combining occurrence and abundance distribution models of Great Bustard for conservation: A global research template from Bohai Bay?

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Species distribution models (SDMs) have become important and essential tools in conservation and management. However, SDMs built with count data, commonly referred to as species abundance models (SAMs), are still less used so far. SDMs are increasingly used now in conservation decisions, whereas SAMs are still not widely employed. Species occurrence and abundance do not frequently display similar patterns, often they are not even well correlated. This leads to an insufficient or misleading conservation. How to combine information from SDMs and SAMs all together for unified conservation remains a challenge. In this study, we put forward for the first time a priority protection index (PI). The PI combines the prediction results of occurrence and abundance models. We used the best-available presence and count records for an endangered farmland species, Great Bustard (*Otis tarda dybowskii*) in Bohai Bay, China, as a case study. We then applied the advanced Random Forest algorithm (Salford Systems Ltd. implementation), a powerful machine learning method, with eleven predictor variables to forecast the spatial occurrence as well as the abundance distribution. The results show that the occurrence model had a decent performance (ROC: 0.77) and the abundance model had a RMSE 26.54. It is of note that environmental variables influenced bustard occurrence and abundance differently. We found that occurrence and abundance models display different spatial distribution patterns. Still, combining occurrence and abundance indices to produce a priority protection index (PI) used for conservation could guide the protection of the areas with high occurrence and high abundance (e.g. in Strategic Conservation Planning). Due to the widespread use of SDMs and the rel. easy subsequent employment of SAMs these findings have a wide relevance and applicability, worldwide. We promote and strongly encourage to further test, apply and update the priority protection index (PI) elsewhere in order to explore the generality of these findings and methods readily

available now for researchers.

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15

16 **ABSTRACT**

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18 and management. However, SDMs built with count data, commonly referred to as species  
19 abundance models (SAMs), are still less used so far. SDMs are increasingly used now in  
20 conservation decisions, whereas SAMs are still not widely employed. Species occurrence and  
21 abundance do not frequently display similar patterns, often they are not even well correlated. This  
22 leads to an insufficient or misleading conservation. How to combine information from SDMs and  
23 SAMs all together for unified conservation remains a challenge. In this study, we put forward for  
24 the first time a priority protection index (PI). The PI combines the prediction results of occurrence  
25 and abundance models. We used the best-available presence and count records for an endangered  
26 farmland species, Great Bustard (*Otis tarda dybowskii*) in Bohai Bay, China, as a case study. We  
27 then applied the advanced Random Forest algorithm (Salford Systems Ltd. implementation), a  
28 powerful machine learning method, with eleven predictor variables to forecast the spatial  
29 occurrence as well as the abundance distribution. The results show that the occurrence model had  
30 a decent performance (ROC: 0.77) and the abundance model had a RMSE 26.54. It is of note that  
31 environmental variables influenced bustard occurrence and abundance differently. We found that  
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33 occurrence and abundance indices to produce a priority protection index (PI) used for conservation  
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35 Conservation Planning). Due to the widespread use of SDMs and the rel. easy subsequent

36 employment of SAMs these findings have a wide relevance and applicability, worldwide. We  
37 promote and strongly encourage to further test, apply and update the priority protection index (PI)  
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41 **Keywords:** conservation decision, occurrence model, abundance model, Great Bustard (*Otis tarda*  
42 *dybowskii*), machine learning method, Random Forest

43

## 44 INTRODUCTION

45 The knowledge of species occurrence and abundance distribution makes for a fundamental  
46 information for conservation biology (VanDerWal et al., 2009; Drew et al., 2011; Primack, 2012;  
47 Johnston et al., 2015). Understanding how environmental factors are related to species occurrence  
48 and abundance distribution explicit in time and space represent a priority in current biodiversity  
49 conservation (Drew et al., 2011; Martín et al., 2012).

50 Species distribution models (SDMs) are empirical ecological models that relate species  
51 observations to environmental predictors (Guisan & Zimmermann, 2000); usually that is done with  
52 machine learning algorithms (Drew et al., 2011, see Mi et al., 2017 for an application). They have  
53 become important and essential tools in ecology, biogeography, climate change research,  
54 conservation and management based on their spatial occurrence prediction (Peterson et al., 2002;  
55 Guisan & Thuiller 2005; Elith et al., 2006; Araújo & New 2007; Mi et al., 2016). SDMs built with  
56 count data are called species abundance models (SAMs) (Elith & Leathwick 2009; Barker et al.,  
57 2014; see Yen et al 2004 for an application). SAMs are still less commonly used yet, despite their  
58 greater information for conservation and management. But increasing attention has been paid to  
59 these problems in recent years (e.g. Yen et al., 2004; Martín et al., 2012; Howard et al., 2015;  
60 Ashcroft et al., 2017; Fox et al., 2017).

61 In the past, spatial conservation decisions and plans are usually just based on SDMs (e.g. Suárez-  
62 Seoane et al., 2008; Gray et al., 2009; Adams et al., 2016; Mi et al., 2016). However, despite  
63 statements by Newton (2008), many scholars found species occurrence and abundance distribution

64 not to display similar patterns (Yen et al., 2004; Karlson et al., 2011; Yin & He 2014; Johnston et  
65 al., 2015). Therefore, conservation decisions only based on SDMs predictions are insufficient and  
66 may even be misleading, so do SAMs. In the future, one time-critical challenge and associated  
67 progress will be centered how to combine the useful information that SDMs and SAMs each offer  
68 for conservation.

69 In this study we chose the endangered Great bustard (*Otis tarda dybowskii*) wintering in  
70 Cangzhou at the North China Plain near Bohai bay as a case study. This area is one of the most  
71 important wintering grounds for this species (about 300 individuals, c.13.6~20.0 % of China's  
72 total wintering population (Goroshko 2010; Meng 2010). Using the Great Bustard as a case study  
73 would contribute to our conservation knowledge about habitat use of a threatened farmland species  
74 and for a better policy. By studying not only the spatial occurrence and the abundance patterns,  
75 but also combining these two model types together as a role model for predictive modeling and its  
76 inference would potentially have wider conservation implications. Our overall objective of this  
77 research was to (1) assess and develop models to predict accurately the patterns of bustard  
78 occurrence and abundance; (2) infer on environmental variables that influence occurrence and  
79 abundance of this species; (3) combine occurrence and abundance models as a new contribution  
80 to conservation decisions; and (4) investigate the overall relationship among predicted occurrence,  
81 predicted abundance and observed abundance. Well-tested and suited methods from this research  
82 could be useful for the conservation of Great Bustard, but also other rare species and biodiversity  
83 in general where SDMs and SAMs can be employed.

84



## 85 MATERIALS AND METHODS

### 86 Study area

87 This study was conducted at the wintering grounds of endangered Great Bustards in Cangzhou,  
88 southeast of the Heibei Province in the wider Bohai Bay (Fig. 1). It is located at 38°12'57" -  
89 38°36'51" latitude and at 116°50'48" - 117°24'03" longitude in the warm temperate, semi-humid  
90 monsoon climate zone, which features the slightly marine climatic characteristic of the Bohai Sea  
91 region. The topographical and climate condition varies little in the study area. The total study area  
92 is 2,191.4 km<sup>2</sup>, consisting of farmland (1,675.1 km<sup>2</sup>; 76.4%), residential area (330.5 km<sup>2</sup>, 15.1%),  
93 open water (23.5 km<sup>2</sup>; 1.1%) and other unspecified land uses (e.g. home lots, sheds).

94 **Put Fig. 1 Here**

95 Most of the farms in this region produce cereal, which is grown in a 2-year rotation system. In  
96 the first year, winter cereal is cultivated from early September to the end of April the following  
97 year. Then, corn is cultivated between the end of April to early September of the same year. The  
98 study area was chosen (Fig. 1) because of its large numbers (about 300 individuals, c.13.6 ~20 %  
99 of China's total wintering population (Goroshko 2010; Meng 2010). This area is the world's largest  
100 wintering ground of the endangered *O. t. dybowskii*. This area is representative of the typical  
101 farmland situation in the North China Plain. In addition, accurate Great Bustard census data,  
102 geographic information system (GIS) data coverages and satellite imagery were readily available.

103 Bird census data

104 Spatial occurrence and abundance data for Great Bustards were used to develop models. A Great  
105 Bustard census was winter survey conducted during November 2013 to March 2014. In the study  
106 area, we travelled with a small four-wheel-drive tractor along fixed routes, using speeds of 10-30  
107 km/hour. Our team consisted of two experienced observers (one surveyor and one local resident)  
108 counting bustards and with a good knowledge of the area to be surveyed. When a flock was found,  
109 we drove slowly and stopped on the location at a 100 - 500 m distance from bustard flocks,  
110 recording its size, location, habitat type and basic behavior. This resulted in a good detection of  
111 birds and flocks in the study area because birds can be seen already from long distances (~3km)  
112 but also when flying away. The actual animal coordinates were obtained by Google Earth when  
113 combing it with our recorded location. Each census was done from dawn to dusk. During the study,  
114 we identified 94 bustard sites in the study area. To our knowledge, this census data were the best  
115 available ones in China for bustards.

116 GIS environmental layers

117 Based on environmental conditions in our study area, we selected eleven habitat and landscape  
118 (environmental) variables to construct models predicting occurrence and abundance (Table 1). In  
119 order to obtain these variables, we acquired the basemap from Google Earth (using Daogle, an  
120 open source software made by a Chinese individual <http://www.daogle.com/>; as used and  
121 explained in Mi et al., 2014) and derived otherwise unavailable high resolution landscape  
122 inventory information about open water pools, rivers, residential areas, national roads, provincial

123 roads, expressway, farmland road, ditch and farmland areas from the base map. Next we  
124 constructed a distance layer for these variables (except for the farmland area) using the Euclidean  
125 Distance tool in ArcGIS 10.1 with a 30 m×30 m spacing. This high pixel resolution was chosen in  
126 order to be consistent with remote sensing variable resolution we used.

#### 127 Satellite images

128 A range of the best cloud-free HJ-1A/B (HuanJing (HJ)) satellite images  
129 (<http://218.247.138.121/DSSPlatform/index.html#>) at a 30 m×30 m resolution was obtained for  
130 each month for November 2013 to March 2014 in order to calculate the normalized difference  
131 vegetation indices (NDVI) signature for each pixel. The HJ-1A/B CCD data were run for  
132 radiometric calibration, atmospheric correction and geometric correction in order to obtain surface  
133 reflectance data and subsequent NDVI data. Radiometric calibration was finished using 2014 HJ-  
134 1A/B CCD absolute radiometric calibration coefficients provided by the China Centre for  
135 Resources Satellite Data and Application. For this study, we used maximum and mean NDVI to  
136 represent the vegetation condition (Osborne et al., 2001).

137 **Put Table 1 Here**

## 138 Model development

139 We employed an advanced machine learning technique, Random Forest, to model the  
140 occurrence as well as abundance distribution of Great Bustards. Breiman (2001)'s Random Forest  
141 implementation in SPM7 by Salford Systems Ltd is robust to over-fitting and is widely recognized  
142 to produce very good predictive models. Hence, it is increasingly applied to species distribution  
143 modelling (Cutler et al., 2007; Drew et al., 2011; Mi et al., 2016 for an application using bustards  
144 in China). Though Random Forest performed the best to predict abundance itself (see Appendix  
145 1), testing the feasibility for other data was essential for good certainty. So for an assessment on  
146 the robustness of the model we pooled data from 2013 and 2014, and then used 80% abundance  
147 data as training data and the remaining 20% as testing data. When we constructed initial abundance  
148 models with all eleven environmental predictors, model performance is not so good ( $R^2$  was small).  
149 Likely that has to do with the regression settings in Random Forest algorithm. For a better outcome  
150 we assessed a "stepwise" setting in SPM for whole abundance data (100%) to re-run models, and  
151 found better results. In that way, we identified a multivariate set of four environmental predictors  
152 (distance to expressway, distance to national road, distance to pool, MNNDVI), which have the  
153 best performance (biggest  $R^2$ ). Using these four predictors, we re-constructed the abundance model  
154 based on the training data (80%) and validated it with testing data (20%). We found that the  
155 regression model performance was acceptable but fair ( $R^2 = 0.551$ ) between observation and  
156 simulation abundance. Thus, we constructed the final abundance model based on the above four  
157 selected variables and with the entire observation data. In order to obtain an abundance index more  
158 close to observations we adjusted the simulation abundance according to the linear regression  
159 between observation and simulation abundance (Fig. 2a).

160

Put Fig. 2 Here

161 Further, Random Forest was also applied to rank the relative importance of environmental  
162 variables. In SPMv7, partial dependence plots are not directly implemented in Random Forest yet,  
163 but can easily be obtained from R or are mimicked in TreeNet model as a Random Forest run.  
164 Thus, we used TreeNet with bagging settings to create partial dependence plots for each variable  
165 of the occurrence and abundance models.

166 About 10,000 pseudo-absence points were taken by random sampling across study areas using  
167 the freely available Geospatial Modeling Environment (GME) software  
168 (<http://www.spatial ecology.com/gme/>) for distribution models. In SPMv7 we set balanced class  
169 weights, grew each model to 1,000 classification trees for occurrence model and 1,000 regression  
170 trees for abundance model, and used all other software default settings. We extracted the habitat  
171 information from the environmental layers for presence and pseudo-absence points for Great  
172 Bustards in GME, and then created a model file in SPM7 called a 'grove' containing the algorithm  
173 quantifying patterns of occurrence for scoring all pixels in the study area. We also extracted the  
174 habitat information from the same environmental layers for abundance points, and then generated  
175 a 'grove' file for abundance to score abundance estimates for each pixel in the study area.

176 For spatial occurrence and abundance distribution visualization, we applied the SPM7 grove  
177 files to a regular lattice of points (pixels; also attributed to the environmental variables) spaced at  
178 30 m intervals across the study area. Model outputs generated relative indices of occurrence (RIO;  
179 an index of pixels from 0 to 1 representing a relative index belonging to the 'occurrence' class)  
180 and a relative abundance index (simulation abundance) for each point in the regular lattice based  
181 on its underlying environmental variables. We also adjusted the predicted abundance based on a  
182 linear regression as constructed in the previous model development steps (Fig. 2a). For a better  
183 continuous spatial visualization, the RIO and predicted abundance values were smoothed between

184 neighboring points across the extent of the study area using the Inverse Distance Weighting (IDW)  
185 tool in ArcGIS 10.1. This yielded spatially continuous predictive distribution and abundance raster  
186 maps of Great Bustard.

187 Model validation

188 The Random Forest performance was first assessed internally using a set of ‘out-of-bag’ (OOB)  
189 training points (OOB; a specific concept used with Random Forest models to describe a subset of  
190 points not used initially for model fitting; Breiman 1996, Breiman 2001). Using this out-of-bag  
191 dataset, the receiver-operating characteristic (ROC) and RMSE were used to calculate predictive  
192 performance of occurrence and abundance models, respectively (Zweig and Campbell 1993;  
193 Fielding and Bell 1997; Huettmann and Gottschalk 2010).

194 Priority protection analysis

195 In order to have a more suitable and scientific protection plan for the endangered Great Bustard,  
196 in this study we put forward for the first an index called the priority protection index (PI), which  
197 combines the predicted results of SDM and SAM. This index is calculated by the following  
198 equation for each site:

$$PI = \frac{RIO \times RA}{\max (RIO \times RA)} \quad (1)$$

199 where **PI** = Priority protection index (an index of pixels from 0 to 1 representing the priority of  
200 conservation), **RIO** = relative index of occurrence, and **RA** = relative abundance (simulation  
201 abundance). In our study, we computed the PI for the whole study area based on RIO and the  
202 adjusted RA value of each grid cell by spatial occurrence and abundance maps. Then we used the  
203 IDW tool in ArcGIS 10.1 to generate spatially continuous priority protection index (PI) raster  
204 maps. In this equation we did not consider the weighting of biotic and socioeconomic variables.

205 So the justification and use of the PI should be explained a little more: When combining SDM  
206 with SAM one will not find a straight forward relationship between occurrence and abundance  
207 (see Yen et al. 2004 for an example). What the PI will do, but what has not been achieved before  
208 much, is to essentially model that relationship and provide a combined view of occurrence index  
209 and abundance index explicit in space and time. Achieving this can thereby help to prioritize pixels  
210 better with let's say high occurrence index and low abundances on pixels etc.

## 211 **RESULTS**

### 212 Model performance

213 Our distribution model obtained a decent performance (ROC: 0.77) according to Fielding and Bell  
214 (1997), and the abundance model had RMSE 26.54 (RMSE is unit-less). Such model predictions  
215 allow us to infer from such models and how they are built.

### 216 Variable importance

217 Table 2 presents the variable importance ranking of occurrence and abundance models obtained  
218 from the Random Forest method. We found that the area of farmland, distance to residential area  
219 (buildings), to ditch and to expressway were the top four most important variables influencing  
220 bustard occurrence. Those come as a multivariate package. The NDVI which represents vegetation  
221 condition was less important than the other nine predictors. As for the abundance model, the most  
222 important factors were distance to national road and to expressway, followed by water factors  
223 (distance to pool) and food-related factors (MNNDVI)

224 **Put Table 2 Here**

### 225 Partial dependence plots

226 Partial dependence plots could interpret the functional relationships and effects of each variable

227 by representing a variable's marginal effects on the response (Elith et al., 2008; Johnstone et al.,  
228 2010). It helps to find the signal in the data; Fig. 3a indicated that the occurrence preference of  
229 bustards for farmland area was between 0.6 and 7.5 km<sup>2</sup>. Distance to residential area ranging from  
230 250 to 2,500 m (Fig. 3b), distance to ditch ranging from 100 to 4,500 m (Fig. 3c), and distance to  
231 expressway from 6,000 to 19,000 m (Fig. 3d) were bustard preferences. While for abundances,  
232 more individuals would occur beyond 2,300 m, but less than 9,500 m away from national roads  
233 (Fig. 3e), and be found in the range between 7,000 and 11,000 m away from expressway (Fig. 3f).  
234 Moreover, this species kept themselves away from pools (larger than 1,500 m, Fig. 3g) and with  
235 more vegetation (mean NDVI during the investigation larger than 0.13, Fig. 3h). The information  
236 for other variables, more marginal, can be found in Appendix 2.

237

Put Fig. 3 Here

238 Occurrence, abundance distribution patterns and priority protection

239 Fig. 4 shows the maps of RIO (relative index of occurrence), adjusted RA (relative abundance)  
240 and PI (priority protection index). From the RIO map (Fig. 4a), we found that the distribution area  
241 of high RIO of bustards is high. The regions of high occurrence possibility of bustards were  
242 concentrated in the south-central study area; and the whole habitats represented a fragmented  
243 distribution. The abundance distribution had a different pattern, showing high populations  
244 occurring in the central and northwestern study area (Fig. 4b). Based on the occurrence and  
245 abundance distribution results, we used equation (1) and obtained the result of Fig. 4c. It displays  
246 that a high PI is located in the center, north and northeast of the study area and it shows a sporadic  
247 fragmented distribution which would be the priority protection site if a conservation decision is to  
248 be made.

249

Put Fig. 4 Here



250 **DISCUSSION**

251 The occurrence and abundance models of Great Bustard developed here were designed to  
252 identify relevant locations for where to prioritize conservation, and to assess the effects of each  
253 variable that influenced this species occurrence and abundance (Fig. 3). Area of farmland, distance  
254 to residential area, distance to ditch and to expressway were among the top four most important  
255 predictors for bustard occurrence in a multivariate perspective; while for the abundance model  
256 they consisted of another multivariate package of distance to national road, distance to  
257 expressway, distance to pool and mean NDVI (Table 2). We found that high RIO habitats had a  
258 fragmented distribution throughout the entire study area (Fig. 4a). The abundance model showed  
259 that high population usually occurred in the central and northwestern part of our study area (Fig.  
260 4b). The center, north and northeast of the study area with a high priority protection index (PI) and  
261 with a severely fragmented distribution should be the priority site for protection (Fig. 4c). This not  
262 only confirms our own records but with the help of the PI can now be quantified and modeled  
263 further for an effective conservation!

264 In our study area, human disturbance was very strong, such as density of roads and residential  
265 areas (Fig. 1). During our study we also found other threats to this endangered species: farmers  
266 grazed their sheep; famers sprinkled poison baits in the wheat field to avoid sheep entering; some  
267 bird photographers pursued bustards by walking or following on motor vehicles to take photos,  
268 which they wanted to show off to others; hunters with dogs chasing hare and ring-necked pheasant  
269 during day and night; some local people hunted bustards; increasing power lines setting in  
270 agriculture land, bustards sometimes collided with wires and were injured or even died when  
271 starting to fly in foggy days or when in a hurry (Janss & Ferrer 2000); and the interference of  
272 firecracker sounds during Chinese Spring Festival as well as oil rigs and wind farms. Though

273 carrying a high disturbance and for a stress synthesis (e.g. “death by thousand cuts”), still, a large  
274 number of wintering bustards (about 300, c. 13.6 ~20.0 % of China’s total wintering population;  
275 Goroshko 2010; Meng 2010) wintered in this area. In times of climate change, it can be assumed  
276 the population widens (Mi et al., 2016). Thus, this is an area of essential importance for bustards  
277 in China either way. A feasible conservation plan should therefore be made, based on our model  
278 prediction result, combined with local public customs and financial support and a wider buy-in. In  
279 our opinion, improved education on animal protection to local people as we usually did over the  
280 years would be useful. The same applies to increasing budgets, enforcement and frequency of  
281 patrol by the local management and conservation NGOs in the region with high PI value and the  
282 local community, with corresponding government financial support. Patrol route designation in  
283 the field should avoid getting too close to bustards though, so as not to disturb and stress the regular  
284 wintering activities of bustards. For the benefit of this species and its habitats we suggest to not  
285 change crop farmland into nursery farmland; and we encourage farmers to harvest their crops with  
286 a machine, which is a more beneficial harvesting method for bustards based on our previous  
287 research results (Mi et al., 2014). We also highly recommend, if possible, to bury power lines into  
288 the ground and to collect hunting guns from local public.

289 In this study, occurrence and abundance did not display identical spatial distribution patterns  
290 which was reported in some previous studies (Conlisk et al., 2007; Karlson et al., 2011; Yin & He  
291 2014; Johnston et al., 2015). There is actually no reason to assume a presence site just shows one  
292 animal individual, or a linear relationship between RIO and abundance. Technically-speaking,  
293 ‘presence’ can mean 1-infite animals and details depend on the actual pixel set-up and how it fits  
294 into the obtained model. So while the relationship is not automatically clear this could be due to  
295 several reasons and depending on specific habitat details: Firstly, environmental variables that

296 contributed to occurrence and abundance were different, as Table 2 indicated. Secondly, predictor  
297 preference in bustard occurrence and abundance models were different. For instance, bustards  
298 occur at a distance to expressway from 6,000 to 19,000m (Fig. 3d), while most populations occur  
299 between 7,000 and 11,000m from expressway for abundance (Fig. 3f) (see more details in Fig. 3  
300 and Appendix 2). Thirdly, they differed in their spatial distribution for occurrence and abundance  
301 (Fig. 4a, b). Based on the analysis of overlaying observation sites with RIO and observation  
302 abundance (Fig. 5a, b), estimated relative index of occurrence (RIO) do not consistently relate with  
303 the relative index of abundance (Fig. 5a). All locations of observed abundance had high RIO (Fig  
304 5a), and the relationships between occurrence and abundance estimates were nonlinear (Fig. 5b).  
305 These differences may represent a mixture of effects reflecting differences between the underlying  
306 biological processes that give rise to specific abundance and occurrence at a pixel, as well as  
307 limitations imposed by the data and methodology to estimate these patterns (Johnston et al., 2015;  
308 see Buckland et al., 2016 for Distance Sampling and detectability problems). In addition, how to  
309 understand the inconsistency between these two indices of plant prediction is a problem waiting  
310 to be resolved further. For instance, between crop occurrence index (equal to habitat suitability  
311 index) and crop abundance (e.g. production).

312

Put Fig. 5 Here

313 When treating all presences as equal in species distribution models (SDMs; occurrence model,  
314 habitat niche model) -regardless of the abundance of individuals that the habitat supports - this  
315 could provide us with information on the suitability of habitat loss (Howard et al., 2014). Applying  
316 models based on abundance data even at a relatively coarse scale can help to predict spatial patterns  
317 of occurrence modelled with even greater refinement (Howard et al., 2014). Conservation decision-  
318 making should use as much knowledge and information as possible to optimize the benefits of

319 conservation action (Sutherland et al., 2004; Segan et al., 2011). The use of species distribution  
320 models (SDMs) of occurrence has been an important tool in optimizing the selection of protected  
321 areas (Franklin 2013; Guisan et al., 2013, Mi et al., 2016; Han et al., 2017) based on the ecological  
322 niche space (Drew et al., 2011), but relative abundance is often perceived a more relevant metric  
323 because it can quantify animals on a pixel, and thus, populations (Johnston et al., 2015). Modeling  
324 abundance requires methods that can handle large numbers of zero counts as well as the rare, but  
325 important, high counts (Welsh et al., 1996) without a solid research design, according to frequentist  
326 statistics. However, Yen et al., (2004), Magness et al., (2008) and Fox et al., (2017) showed already  
327 how machine learning can change this perspective and provide very powerful solutions.

328 High counts and their locations are particularly important because the pixels with the highest  
329 densities of animals are potentially of greatest interest for conservation planning (Johnston et al.,  
330 2015). In our study, we found that the regressions in Random Forest performed imperfectly for  
331 low and high counts (Fig. 2b) although it showed a highly linear relationship between observed  
332 and simulation abundance ( $R^2=0.844$ ; Fig 2a). Therefore, we argue that the regression method in  
333 Random Forest algorithm should optimize low and high count predictions. We recommend to  
334 classify abundances in bins (e.g. high, medium, low with associated abundance estimates) because  
335 Random Forest is exceptionally strong for classification problems. This remains an open field of  
336 research, for now. However, we find our progress remains substantial.

337 Abundance data could also provide valuable baselines against which to assess future changes  
338 (Cumming 2007) (e.g. climate change, land use change). Such changes in abundance will be much  
339 more rapidly apparent, and hence more rapidly detected than changes in presence-absence patterns  
340 across ranges (Gregory et al., 2005). However, only a few spatial distribution modelers derived  
341 models with the collection of abundance data (e.g. Yen et al. 2004, Fox et al. 2017). This may be

342 because collection of abundance data is more cost or resource demanding than collecting presence  
343 - absence data especially for highly mobile animals. Such data are sophisticated in structure and  
344 research design, and still they are rarely shared (see in GBIF.org). We therefore recommend that  
345 abundance data could be collected (easily to be turned into presence-absence data, too), even at  
346 only relatively coarse numerical scales because the benefits are considerable (as stated by Howard  
347 et al., 2014). One thing that should be mentioned is that plenty of abundance data and (non-linear  
348 regression) models did not perform well and abundance were extremely difficult to predict (Oppel  
349 et al., 2012). Finding the underlying causes that influence abundance model accuracy and  
350 constructing more accurate models would be extreme important and useful in future applications  
351 towards individual-based policy applications.

352 For a spatial priority protection of mobile species, one should note that high numbers of  
353 individuals are not always present in the same habitats and pixels, instead low numbers may occur  
354 in one place many times. And this may have implications for spatial priority protection for mobile  
355 species. Previous studies have used analytical approaches to deal with some of these challenges  
356 (e.g. Nichols et al., 2009; Kery & Andrew Royle 2010; Oppel et al., 2012; Jiguet et al., 2013).  
357 However, no general modeling framework has been proposed for dealing with all of these  
358 analytical challenges simultaneously. This is exactly where our PI offers progress. We also thought  
359 the situation of mobile species selecting habitats could be divided into five scenarios: higher  
360 numbers and multi frequency, higher numbers and lower frequency, low numbers and multi  
361 frequency, low numbers and low frequency, none. When a conservation plan is made for a species,  
362 one should consider not only occurrence index and frequency, but also abundance. Here we  
363 proposed the priority protection index (PI; equation (1) and Fig. 4) based on the distribution of  
364 occurrence and abundance pattern as more helpful for a fast priority protection plan than indices

365 and it's only based on distribution of occurrence or abundance.

366 To date, quantitative estimates of population size during global and local changes have actually  
367 proven to be difficult to forecast. This is a major hindrance for effective management, as population  
368 size and trend are considered among the best correlates of extinction risk (O'Grady et al., 2004).  
369 Such measures are commonly used in determining the conservation status of a species (e.g. IUCN  
370 (2001)). We argue that habitat loss remains the one and only powerful metric that can be obtained  
371 quickly on a landscape-scale in the absence of proper trends and abundances (e.g. Drew et al.  
372 2011). The relationship between predicted environmental suitability and abundance - as presented  
373 here - may provide us with a possible method for predicting population size and its changes  
374 associated with distributional changes, particularly appropriate for non-mobile species (e.g. plants,  
375 fungi). However, this method is not particularly suitable for mobile species, especially for highly  
376 mobile species such as many birds, bats, and flying insects. They may move over a large landscape  
377 within just a single day, and abundance and the environment can vary seasonally and spatially.  
378 When computing population size or population density using abundance, the primary task will be  
379 how to determine the unit area of investigation and for conservation management.

380 This study is the first that has combined model-predicted occurrence (representing species  
381 distribution model) and abundance indices (representing species abundance model) to produce a  
382 priority protection index (PI), which may contribute to spatial conservation and management  
383 decisions worldwide. We strongly encourage other researchers to test, apply and update the priority  
384 protection index (PI) to explore the generality of these findings further.

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389

390 **REFERENCES**

- 391 Adams MP, Saunders MI, Maxwell PS, Tuazon D, Roelfsema CM, Callaghan DP, Leon J,  
392 Grinham AR, and O'Brien KR. 2016. Prioritizing localized management actions for seagrass  
393 conservation and restoration using a species distribution model. *Aquatic Conservation Marine  
394 and Freshwater Ecosystems* 26:639-659.
- 395 Araújo MB, New M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology and  
396 Evolution* 22:42-47.
- 397 Ashcroft MB, King DH, Raymond B, Turnbull JD, Wasley J, and Robinson SA. 2017. Moving  
398 beyond presence and absence when examining changes in species distributions. *Global  
399 Change Biology* 23:2929-2940.
- 400 Barker NKS, Cumming SG, Darveau M. 2014. Models to predict the distribution and abundance  
401 of breeding ducks in Canada. *Avian Conservation and Ecology* 9:7.
- 402 Breiman L. 1996. Bagging predictors. *Machine learning* 24:123-140.
- 403 Breiman L. 2001. Random forests. *Machine learning* 45:5-32.
- 404 Buckland ST, Rexstad EA, Marques TA, and Oedekoven CS. 2016. Distance Sampling: Methods  
405 and Applications. *Methods in Statistical Ecology* 63:152-153.
- 406 Conlisk E, Conlisk J, Harte J. 2007. The impossibility of estimating a negative binomial clustering  
407 parameter from presence - absence data: a comment on He and Gaston. *The American  
408 Naturalist* 170:651-654.
- 409 Cumming GS. 2007. Global biodiversity scenarios and landscape ecology. *Landscape Ecology*  
410 22:671-685.
- 411 Cutler DR, Edwards JrTC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler, JJ. 2007. Random  
412 forests for classification in ecology. *Ecology* 88:2783-2792.



- 413 Drew CA, Wiersma Y, Huettmann F. 2011. Predictive species and habitat modeling in landscape  
414 ecology: concepts and applications. Springer, London.
- 415 Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F,  
416 Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura  
417 M, Nakazawa Y, Overton JMM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira  
418 R, Schapire RE, Soberón J, Williams S, Wisz MS, and Zimmermann NE. 2006. Novel  
419 methods improve prediction of species' distributions from occurrence data. *Ecography*  
420 29:129-151.
- 421 Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. *Journal of*  
422 *Animal Ecology* 77: 802-813.
- 423 Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction  
424 across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677-697.
- 425 Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in  
426 conservation presence/absence models. *Environmental conservation* 24:38-49.
- 427 Fox CH, Huettmann F, Harvey GKA, Morgan KH, Robinson J, Williams R, Paquet PC. 2017.  
428 Predictions from machine learning ensembles: marine bird distribution and density on  
429 Canada's Pacific coast. *Marine Ecology Progress Series* 566:199-216.
- 430 Franklin J. 2013. Species distribution models in conservation biogeography: developments and  
431 challenges. *Diversity and Distributions* 19:1217–1223.
- 432 Goroshko OA. 2010. Present status of population of Great Bustard (*Otis tarda dybowskii*) in  
433 Dauria and other breeding grounds in Russia and Mongolia: distribution, number and  
434 dynamics of population, threats, conservation. First International Symposium on  
435 Conservation of Great Bustard, Beijing (in Chinese).

- 436 Gray TN, Borey R, Hout SK, Chamnan H, Collar NJ, and Dolman PM. 2009. Generality of models  
437 that predict the distribution of species: conservation activity and reduction of model  
438 transferability for a threatened bustard. *Conservation biology* 23:433–439.
- 439 Gregory RD, Strien AV, Vorisek P, Meyling AWG, Noble DG, Foppen RP, Gibbons DW. 2005.  
440 Developing indicators for European birds. *Philosophical Transactions of the Royal Society*  
441 of London B: Biological Sciences 360:269-288.
- 442 Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat  
443 models. *Ecology Letters* 8:993-1009.
- 444 Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ,  
445 Brotons L, McDonald-Madden E, Mantyka-Pringle C. 2013. Predicting species distributions  
446 for conservation decisions. *Ecology Letters* 16:1424-1435.
- 447 Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological*  
448 *Modelling* 135:147-186.
- 449 Han X, Guo Y, Mi C, Huettmann F, and Wen L. 2017. Machine Learning Model Analysis of  
450 Breeding Habitats for the Black-necked Crane in Central Asian Uplands under Anthropogenic  
451 Pressures. *Scientific Reports* 7:6114.
- 452 Howard C, Stephens PA, Pearce-Higgins JW, Gregory RD, Willis SG. 2014. Improving species  
453 distribution models: the value of data on abundance. *Methods in Ecology and Evolution*  
454 5:506-513.
- 455 Howard C, Stephens PA, Pearce - Higgins JW, Gregory RD, Willis SG. 2015. The drivers of avian  
456 abundance: patterns in the relative importance of climate and land use. *Global Ecology and*  
457 *Biogeography* 24:1249-1260
- 458 Huettmann F, Gottschalk T. 2010. Simplicity, Model Fit, Complexity and Uncertainty in Spatial

- 459 Prediction Models Applied Over Time: We Are Quite Sure, Aren't We? Springer New York.
- 460 IUCN. 2001. UCN red list categories and criteria: version 31 Prepared by the IUCN Species  
461 Survival Commission.
- 462 Janss GFE, Ferrer M. 2000. Common Crane and Great Bustard Collision with Power Lines:  
463 Collision Rate and Risk Exposure. *Wildlife Society Bulletin* 28:675-680.
- 464 Jiguet F, Thomas C, Cook A, Newson S, Ockendon N, Rehsch M, Roos S, Thaxter C, Brown A,  
465 Crick H. 2013. Observed and predicted effects of climate change on species abundance in  
466 protected areas. *Nature Climate Change* 3:1055-1061.
- 467 Johnston A, Fink D, Reynolds MD, Hochachka WM, Sullivan BL, Bruns NE, Hallstein E,  
468 Merrifield MS, Matsumoto S, Kelling S. 2015. Abundance models improve spatial and  
469 temporal prioritization of conservation resources. *Ecological Applications* 25:1749-1756.
- 470 Johnstone JF, Hollingsworth TN, Chapin FS, Mack MC. 2010. Changes in fire regime break the  
471 legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*  
472 16:1281-1295.
- 473 Karlson RH, Connolly SR, Hughes TP. 2011. Spatial variance in abundance and occupancy of  
474 corals across broad geographic scales. *Ecology* 92:1282-1291.
- 475 Kery M, Andrew RJ. 2010. Hierarchical modelling and estimation of abundance and population  
476 trends in metapopulation designs. *Journal of Animal Ecology* 79:453-461.
- 477 Magness DR, Huettmann F, Morton JM. 2008. Using Random Forests to provide predicted species  
478 distribution maps as a metric for ecological inventory and monitoring programs. pp 209-229  
479 In Smolinski TG, Milanova MG, Hassanien AE *Applications of Computational Intelligence*  
480 in Biology: Current Trends and Open Problems *Studies in Computational Intelligence*, Vol  
481 122, Springer-Verlag Berlin, Heidelberg.

- 482 Martín B, Alonso JC, Martín CA, Palacín C, Magaña M, Alonso J. 2012. Influence of spatial  
483 heterogeneity and temporal variability in habitat selection: A case study on a great bustard  
484 metapopulation. *Ecological Modelling* 228:39-48.
- 485 Meng D. 2010. Study on the Rescue to Great Bustard in Cangzhou, Hebei. First International  
486 Symposium on Conservation of Great Bustard, Beijing (in Chinese).
- 487 Mi C, Huettmann F, Guo Y. 2014. Obtaining the best possible predictions of habitat selection for  
488 wintering Great Bustards in Cangzhou, Hebei Province with rapid machine learning analysis.  
489 *Chinese Science Bulletin* 59:4323-4331.
- 490 Mi C, Huettmann F, Guo Y. 2016. Climate envelope predictions indicate an enlarged suitable  
491 wintering distribution for Great Bustards (*Otis tarda dybowskii*) in China for the 21st century.  
492 *PeerJ* 4:e1630.
- 493 Mi C, Huettman F, Guo Y, Han X, Wen L. 2017. Why choose Random Forest to predict rare  
494 species distribution with few samples in large undersampled areas? Three Asian crane species  
495 models provide supporting evidence. *PeerJ* 5:e2849.
- 496 Newton I. (2008) *Migration Ecology of Birds*. London, UK: Academic Press.
- 497 Nichols JD, Thomas L, Conn PB. 2009. Inferences about landbird abundance from count data:  
498 recent advances and future directions pp 201-235 In Thomson DL, Cooch EG, Conroy MJ  
499 *Modeling demographic processes in marked populations* Springer, US.
- 500 O'Grady JJ, Reed DH, Brook BW, Frankham R. 2004. What are the best correlates of predicted  
501 extinction risk? *Biological Conservation* 118:513-520.
- 502 Oppel S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, Louzao M. 2012.  
503 Comparison of five modelling techniques to predict the spatial distribution and abundance of  
504 seabirds. *Biological Conservation* 156:94-104.

- 505 Osborne PE, Alonso J, Bryant R. 2001. Modelling landscape - scale habitat use using GIS and  
506 remote sensing: a case study with great bustards. *Journal of Applied Ecology* 38:458-471.
- 507 Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH,  
508 Stockwell DR 2002. Future projections for Mexican faunas under global climate change  
509 scenarios. *Nature* 416:626-629.
- 510 Primack RB. 2012. *A primer of conservation biology*. 5th Edition Sunderland, Massachusetts.  
511 Sinauer Associates.
- 512 Segan DB, Bottrill MC, Baxter PWJ, Possingham HP. 2011. Using conservation evidence to guide  
513 management. *Conservation Biology* 25:200-202.
- 514 Suárez-Seoane S, Morena ELGDL, Prieto MBM, Osborne PE, and Juana ED. 2008. Maximum  
515 entropy niche-based modelling of seasonal changes in little bustard ( *Tetrax tetrax* )  
516 distribution. *Ecological Modelling* 219:17-29.
- 517 Sutherland WJ, Pullin AS, Dolman PM, Knight TM. 2004. The need for evidence-based  
518 conservation. *Trends in Ecology and Evolution* 19:305-308.
- 519 VanDerWal J, Shoo LP, Johnson CN, Williams SE. 2009. Abundance and the environmental  
520 niche: environmental suitability estimated from niche models predicts the upper limit of local  
521 abundance. *The American Naturalist* 174:282-291.
- 522 Welsh AH, Cunningham RB, Donnelly CF, Lindenmayer DB, 1996. Modelling the abundance of  
523 rare species: statistical models for counts with extra zeros. *Ecological Modelling* 88:297-308.
- 524 Yen PPW, Huettmann F, Cooke F. 2004. A large-scale model for the at-sea distribution and  
525 abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season  
526 in coastal British Columbia, Canada. *Ecological Modelling* 171:395-413.
- 527 Yin D, He F. 2014. A simple method for estimating species abundance from occurrence maps.

528           Methods in Ecology and Evolution 5:336-343.

529   Zweig MH, Campbell G, 1993. Receiver-operating characteristic (ROC) plots: a fundamental

530           evaluation tool in clinical medicine. *Clinical Chemistry* 39:561-577.

531

**Table 1** (on next page)

Table

## 1 Tables

2 Table 1 Comparison of features around 94 sites occupied by great bustards and 10 000 random points. Values are means  $\pm$  standard deviations.

Layer	Variable	Description	Bustard sites	Random points
1	Distance to pool	Distance to pool in meter	1179.0 $\pm$ 734.5	1378.0 $\pm$ 910.3
2	Distance to river	Distance to river in meter	2302.0 $\pm$ 1751.2	2630.0 $\pm$ 2483.0
3	Distance to residential	Distance to residential in meter	935.0 $\pm$ 586.8	980.2 $\pm$ 723.8
4	Distance to national road	Distance to national road in meter	5280.0 $\pm$ 4234.2	5855.0 $\pm$ 4036.9
5	Distance to provincial road	Distance to provincial road in meter	8730.0 $\pm$ 5928.7	9217.0 $\pm$ 6112.4
6	Distance to expressway	Distance to expressway in meter	10010 $\pm$ 5750.0	9585.0 $\pm$ 6666.7
7	Distance to farmland road	Distance to farmland road in meter	477.4 $\pm$ 385.3	524.9 $\pm$ 455.8
8	Distance to ditch	Distance to ditch in meter	1522.0 $\pm$ 1722.7	2120.0 $\pm$ 2078.1
9	Area of farmland	Area of farmland in kilometers	3.3 $\pm$ 3.2	5.3 $\pm$ 6.2
10	MNNDVI	The average value of the normalized difference vegetation index from November, 2013 to March, 2014	0.14 $\pm$ 0.04	0.13 $\pm$ 0.05
11	MAXNDVI	The maximum value of the normalized difference vegetation index from November, 2013 to March, 2014	0.23 $\pm$ 0.06	0.21 $\pm$ 0.07

3



4 Table 2 Variables importance ranking of occurrence and abundance models

Ranking	Occurrence model	Abundance model
1	Area of farmland	Distance to national road
2	Distance to residential	Distance to expressway
3	Distance to ditch	Distance to pool
4	Distance to expressway	MNNDVI
5	Distance to pool	--
6	Distance to river	--
7	Distance to provincial road	--
8	Distance to national road	--
9	Distance to farmland road	--
10	MAXNDVI	--
11	MNNDVI	--

5

6

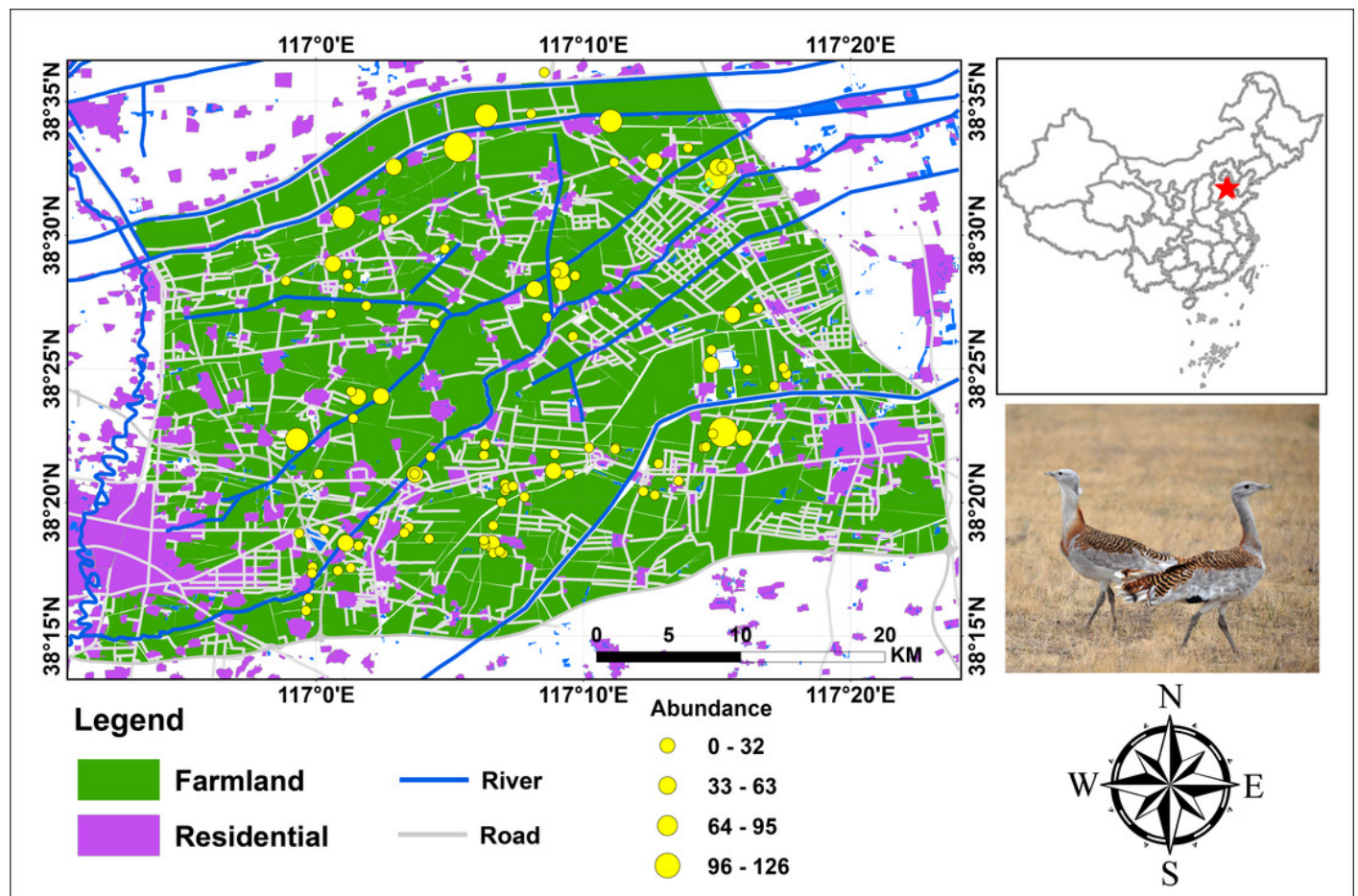
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# Figure 1

Figure 1

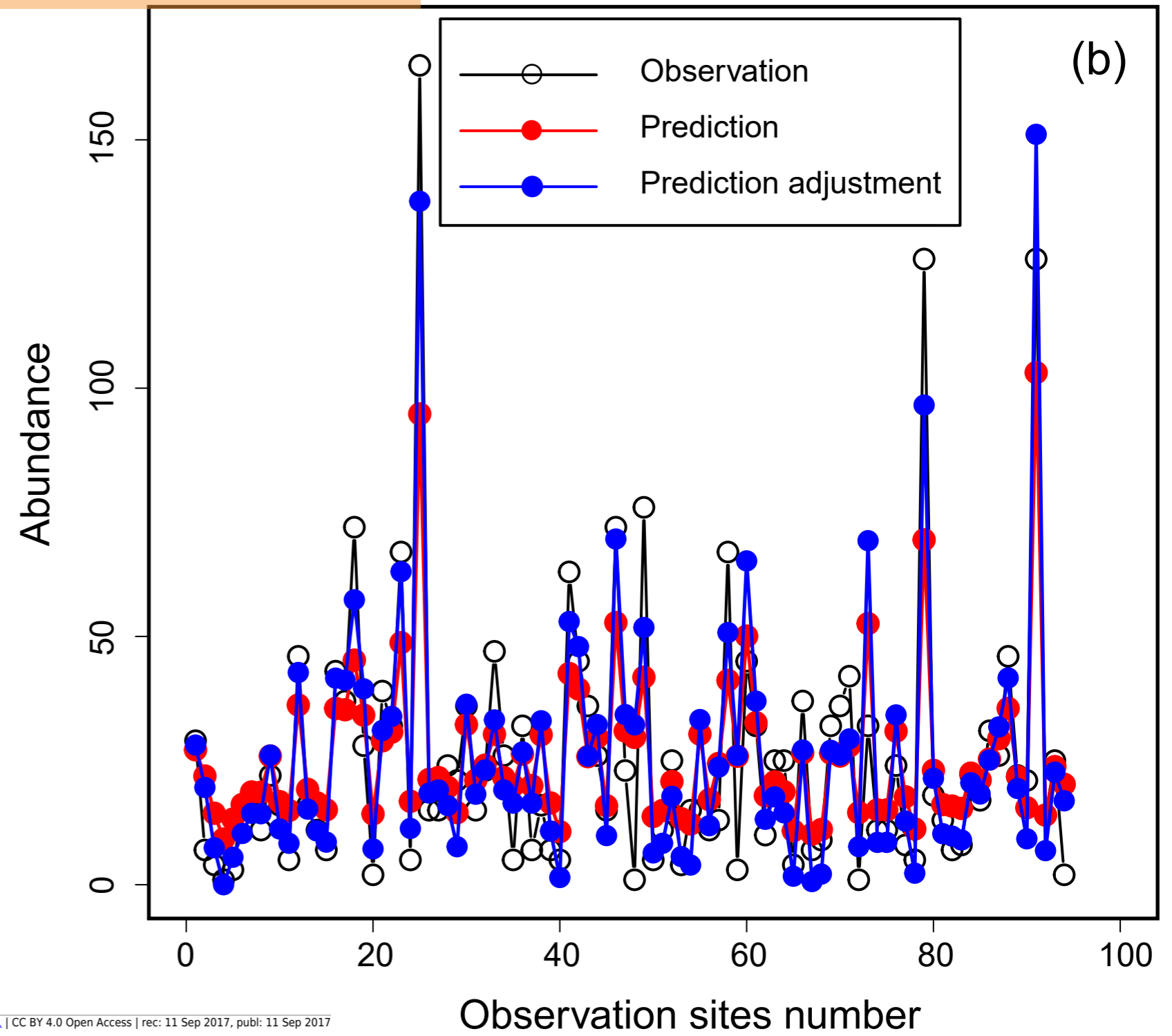
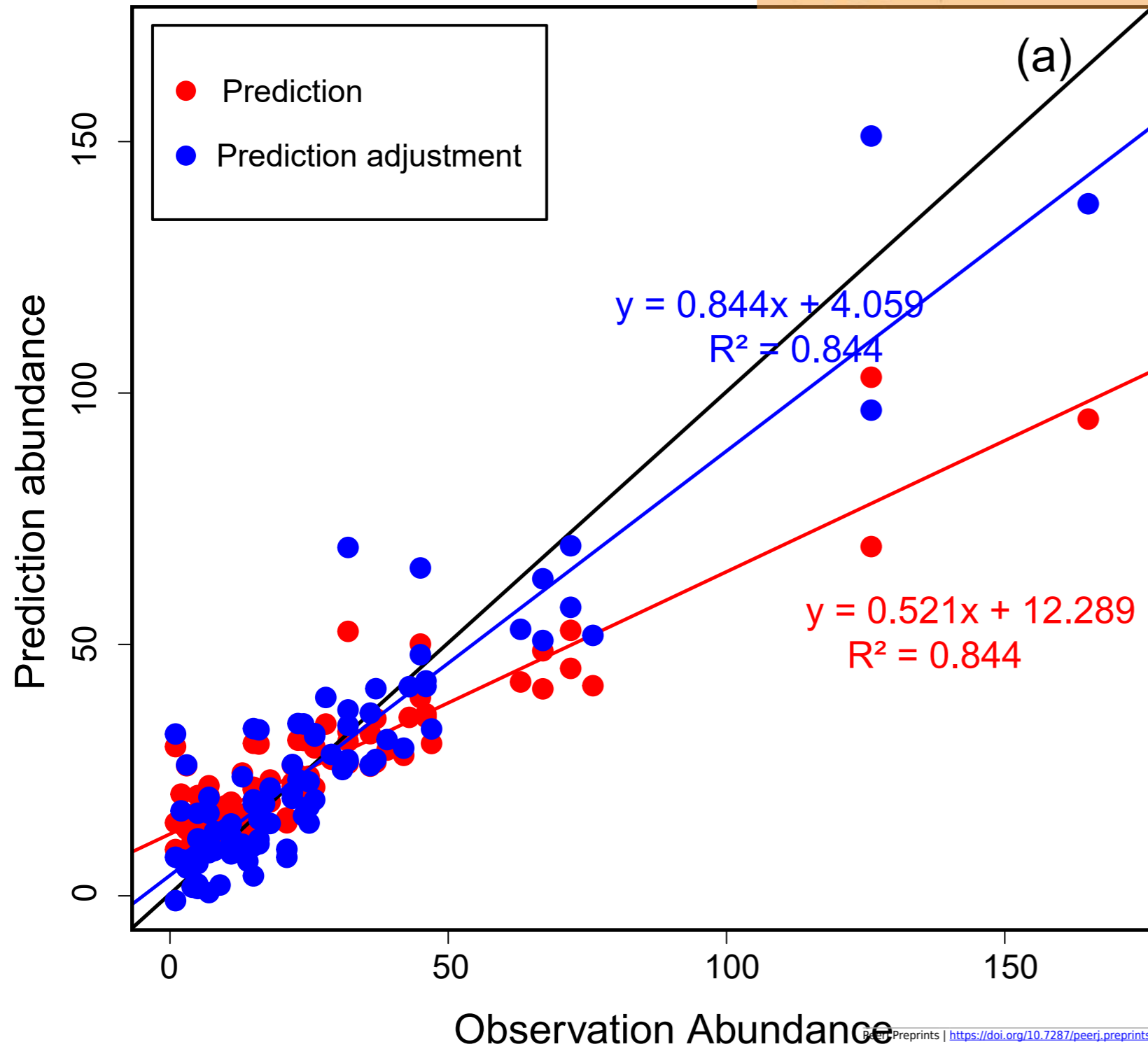
Study area and bird abundance and occurrence data for Great Bustard in Cangzhou, China. Photograph of Great Bustard by Jianguo Fu.



**Figure 2** (on next page)

## Figure 2

Figure 2 The relationship between observation and prediction abundance using Random Forest for Great Bustards. (a) Scatter plot of observation abundance with prediction and adjustment prediction abundance, and (b) lines and points plot of observation, prediction and adjustment prediction abundance.



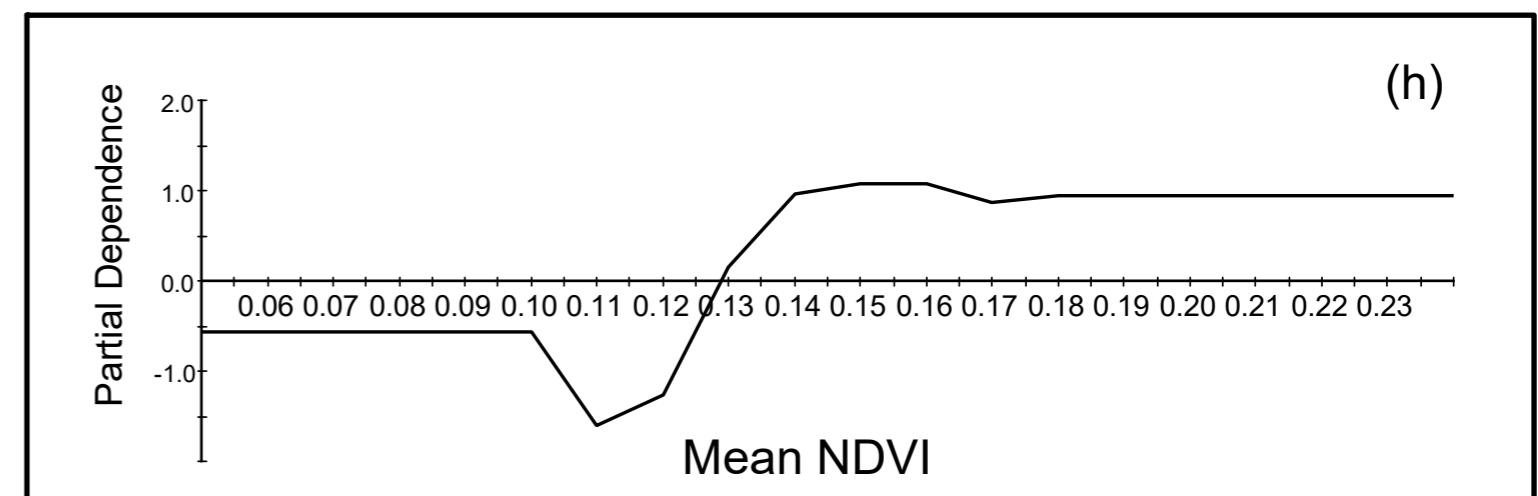
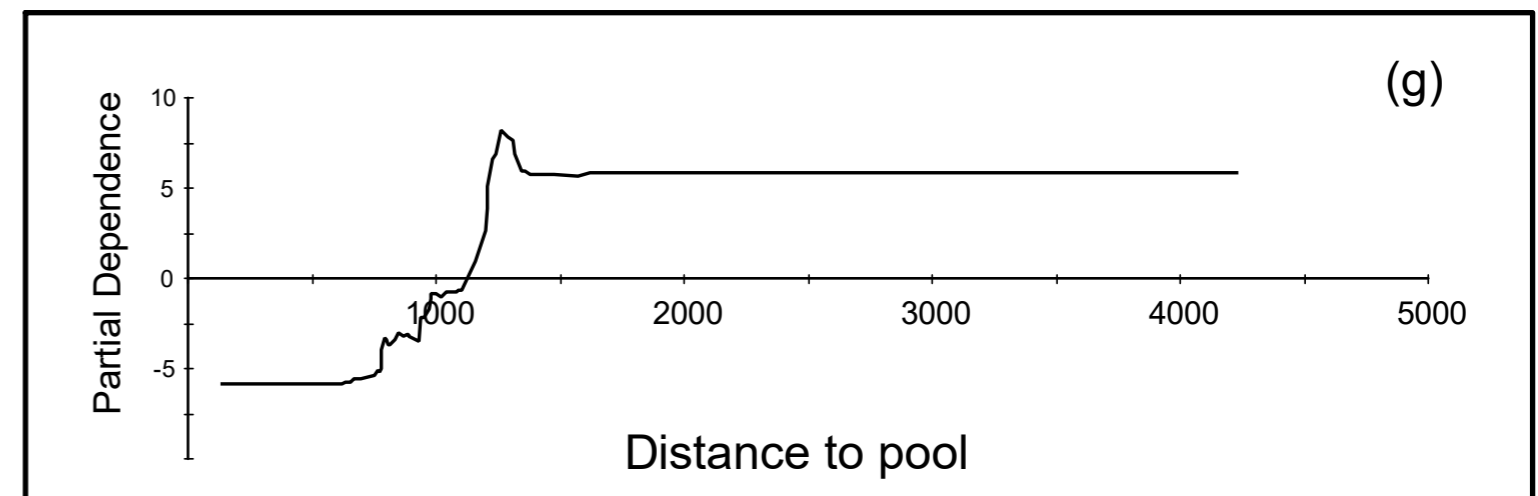
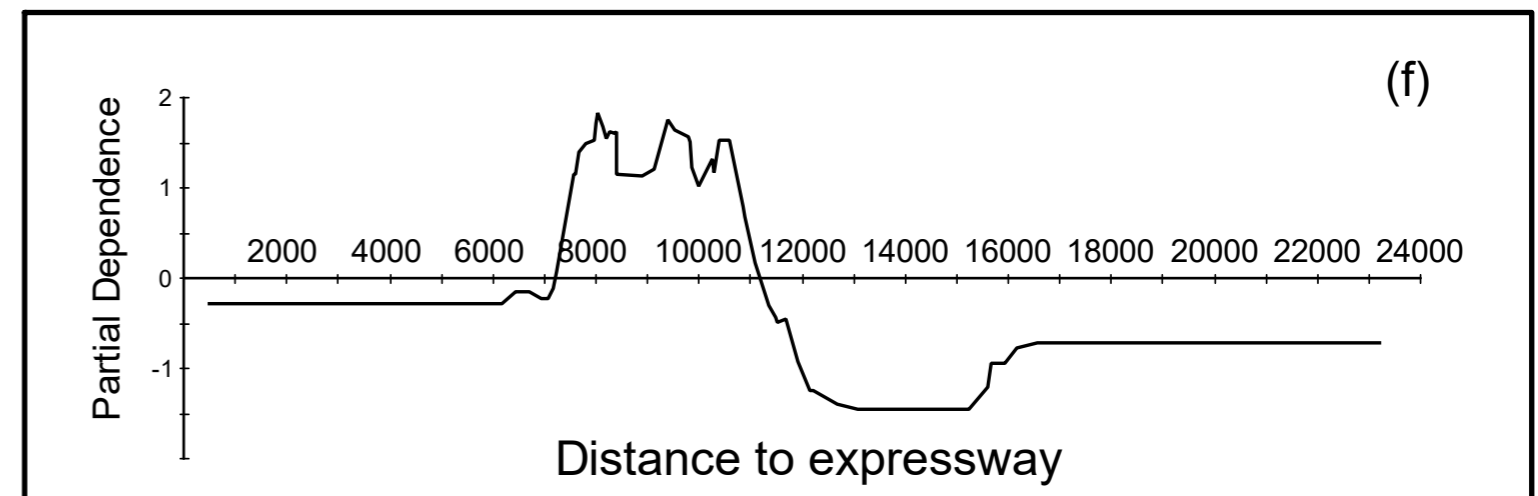
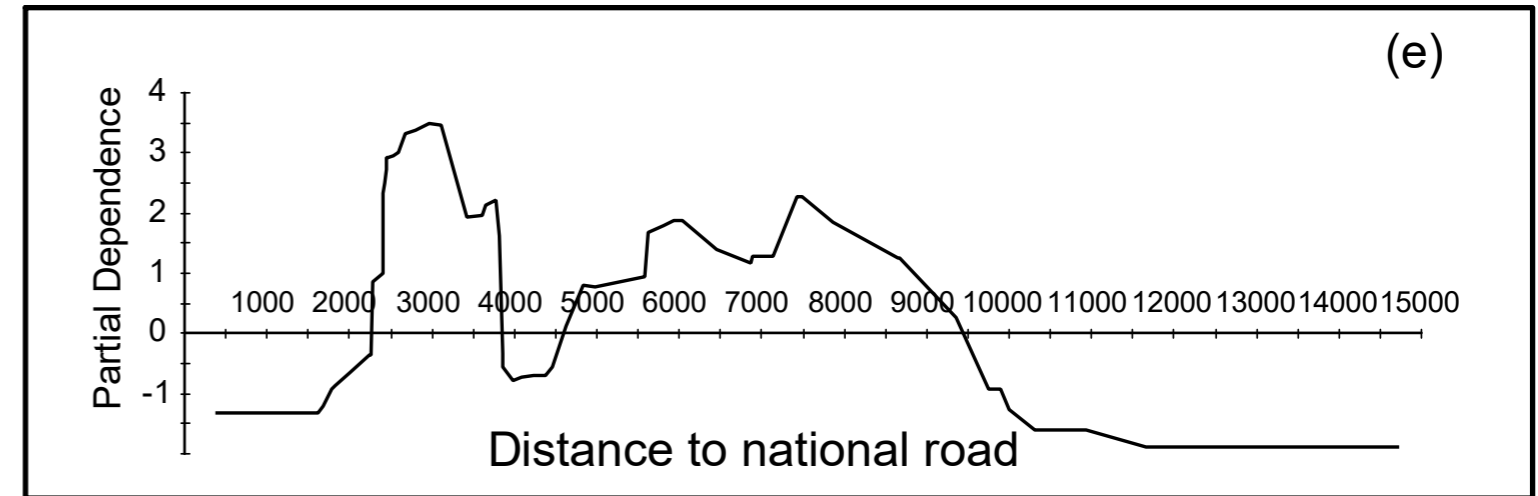
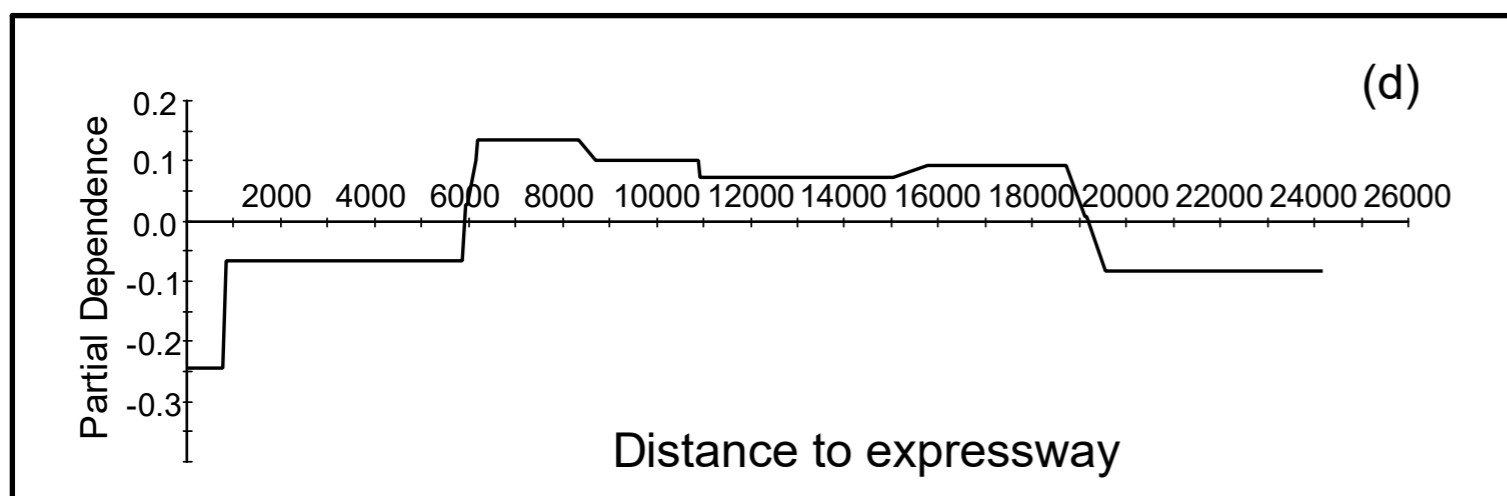
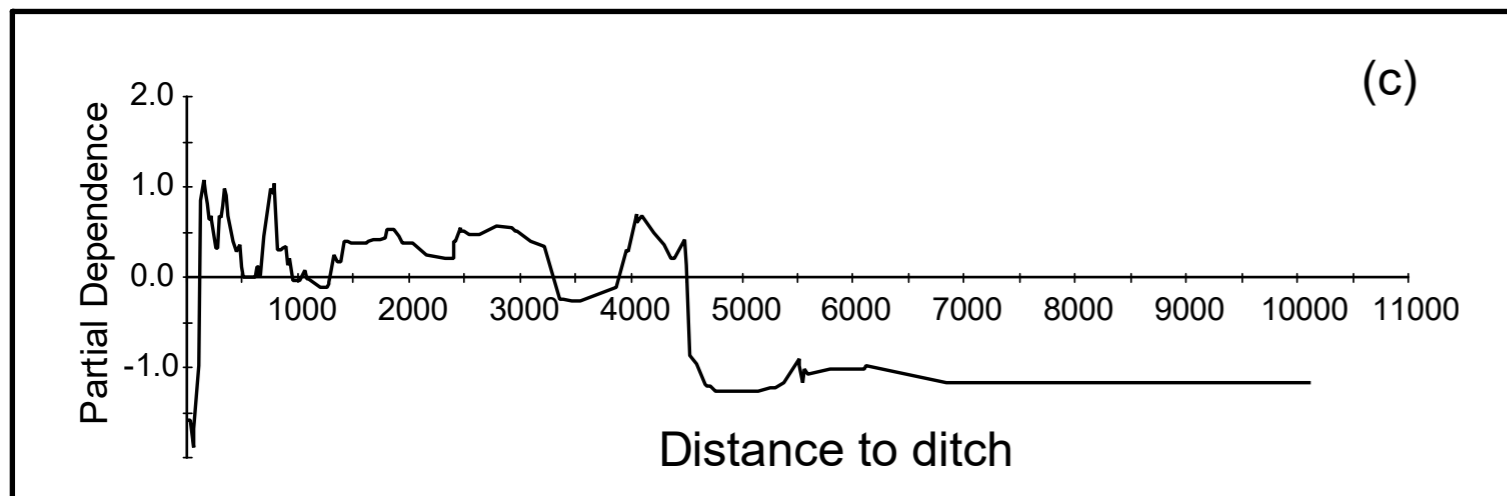
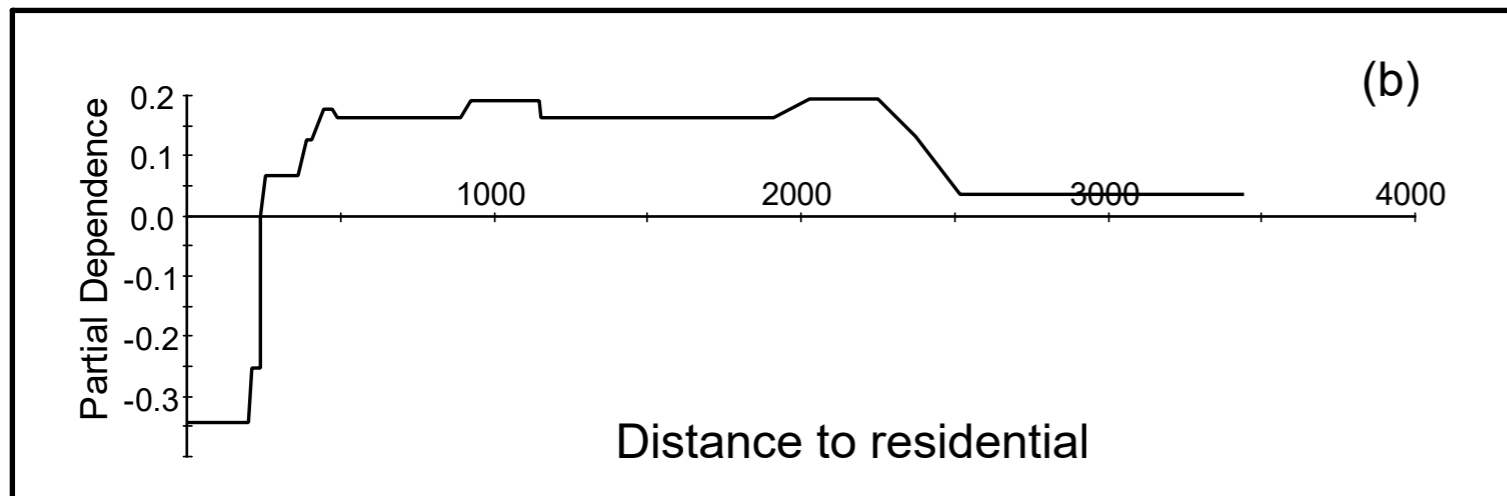
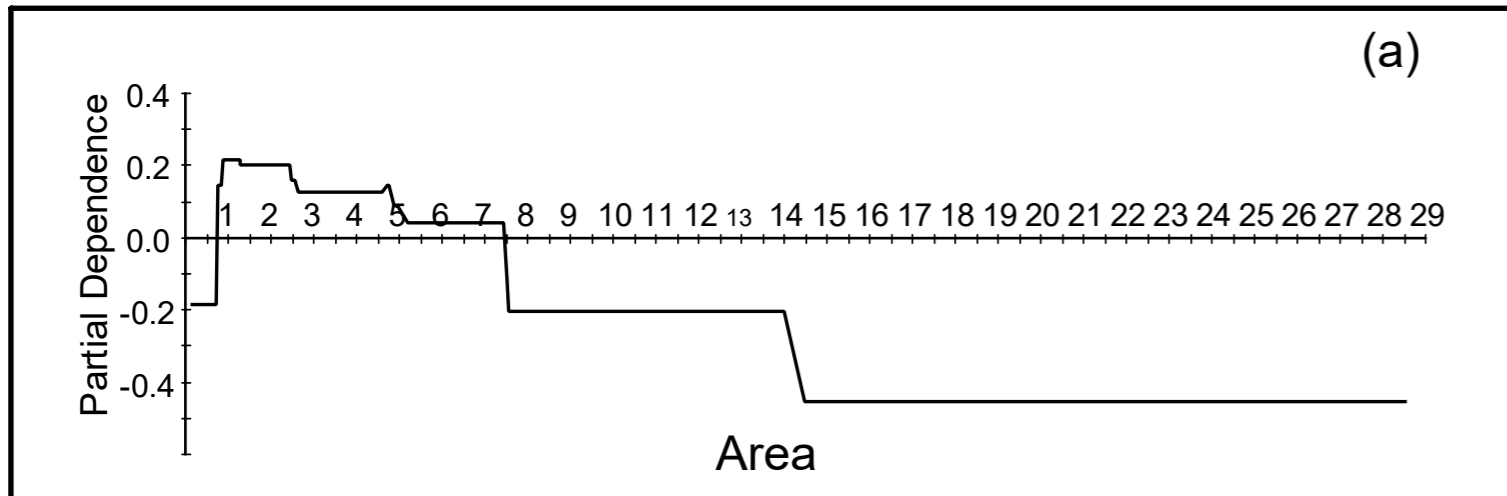
**Figure 3**(on next page)

## Figure 3

Partial dependence plots for the top four most influential variables in the occurrence and abundance distribution models for Great Bustards, respectively: (a) area of farmland in occurrence distribution model; (b) distance to residential in occurrence distribution model; (c) distance to ditch in occurrence distribution model; (d) distance to expressway in occurrence distribution model; (e) distance to national road in abundance distribution model; (f) distance to expressway in abundance distribution model; (g) distance to pool in abundance distribution model; and (h) mean NDVI in abundance distribution model.

## Occurrence model

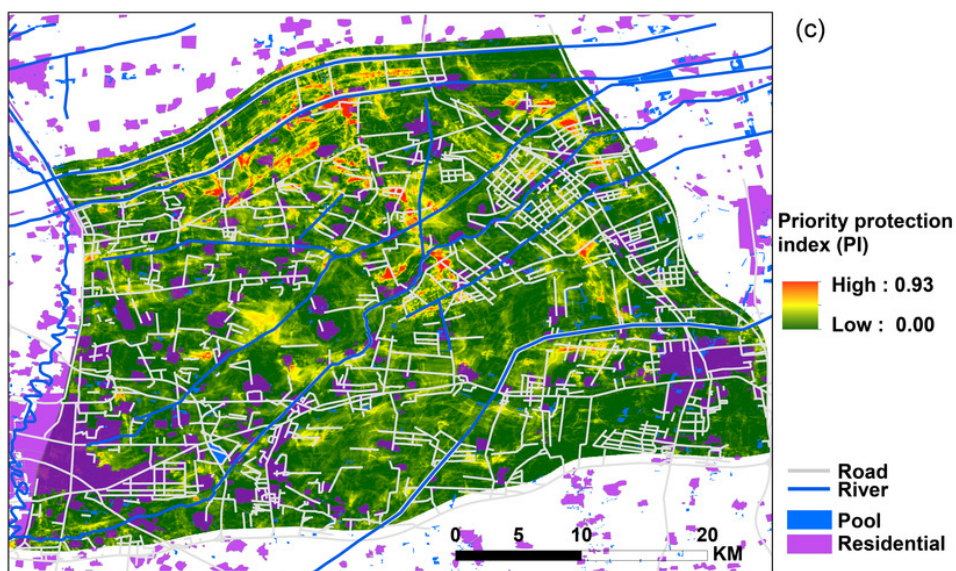
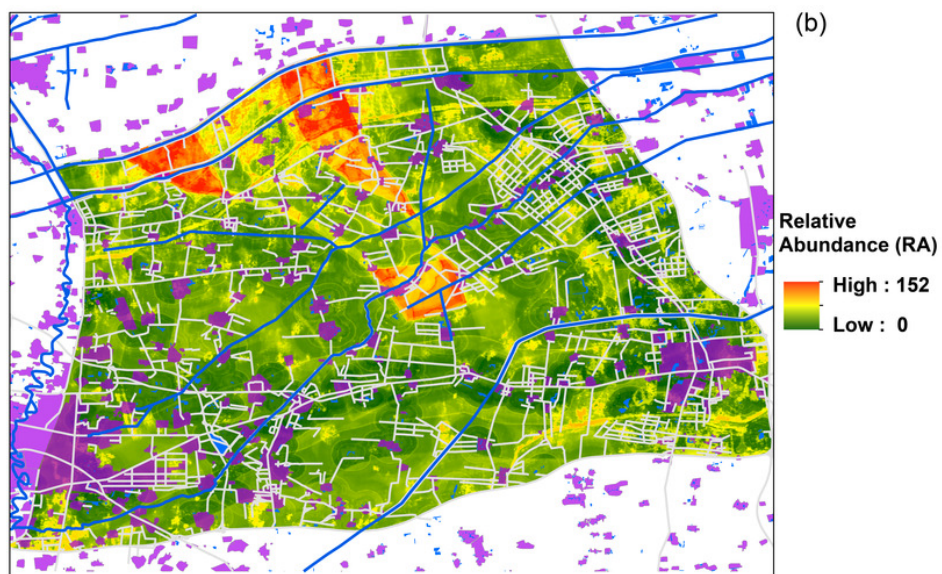
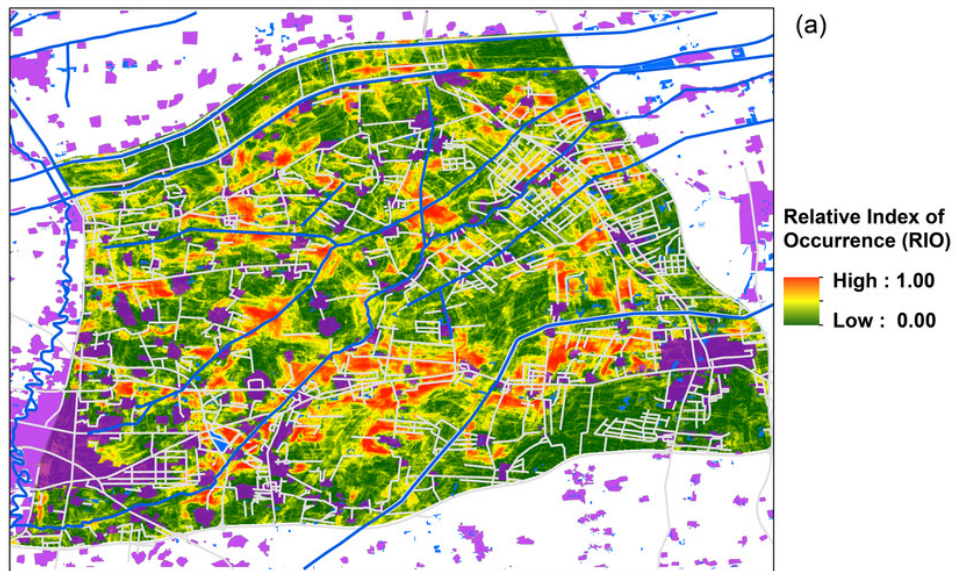
## Abundance model



## Figure 4

### Figure 4

Spatial distribution map of relative index of occurrence (RIO), relative abundance (RA) and priority protection index (PI). (a) Map of relative index of occurrence (RIO); (b) map of adjusted relative abundance (RA); and (c) map of priority protection index (PI).





**Figure 5**(on next page)

## Figure 5

Plots of the relationship between relative index of occurrence (RIO) and observation abundance. (a) Scatter plot between relative index of occurrence (RIO) and observation abundance; and (b) partial dependence plot between relative index of occurrence (RIO) and observation abundance (obtained from TreeNet, non-parametric method).

