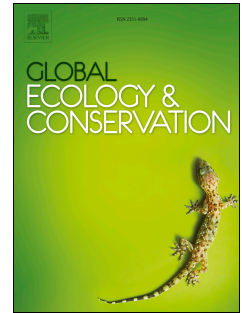# Journal Pre-proof

Using geolocator tracking data and ringing archives to validate citizen-science based seasonal predictions of bird distribution in a data-poor region

Wieland Heim, Ramona J. Heim, Ilka Beermann, Oleg A. Burkovskiy, Yury Gerasimov, Pavel Ktitorov, Kiyoaki Ozaki, Ilya Panov, Martha Maria Sander, Sissel Sjöberg, Sergei M. Smirenski, Alexander Thomas, Anders Tottrup, Ivan M. Tyunov, Mikkel Willemoes, Norbert Hölzel, Kasper Thorup, Johannes Kamp

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1 **Using geolocator tracking data and ringing archives to validate citizen-science based seasonal**

2 **predictions of bird distribution in a data-poor region**

3

4 Running title: Validating bird distribution maps for E Asia

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6 Wieland Heim[*], Ramona J. Heim, Ilka Beermann, Oleg A. Burkovskiy, Yury Gerasimov, Pavel Ktitorov,

7 Kiyoaki Ozaki, Ilya Panov, Martha Maria Sander, Sissel Sjöberg, Sergei M. Smirenski, Alexander

8 Thomas, Anders Tottrup, Ivan M. Tyunov, Mikkel Willemoes, Norbert Hölzel, Kasper Thorup,

9 Johannes Kamp

10

11 WH, RJH, IB, NH, JK: Institute of Landscape Ecology, University of Münster, Germany; OAB: Sakhalin

12 Energy, Investment Company LTD, Yuzhno-Sakhalinsk, Russia; YG: Kamchatka Department of Pacific

13 Geographical Institute, Far-eastern Branch of Russian Academy of Science, Petropavlovsk-

14 Kamchatskiy, Russia; PK: [1]Institute of Biological Problems of the North, Far-eastern Branch of Russian

15 Academy of Science, Magadan, Russia, [2]Birds Russia, Yuzhno-Sakhalinsk, Russia; KO: Yamashina

16 Institute for Ornithology, Chiba, Japan; IP: [1]Bird Ringing Centre of Russia, IPEE RAS, [2]Biological Station

17 Rybachy, ZIN RAS; MMS: Department of Life Sciences and Systems Biology, University of Turin, Italy;

18 SS, KT: Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen,

19 Denmark; SMS: Muraviovka Park for Sustainable Land Use, Blagoveshchensk, Russia; AlT: School of

20 Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen,

21 China; IMT: Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch,

22 Russian Academy of Sciences, Vladivostok, Russia; MW: Department of Biology, Lund University,

23 Sweden; AnT: Natural History Museum of Denmark, University of Copenhagen, Denmark, JK:

24 University of Göttingen, Department of Conservation Biology, Bürgerstr. 50, 37073 Göttingen

25 [*]corresponding author: wieland.heim@uni-muenster.de

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38

39 **Keywords:** East Asian Flyway; eBird; MaxEnt; migration; species distribution model; tracking

40

41 **Abstract**

42 Unstructured citizen-science data are increasingly used for analysing the abundance and distribution

43 of species. Here we test the usefulness of such data to predict the seasonal distribution of migratory

44 songbirds, and to analyse patterns of migratory connectivity.

45 We used bird occurrence data from eBird, one of the largest global citizen science databases, to

46 predict the year-round distribution of eight songbird taxa (*Agropsar philippensis*, *Calliope calliope,*

47 *Cecropis daurica*, *Emberiza aureola, Hirundo rustica, Locustella certhiola, Oriolus chinensis, Saxicola*

48 *torquatus stejnegeri*) that migrate through East Asia, a region especially poor in data but globally

49 important for the conservation of migratory land birds. Maximum entropy models were built to

50 predict spring stopover, autumn stopover and wintering areas. Ring recovery and geolocator tracking

51 data were then used to evaluate, how well the predicted occurrence at a given period of the annual

52 cycle matched sites where the species were known to be present from ringing and tracking data.

53 Predicted winter ranges were generally smaller than those on published extent-of-occurrence maps

54 (the hitherto only available source of distribution information). There was little overlap in stopover

55 regions. The overlap between areas predicted as suitable from the eBird data and areas that had

56 records from geolocator tracking was high in winter, and lower for spring and autumn migration. Less

57 than 50 % of the ringing recoveries came from locations within the seasonal predicted areas, with the

58 highest overlap in autumn. The seasonal range size of a species affected the matching of

59 tracking/ringing data with the predictions. Strong migratory connectivity was evident in Siberian

60 Rubythroats and Barn Swallows. We identified two migration corridors, one over the eastern

61 mainland of China, and one along a chain of islands in the Pacific.

62 We show that the combination of disparate data sources has great potential to gain a better

63 understanding of the non-breeding distribution and migratory connectivity of Eastern Palearctic

64 songbirds. Citizen-science observation data are useful even in remote areas to predict the seasonal

65 distribution of migratory species, especially in periods when birds are sedentary and when

66 supplemented with tracking data.

67

68 **1. Introduction**

69 Species distribution models (SDMs) have been proven to be useful tools to understand the spatio-

70 temporal occurrence of species, and allow to predict their distribution in areas that are poorly

71 covered by observational data (Guisan & Thuiller 2005). Observations from citizen scientists are

72 available in ever-increasing numbers, and commonly used for SDMs (Kéry et al. 2010; van Strien et al.

73 2013; Tye et al. 2017; Fink et al. 2020). However, the usefulness of such data for assessing abundance

74 and distribution remains controversial (Conrad & Hilchey 2011; Kamp et al. 2016), as several

75 systematic errors can affect the results. First, species identification might be wrong (Lotz & Allen

76 2007). Second, the data might be biased towards conspicuous species (due to uneven detection

77 probability), towards species-rich or easy-to-reach areas (resulting in spatial bias), and towards

78 certain times of the day or year (resulting in temporal bias) (Boakes et al. 2010; Bird et al. 2014). To

79 increase data quality, some citizen-science databases have established standard protocols and a

80 rigorous quality check (Bonter & Cooper 2012; Freitag et al. 2016). Novel analytical techniques allow

81 to correct for observer bias (Johnston et al. 2018, 2020), spatial bias (Hochachka et al. 2012) and

82 differences in detection probability (Isaac et al. 2014; Guillera-Arroita 2017).

83   The prediction of seasonal distributions or periods of movement for highly mobile and migratory

84 species remains challenging. Species may widen or change their niche during different times of the

85 annual cycle, which is a common pattern in migratory fish (Forseth et al. 1999; Weng et al. 2005),

86 mammals (Cherel et al. 2007, 2009) and birds (e.g. Martínez-Meyer et al. 2004; Nakazawa et al.

87 2004). Phenological changes in behaviour (such as density-dependent singing activity during the

88 breeding season and on spring migration in songbirds) can cause variation in detection probability

89 (Warren et al. 2013).

90 The combination of tracking and citizen-science data holds a high potential to improve species

91 distribution models. Laughlin et al. (2013) used observation data from different sources to determine

92 habitat use and stopover sites of Tree Swallows *Tachycineta bicolor*. However, the authors did not

93 model the spatial distribution based on the observation data, but used them only to analyse

94 temporal migration patterns. In contrast to field observations based on citizen science, individual

95 tracking data are spatially unbiased, and can therefore be used to model species distributions in

96 regions of low observer density (Jiguet et al. 2011; Gschweng et al. 2012; Williams et al. 2017). But

97 the availability of tracking data is usually limited to larger species and few individuals (Bridge et al.

98 2011). Alternatively, bird ringing data can be used to predict seasonal distributions, but information

99 on recovery probabilities needs to be available (Thorup & Conn 2009). In many parts of the world,

100 few ringing recoveries are available for most species (Clark et al. 2009).

101 The increasing spatial and temporal resolution of citizen-science data allows the modelling of

102 migratory movements in unprecedented temporal and spatial resolution (Hurlbert & Liang 2012;

103 Sullivan et al. 2014; Supp et al. 2015). The potential for predicting seasonal priority areas for the

104 conservation of rare species by using citizen-science observations is huge (Devictor et al. 2010).

105 However, the inclusion of individuals from resident populations might affect the predictions (Supp et

106 al. 2015), and biased predictions might result in ineffective conservation measures (Loiselle et al.

107 2003). Citizen-science based models of seasonal distributions have not been evaluated by comparing

108 the predictions with spatially unbiased tracking data so far.

109 The East Asian-Australasian flyway holds the highest number of migratory land birds, including the

110 highest number of globally threatened species of any flyway (Yong et al. 2015). Habitat loss due to

111 deforestation (Brooks et al. 1999; Wilcove et al. 2013; Estoque et al. 2019),the conversion to

112 cropland and agricultural management intensification are major drivers of biodiversity loss (Kehoe et

113 al., 2017; Zhao et al., 2006). During the past four decades such land use change happened across vast

114 areas in East and South East Asia and has been linked to declines in migratory land birds (Higuchi &

115 Morishita 1999). Russia, where most of the migratory species breed (Ravkin & Ravkin 2005; Yong et

116 al. 2015), showed an opposite development with large scale abandonment of agricultural land since

117 the break-down of the Soviet Union (Lesiv et al. 2018). Unsustainable trapping for consumption

118 (Kamp et al. 2015), cage bird trade (Shepherd et al. 2016) and religious purposes ("merit release",

119 Gilbert et al. 2012) has further contributed to the rapid population declines of several songbird

120 species that move along the East Asian flyway.

121 Species-specific causes and mechanisms for these declines are still poorly understood, as knowledge

122 on land bird migration routes, stopover sites and wintering grounds in East and South-East Asia is still

123 rudimentary (Amano & Yamaura 2007; Yong et al. 2015). Key to the conservation of migratory

124 animals is the linking of breeding, stopover and wintering areas, known as migratory connectivity

125 (Marra et al. 2011). For Asia, data is available for large birds such as geese (Palm et al. 2015) and

126   bustards (Combreau et al. 2011), but data on migratory connectivity in songbirds is lacking (Yong et

127   al. 2015).

128   Several million birds have been marked with metal rings in Asia since the 1950´s. However, the last

129   large-scale analysis of ringing and recovery data from Asia was published almost 50 years ago

130   (McClure 1974). Moreover, new technology has revolutionized bird migration research: Light-level

131   based geolocators enable us to follow the migration of songbirds down to 10 g body weight, which

132   are too small to carry satellite transmitters (Bridge et al. 2011). Dozens of geolocation studies were

133   conducted in the American and European-African flyways, but only few published results are

134   available for the Asian migration routes (McKinnon & Love 2018).

135   Here, we use observational data from citizen scientists to predict the seasonal distribution of

136   songbird species that migrate along the East Asian route. We then validate the predicted

137   distributions with bird ringing and tracking data.

138   Our aims were A) to test the usefulness of citizen-science observation data to predict the seasonal

139   distribution of migratory species in a data-poor region by validating it with ringing and tracking data,

140   and B) to analyse migratory connectivity and patterns of non-breeding distribution of a set of East

141   Asian songbirds.

142

143   **2.   Materials and Methods**

144   *2.1 Study region*

145   Our study region covered the area that is likely to be reached by birds migrating in the East Asian

146   flyway: eastwards from the Ural Mountains to Kamchatka (from 60° to 160° longitude) and

147   northward from Indonesia to the Arctic Circle (-10° to 60° latitude).

148   *2.2 Predicting seasonal species' distributions*

149 We built maximum entropy (MaxEnt) models, a class of SDMs allowing to model the geographic

150 distribution with presence-only data (Phillips et al. 2006), using the R package dismo (Hijmans et al.

151 2016b).

152 To feed our models, we used unstructured citizen science data from eBird, the world's largest

153 database of bird observations (Sullivan et al. 2009; La Sorte & Somveille 2019). We selected all land

154 bird species for which also tracking data were available (see below), namely Yellow-breasted Bunting

155 *Emberiza aureola*, Siberian Rubythroat *Calliope calliope*, Pallas´s Grasshopper Warbler *Locustella*

156 *certhiola*, Barn Swallow *Hirundo rustica*, Red-rumped Swallow *Cecropis daurica*, Black-naped Oriole

157 *Oriolus chinensis*, Stejneger´s Stonechat *Saxicola torquatus stejnegeri* and Chestnut-cheeked Starling

158 *Agropsar philippensis*. We downloaded all observations available up to October 2018. We defined

159 April and May as spring migration, September and October as autumn migration, and November to

160 March as wintering periods. We used two approaches to correct for spatial bias in the eBird

161 observation data. First, we randomly selected only one observation per grid cell (see below) for each

162 species and season (Kramer-Schadt et al. 2013). Such systematic sampling has been shown to be the

163 most efficient method for correcting sampling bias (Fourcade et al. 2014). Second, we included a bias

164 file (representing the sampling probability surface based on available species records, Fourcade et al.

165 2014) as most observations come from densely populated areas and places where birdwatchers

166 congregate (Boakes et al. 2010). Models containing a bias file had a poorer fit than those without

167 bias correction (Suppl. 1), therefore the bias grid was not used in the final models. An overview of the

168 sample sizes per species and season is given in Table 1. MaxEnt models rely on a comparison of

169 probability densities of presence-only records with background data (Elith et al. 2011). For each

170 model, we sampled 10,000 random points across the study area and considered these background

171 locations.

172 As predictors, we used climatic variables (Fick & Hijmans 2017) and altitude (Jarvis et al. 2008), which

173 are the main factors that determine large-scale distributional patterns in birds (Rahbek & Graves

174 2001). From the BioClim dataset (Fick & Hijmans 2017), we extracted mean monthly precipitation,

175   maximum monthly temperature and mean monthly water vapour pressure, and calculated the

176   average mean for all seasons (autumn, winter, spring) for all available years (1970-2000). We also

177   calculated the mean Normalized Difference Vegetation Index (NDVI) for each season based on the

178   MODIS product MOD13C1 (Didan 2015). Many songbirds are known to track seasonal resource

179   availability (Thorup et al. 2017), and the NDVI has been shown to be correlated with migration

180   phenology (Robson & Barriocanal 2011), including in Siberian Rubythroats migrating along the East

181   Asian flyway (Heim et al. 2018). Additionally, we included land cover (10 classes, 30 m resolution) as

182   a predictor variable (downloaded from http://www.globallandcover.com, Chen et al. 2017) as it

183   influences species distributions on regional scales (Thuiller et al. 2004). All layers were resampled to

184   a resolution of 0.05 degrees (approximately 5.55 by 5.55 km at equator) using the *resample* function

185   from the R package raster.

186   We built separate models for spring migration, autumn migration and winter based on the seasonal

187   records from eBird as defined above, including the climatic and NDVI data from the respective

188   months (Williams et al. 2017). For land cover and altitude, the same layers were used for all seasons.

189   Model performance was assessed using the area under a receiver-operator curve (AUC) and Cohen´s

190   Kappa (Manel et al. 2001). We used three different thresholds to translate the gradual predictions of

191   habitat suitability into binary presence-absence maps to map the range predicted as suitable:

192   maximum kappa, maximum specificity and sensitivity, and zero omissions of presence points from

193   the predicted range. Predicted values above the corresponding threshold were interpreted as

194   suitable range, while values below the threshold were interpreted as unsuitable range (Jiménez-

195   Valverde & Lobo 2007). We chose the most sensitive threshold for each seasonal model that would

196   minimize the predicted range to gain maximum specificity. Preparation of the layers was done using

197   the R packages raster (Hijmans et al. 2016a), rgdal (Bivand et al. 2015), rJava (Urbanek 2009) and

198   rgeos (Bivand et al. 2016).

199   *2.3 Validating predictions of seasonal distributions*

200   To validate the MaxEnt seasonal range predictions, we used different sources of data (Figure 1):

201   Published and unpublished geolocation tracking data, and ringing recoveries. Geolocation data are

202   spatially unbiased, but the precision of the location estimates varies strongly due to shading by

203   vegetation, bird behaviour, length of stay at a given site and time of the year (Lisovski et al. 2012).

204   Ringing recovery data are spatially biased towards areas of higher activities of ringers and more

205   densely populated areas with a higher detection probability of dead birds (Thorup et al. 2014).

206   Geolocation data were available from our own field studies (6 species, Heim et al. 2018, Heim et al.

207   unpublished, Figure 2) and were analyzed using the R package GeoLight (Lisovski & Hahn 2012). All

208   positions with a minimum stopover duration of five days were considered, for details see Suppl. 2

209   and Heim et al. (2018). Geolocation data for two more species were gathered from publications

210   (Koike et al. 2016; Yamaura et al. 2017).

211   Ringing data were obtained from the national ringing archives of Russia (Moscow Bird Ringing

212   Centre) and the ringing recovery archive of the Ministry of the Environment, Tokyo, Japan, managed

213   by the Yamashina Institute for Ornithology, Abiko, Chiba, Japan. Additional ringing recovery data

214   were gathered from McClure (1974). We only included long-distance recoveries (≥200 km between

215   ringing and recovery site) within our study area.

216   To identify out-of-range predictions, we overlaid our predictions with coarse extent-of-occurrence

217   (EOO) maps available from BirdLife International (BirdLife International 2019). These maps were

218   available for winter distribution as well as for spring and autumn combined. We calculated the

219   overlap between the predictions and the EOO maps using the *gArea* function in R package rgeos

220   (Bivand et al. 2016). We give both the percentage of the predicted areas covered by the EOO maps,

221   and the percentage of the EOO map extent covered by the predictions.

222   To externally validate our seasonal range predictions, we calculated the proportion of geolocator

223   positions and ring recoveries that fell onto the area predicted as suitable in the given season (for

224   season definitions see above). For geolocator positions, we used mean coordinates (Suppl. 3). To

225   incorporate uncertainty associated with the estimated mean coordinate, we identified the area

226   covered by the range of the latitude and longitude standard deviation of the mean coordinate

227   (resulting in polygons of varying size). We then evaluated whether these polygons showed any

228   overlap with the area predicted as suitable by the MaxEnt model.

229   In a second step, we modelled the probability of our validation locations to fall within the predicted

230   ranges using generalized linear mixed-effect models (GLMMs) in R package lme4 (Bates et al. 2014).

231   We used models with a binomial error distribution and logit link (i.e. binary logistic regression).

232   Locations that fell within the predicted range were considered successes (1), locations that were out

233   of range were considered failures (0). Data type (geolocator or ringing data), season (winter, spring

234   and autumn) were fitted as fixed independent effects. The extent of the seasonal predicted range

235   was fitted as covariate. Species identity was included as random effect. We built two sets of

236   candidate models, one defining the matching/non-matching of the tracking locations with the

237   predicted distribution by the mean coordinates of the geolocation fixes, the other using a polygon of

238   the mean coordinate plus the area added by considering the standard deviation. Model assumptions

239   were graphically tested using residual plots in the DHARMa package (Hartig 2019). Goodness of fit

240   was examined with the conditional and marginal R^2 (Nakagawa & Schielzeth 2013).

241   *2.4 Connectivity analyses*

242   We analysed migratory connectivity by correlating the longitude of the location during breeding

243   season with the longitude during the non-breeding season for ring recoveries and geolocation

244   positions (Trierweiler et al. 2014) using a Pearson´s product moment correlation coefficient. A

245   significant correlation would indicate high migratory connectivity, i.e. the use of population-specific

246   routes (Finch et al. 2017). If more than one site was available for one individual, we chose the final

247   winter site with the longest duration of stay. To estimate the strength of migratory connectivity we

248   conducted a Mantel test (with 9,999 random permutations) using the R package ade4 (Dray & Dufour

249   2007; Ambrosini et al. 2009).

250   **3. Results**

251   *3.1 Predicted distributions*

252   The predicted non-breeding ranges covered almost exclusively South and South-East Asia in all

253   species, only very few suitable areas were predicted in Russia, Kazakhstan, Mongolia and NW China

254   (Fig. 3). A migration corridor through Central Asia, appearing as a high predicted suitability in spring

255   and/or autumn west of the Himalayas, was only found for Barn Swallow and Red-rumped Swallow

256   (Fig. 3). The predictive performance of the models varied across seasons and species, but was

257   acceptable in all cases (AUC > 0.75, Tab. 2). Models with more presence points exhibited the best fit

258   (Tab. 2). The predicted ranges were smallest when using the threshold that maximized kappa (Suppl.

259   1). This threshold was used for all range maps and further calculations. The size of the predicted

260   ranges varied considerably (range: 22-900 grid cells) and seasonal differences were also species-

261   specific (Fig. 3). Smallest ranges were predicted for the Chestnut-cheeked Starling during autumn and

262   winter and for the Yellow-breasted Bunting during autumn, largest ranges were predicted for Barn

263   Swallow and Red-rumped Swallow in all seasons.

264   *3.2 Geolocator tracks*

265   We gathered 171, 43 and 28 geolocation positions of 8 species for autumn, winter and spring,

266   respectively (Tab. 1, Suppl. 3).

267   All individuals of all species tagged in the Russian Far East migrated south-westward in autumn,

268   stopped over in China and wintered in South-East Asia (Fig. 3). No movements were detectable

269   during winter, except for one Yellow-breasted Bunting which moved in February from southern

270   Myanmar to the north of the country. All winter locations were located on the Indochinese peninsula

271   and adjacent China (Yunnan province), except for the Yellow-breasted Buntings, which wintered

272   more to the west in Myanmar or northeast India. Spring migration data were only available for three

273   species: one single Pallas´s Grasshopper Warbler and one Black-naped Oriole used almost identical

274   stopover areas for their return migration, whereas all Siberian Rubythroats moved slightly more to

275 the east, with the stopover sites situated in southern China and not in northern China as during

276 autumn migration.

277 The standard deviation of positions was highest for latitude during autumn (Suppl. 3), as most

278 species migrate around the autumnal equinox.

279 *3.3 Ring recoveries*

280 Long-distance ring recoveries were available for six of the included species (Tab. 1). Siberian

281 Rubythroats and Barn Swallows ringed during the breeding season or on migration in Japan and

282 easternmost Russia (Sakhalin, Kamchatka) were mainly recovered in winter in Taiwan and the

283 Philippines, and vice versa (Fig. 3). A Yellow-breasted Bunting ringed on the breeding grounds in

284 Kamchatka was recovered during autumn migration near Beijing in mainland China, and one

285 Stejneger´s Stonechat migrated from southern Japan to South Korea in autumn. Birds ringed in the

286 Russian Far East (mainland) were exclusively recovered on the South-East Asian mainland, and vice

287 versa. For Barn Swallow, Red-rumped Swallow and Chestnut-cheeked Starling geolocation and

288 ringing recovery data were available from the same areas of origin, and the main direction of

289 migratory movements was similar in all cases.

290 *3.4 Validation*

291 The predicted ranges were generally smaller than the distribution ranges given by BirdLife, and on

292 average covered only 40 % (± 28 %, range: 5-80 %) of the BirdLife winter distributions (Tab. 4). On

293 average, only 61 % (± 29 %, range: 7-90 %) of the area predicted as suitable ranges were within the

294 BirdLife ranges. Very low overlap (< 10 %) was found for the Chestnut-cheeked Starling, whereas

295 good concordance (> 70 %) was evident for Siberian Rubythroat and Red-rumped Swallow.

296 The proportion of the mean geolocation positions that fell onto the predicted range was rather low

297 in all seasons for all species combined (23, 35 and 18 % for autumn, winter and spring, respectively,

298 Tab. 3). We found species-specific differences – between 0 and 100 % of the exact positions (without

299 standard deviation of the coordinates) were within the predicted species´ ranges. When including the

300 standard deviation of the geolocation positions, most of the positions were within the predicted

301 range (51, 67 and 78 % for autumn, winter and spring, respectively, Tab. 3). SDM prediction showed

302 highest overlap with the geolocator positions in winter, and least overlap in autumn. Highest overlap

303 was found for the Siberian Rubythroat, whereas most locations were outside of the predicted range

304 for the Chestnut-cheeked Starling.

305 Only around a third of the ringing and recovery sites were situated within the corresponding seasonal

306 predicted range (37, 32 and 34 % for autumn, winter and spring, respectively, Tab. 3). Species-

307 specific differences were high, ranging from 0 to 100 %, but seasonal differences were low. Detailed

308 results of the comparisons can be found in Table 3 and Supplement 5.

309 Our models revealed that the probability of a point falling onto the predicted range was dependent

310 on the seasonal range size (Tab. 5), while the random factor *species* explained little or no variance.

311 Seasonal effects on the probability were only found when the mean coordinates of geolocation

312 positions were considered, while the data type had only a significant effect when the standard

313 deviation around geolocation points was included (Tab. 5). However, both models explained only

314 very little of the overall variance ($R^2 < 0.05$, Tab. 5).

315 *3.5 Migratory connectivity*

316 We had sufficient data to analyse migratory connectivity in two species. The longitudes of breeding

317 and non-breeding sites were positively correlated in both Siberian Rubythroat (Pearson´s, r = 0.91, p

318 < 0.001, n = 14 individuals) and Barn Swallow (r = 0.53, p < 0.001, n = 110). We found evidence of

319 strong migratory connectivity in the Siberian Rubythroat and to a lesser degree in the Barn Swallow

320 (Mantel correlation coefficients of 0.80 (p < 0.001) and 0.25 (p < 0.001), respectively).

321

322   4. **Discussion**

323   *4.1 Predicted seasonal distributions*

324 We predicted the spatio-temporal occurrence of a set of Eastern Palearctic Passerines during

325 autumn, winter and spring based on unstructured citizen-science data. The predicted distributions

326 varied significantly in their extent. For some species (e.g. Barn and Red-rumped Swallows), huge

327 parts of the study region were predicted suitable, with high overlap between seasons. This pattern is

328 most likely caused by the existence of sedentary populations in the south of the range (BirdLife

329 International 2019), which may bias seasonal predictions (Supp et al. 2015). Strong seasonal

330 differences in occurrence can be more easily detected in true long-distance migrants (Supp et al.

331 2015), such as Yellow-breasted Bunting, Pallas´s Grasshopper Warbler and Stejneger´s Stonechat in

332 our study. In some of the species, migration of the northernmost breeding populations might take

333 place outside of the migration periods that we used for our models (e.g. June and August), and

334 therefore observations of migrating individuals might have been disregarded or mixed up with

335 breeding season observations from southern populations (Supp et al. 2015). This might be the case

336 for the Black-naped Oriole, for which only areas in South-East Asia were predicted suitable, but no

337 stopover areas further north during spring or autumn migration. Our geolocation data revealed

338 pronounced differences in the timing of migration between and within species. For example, some

339 Siberian Rubythroats have already arrived in October at their wintering sites, but one only in

340 December. The precision of the predictions could have been increased by building monthly or full-

341 year models instead of seasonal models (Williams et al. 2017). However, fitting a full-year model

342 would have required many more data points for all months, which were not available from the eBird

343 dataset for most of the studied species. A limited number of presence points will often result in

344 poorer model outcomes, and single erroneous observations can have a stronger impact on the

345 predicted ranges when low numbers of presence records are available for modeling (Wisz et al.

346 2008). Observations of birds outside their usual geographic range, known as vagrants, tend to get

347 more comprehensively reported by birdwatchers (Callaghan et al. 2018). This might explain the

348 model result for the Chestnut-cheeked Starling, where single observations of vagrants from the

349 South-East Asian mainland outside of the known wintering range (Robson 2008) affected our model

350 strongly, leading to a limited overlap of the BirdLife range with our predictions. Furthermore, caused

351 by the rather coarse resolution of our background layers, many coastal sites might have been

352 classified as water (and therefore as unsuitable for the species) by our SDMs. For all other species,

353 the larger part of the predicted distributions overlapped with the BirdLife EOO maps, suggesting an

354 overall good fit. The BirdLife ranges are coarser, and is expected to include unsuitable habitats within

355 the area of occurrence, whereas our modeled predictions might depict the actual distribution more

356 precisely (Graham & Hijmans 2006; Hurlbert & Jetz 2007; Cantú-Salazar & Gaston 2013).

357 Our SDMs predicted some regions to be suitable for most of the studied songbirds, and those might

358 therefore constitute important areas for the conservation of migratory land birds in East Asia (Fig. 3),

359 although the set of species included here is small and not necessarily representative for all East Asian

360 songbirds. During winter, the south-eastern end of mainland South-East Asia and the Ganges-

361 Brahmaputra floodplain in Bangladesh were predicted as suitable for many of the species. Hebei

362 province, surrounding the Chinese capital Beijing, was predicted as the main autumn stopover area

363 for Siberian Rubythroat, Stejneger´s Stonechat, Barn Swallow and the critically endangered Yellow-

364 breasted Bunting. The lower Yangtze River valley was predicted to be an important stopover area

365 during spring for Pallas´s Grasshopper Warbler, and during both spring and autumn seasons for

366 Yellow-breasted Bunting, Siberian Rubythroat, Barn and Red-rumped Swallow as well as Stejneger´s

367 Stonechat. Many of the key stopover areas in eastern China are currently not protected (Lei et al.

368 2019). However, the lack of citizen-science records from western China, where birds might utilize

369 different stopover habitats (caused by climate-driven differences in habitat availability), and the

370 overrepresentation of observations from the densely populated Shanghai and Beijing areas might

371 have biased our predictions (Guillera-Arroita 2017), despite our correction for sampling bias.

372 Parts of the predicted areas of occurrence well beyond the known range limits of the species´ might

373 be suitable, but might not have been colonized so far or are not reachable during migration by the

374 studied species (Engler et al. 2014). This is most likely true for predicted areas outside of the BirdLife

375 range maps in Indonesia for Siberian Rubythroat and Pallas´s Grasshopper Warbler and for areas in

376   South-East India for Siberian Rubythroat, Pallas´s Grasshopper Warbler, Stejneger´s Stonechat and

377   Chestnut-cheeked Starling (Fig. 3).

378   *4.2 Validation of the predictions*

379   The validation with spatially unbiased geolocation positions, ring recoveries and with the available

380   BirdLife range maps suggested that our predictions were more accurate for winter compared to

381   spring or autumn migration. This might be explained by the fact that our study species are much less

382   mobile during winter compared to the migration seasons – only one of the geolocator-tagged birds

383   moved over a longer distance in winter. During migration, birds temporarily use a variety of sites and

384   habitats, which could lead to a decreased precision in model predictions (Williams et al. 2017). The

385   stronger overlap of the model predictions with tracking data during winter might also be caused by

386   inherent seasonal differences in the precision of geolocation data. First, latitude can hardly be

387   estimated during equinox periods (Fudickar et al. 2012), a time coinciding with autumn and spring

388   migration for most species. Second, location errors are decreasing with the length of the stationary

389   period, so that short stopovers during migration can less precisely be determined than long stays on

390   the wintering grounds (Rakhimberdiev et al. 2016).

391   On the contrary, based on our GLMMs, season had no or only a weak effect on the probability that

392   our validation points fell into the predicted ranges. Instead, the range extent was the best predictor.

393   This is most likely linked to seasonal differences in the size of the predicted ranges: in our study,

394   smaller ranges were predicted for autumn migration (Suppl. 4). Narrower distributional ranges or

395   ecological niches during periods of migration are known from many species (e.g. Suárez-Seoane, de

396   la Morena, Prieto, Osborne, & de Juana, 2008).

397   We also found a better overlap of the predicted ranges with point locations of ring recoveries than

398   with the mean geolocation points. While geolocation data are spatially unbiased, the probability of

399   recovery of a ringed bird is linked to human density or targeted ringing activities (Thorup & Conn

400   2009). The bird ringing data used in our study mainly reflects the high activity of Japanese ringing

401   groups, whereas only few recoveries were available for birds migrating over the Asian mainland. The

402   lack of ringing recoveries from e.g. Indonesia is most likely related to limited awareness about bird

403   ringing studies in these regions (McClure, 1974). The same spatial bias might be inherent in the eBird

404   data used for our predictions: most major cities are located along the coasts of East Asia and this is

405   where most birdwatchers are concentrated. This likely led to the perception, that songbirds mainly

406   migrate along coastal flyways (see map in Yong et al., 2015). In particular, geolocator tracking

407   revealed that most of our study species likely migrated over the Asian mainland, with no evidence for

408   migration along the coastlines or long-distance sea crossings (with the exception of the Chestnut-

409   cheeked Starling). This pattern has rarely been demonstrated for Asian songbirds before. There are

410   only few studies that provide data on songbird migration over the East Asian mainland, for example

411   from the Fenghuang mountains in southern China (Han et al. 2007), and from a bird ringing site in

412   south-east Mongolia (Sukhbaatar 2019). The avoidance of sea crossings and migration over mainland

413   is likely a typical, but so far poorly evidenced, characteristic of most East Asian land bird migrants.

414   All birds tracked from mainland East Russia wintered in South-East Asia, but for some of the species,

415   a much larger wintering range was predicted by our models, extending westwards into India. Birds

416   wintering in these areas might originate from the western part of their breeding distribution, from

417   which we lack data. Barn Swallows and Red-rumped Swallows reach India through Central Asia

418   (Gavrilov et al. 2002), but due to the lack of observations from this area it seems unlikely that other

419   species such as the Siberian Rubythroat or Yellow-breasted Bunting would use the Central Asian

420   route across high mountain ranges as well.

421   *4.3 Migratory connectivity*

422   The combination of different data types allowed us to quantify migratory connectivity in selected

423   East Asian songbirds for the very first time. The two analyzed species, Barn Swallow and Siberian

424   Rubythroat, seem to use multiple, population-specific routes. This is unexpected, as high migratory

425   connectivity was found to be uncommon among long-distance migrants from Neotropic and Afro-

426   Palearctic flyways (Finch et al. 2017). Two main migration corridors were used in East Asia:

427   Individuals belonging to populations breeding in mainland East Russia migrate through mainland

428   China and spend the winter in South-East Asia ("mainland corridor"), while birds ringed during the

429   breeding season or on migration in Japan and easternmost Russia (Sakhalin, Kamchatka) were mainly

430   recovered in winter in Taiwan and the Philippines, and vice versa ("island corridor").

431   We found a higher degree of connectivity in the Siberian Rubythroat than in the Barn Swallow. This

432   could be explained either by the lower sample size for the Siberian Rubythroat or by the availability

433   of data from a wider range of different populations (no data were available for Barn Swallows from

434   Kamchatka). Another issue could be the obvious differences in ringing effort, especially during the

435   non-breeding season, which might have affected the results, and the fact that some records in our

436   data set refer to individuals which were still on migration (Ambrosini et al. 2009).

437   Low migratory connectivity could be expected for species in which multiple populations use a

438   common route (Finch et al. 2017). We found that Yellow-breasted Buntings from mainland East

439   Russia use the same autumn stopover area in north-east China as an individual ringed in Kamchatka

440   (Fig. 3). The wintering sites of the geolocator-tagged birds from East Russia are close to the recovery

441   sites of ringed Yellow-breasted Buntings from the northernmost and westernmost ends of its

442   breeding distribution. Therefore, it seems likely that all populations of the Yellow-breasted Bunting

443   use the same migration corridor in East Asia. This could explain why unsustainable harvest in China

444   has led to a disproportionally wide-ranging decline in this species (Kamp et al. 2015). Another taxon,

445   which might share this migration pattern, is the Stejneger's Stonechat - birds from Hokkaido are

446   known to jump to the East Asian mainland before starting to migrate southwards (Yamaura et al.

447   2017), most likely along the same route as their conspecifics from the mainland.

448   The remaining study species likely use only one migration route through East Asia, since they breed

449   either only on the mainland (mainland corridor: Pallas's Grasshopper Warbler, Black-naped Oriole,

450   Red-rumped Swallow) or only on the Japanese archipelago and adjacent Russian islands (island

451   corridor: Chestnut-cheeked Starling).

452   *4.4 Conclusions*

453   The combination of SDMs, ringing and tracking data provided a valuable set of tools to understand

454   the spatio-temporal distribution of birds in a data-poor region. We found that species occurrence

455   during stationary periods in winter can be rather accurately predicted with unstructured citizen-

456   science observation data, while predictions of occurrence during the migration periods were less

457   precise. Ringing and tracking data on the other hand can provide valuable insights into migration

458   routes and migratory connectivity, but sample sizes are often small, and the spatial resolution varies.

459   We argue that all available data sources should be included when assessing seasonal distribution of

460   migratory species.

461   Our results highlight several regions as potential hotspots for migratory land birds, but further

462   studies using geolocators or transmitter tracking will be necessary to pin-point important stopover

463   areas to inform the conservation of Eastern Palearctic Passerines.

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480   **Tables**

481   **Table 1**: Sample sizes for eBird observations, geolocation data and ringing recoveries for the selected

482   target species (excluding data from the breeding season). The number of recoveries of ringed birds is

483   based on data of the ringing schemes of Russia and Japan until 2017.

Species	eBird observations (autumn/winter/spring)	Geolocation (individuals/ positions)	Ringing (long-distance recoveries)
Yellow-breasted Bunting	101/113/93	3/9	3
Siberian Rubythroat	334/467/430	10/21	136
Pallas´s Grasshopper Warbler	129/173/183	1/3	0
Barn Swallow	2619/3328/3475	1/1	200
Red-rumped Swallow	1095/1555/1442	1/1	1
Black-naped Oriole	506/562/621	1/7	0
Stejneger´s Stonechat	168/223/219	12/55	1
Chestnut-cheeked Starling	87/41/127	16/145	8

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491 **Table 2**: Predictive performance of the MaxEnt species distribution models. Given is the number of

492 eBird presence points used for each of the seasonal models (n) and the respective AUC and kappa

493 statistics.

Species	Autumn			Winter			Spring		
	n	AUC	kappa	n	AUC	kappa	n	AUC	kappa
Yellow-breasted Bunting	101	0.82	0.29	113	0.93	0.31	93	0.91	0.30
Siberian Rubythroat	334	0.89	0.39	467	0.95	0.55	430	0.86	0.40
Pallas´s Grasshopper Warbler	129	0.90	0.22	173	0.97	0.56	183	0.89	0.35
Barn Swallow	2619	0.87	0.56	3328	0.91	0.69	3475	0.82	0.51
Red-rumped Swallow	1095	0.88	0.50	1555	0.93	0.68	1442	0.85	0.46
Black-naped Oriole	506	0.91	0.48	562	0.96	0.66	621	0.91	0.51
Stejneger´s Stonechat	168	0.91	0.35	223	0.95	0.50	219	0.90	0.40
Chestnut-cheeked Starling	87	0.96	0.53	41	0.95	0.30	127	0.96	0.50

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501   **Table 3:** Overlap of the seasonal predictions with the coordinates of mean geolocation positions

502   ("geolocation points"), polygons based on the standard deviation around mean geolocation positions

503   ("geolocation points + SD") and the position of ringing recoveries. The first column for each species

504   and season indicates how many of the available points were within the predicted range, the second

505   column the percentage (in %).

Species	Autumn		Winter		Spring	
Geolocation points	*n*	*%*	*n*	*%*	*n*	*%*
Yellow-breasted Bunting	0/5	0.0	1/4	25.0	0/0	NA
Siberian Rubythroat	0/7	0.0	5/8	62.5	4/6	66.7
Pallas´s Grasshopper Warbler	0/1	0.0	1/1	100.0	0/1	0.0
Barn Swallow	0/1	0.0	0/0	NA	0/0	NA
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA
Black-naped Oriole	0/4	0.0	1/1	100.0	0/2	0.0
Stejneger´s Stonechat	6/43	14.0	6/12	50.0	0/0	NA
Chestnut-cheeked Starling	34/110	30.9	0/16	0.0	1/19	5.3
Total	40/171	23.4	15/43	34.9	5/28	17.9
Geolocation points + SD	*n*	*%*	*n*	*%*	*n*	*%*
Yellow-breasted Bunting	3/5	60.0	4/4	100.0	0/0	NA
Siberian Rubythroat	5/7	71.4	8/8	100.0	6/6	100.0
Pallas´s Grasshopper Warbler	0/1	0.0	1/1	100.0	1/1	100.0
Barn Swallow	0/1	0.0	0/0	NA	0/0	NA
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA
Black-naped Oriole	0/4	0.0	1/1	100.0	0/2	0.0
Stejneger´s Stonechat	23/43	53.5	9/12	75.0	NA	NA
Chestnut-cheeked Starling	NA	NA	5/16	31.3	NA	NA
Total	31/61	50.8	29/43	67.4	7/9	77.8
Ringing recoveries	*n*	*%*	*n*	*%*	*n*	*%*
Yellow-breasted Bunting	1/1	100.0	2/2	100.0	0/0	NA
Siberian Rubythroat	77/236	32.6	4/25	16.0	0/9	0.0
Pallas´s Grasshopper Warbler	0/0	NA	0/0	NA	0/0	NA
Barn Swallow	40/77	51.9	39/114	34.2	32/80	40.0
Red-rumped Swallow	0/0	NA	1/1	100.0	0/0	NA

Black-naped Oriole	0/0	NA	0/0	NA	0/0	NA
Stejneger´s Stonechat	1/1	100.0	0/1	0.0	0/2	0.0
Chestnut-cheeked Starling	0/4	0.0	0/0	NA	1/6	16.7
Total	119/319	37.3	46/143	32.2	33/97	34.0

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507 **Table 4:** Validation of the seasonal predictions ("SDM") with existing extent-of-occurrence maps

508 ("EOO", BirdLife International, 2019)**.** Note that we had to combine the predictions for spring and

509 autumn ("Migration") to analyse overlap with the BirdLife EOO maps. The spatial overlap is given in

510 %.

Species	Migration		Winter	
	SDM covered by EOO map	*EOO covered by SDM*	*SDM covered by EOO map*	*EOO covered by SDM*
Yellow-breasted Bunting	NA	NA	55.7	33.5
Siberian Rubythroat	29.2	9.2	70.9	76.2
Pallas´s Grasshopper W.	24.7	11.6	29.6	16.0
Barn Swallow	NA	NA	90.2	58.1
Red-rumped Swallow	NA	NA	85.3	80.0
Black-naped Oriole	NA	NA	73.7	34.3
Stejneger´s Stonechat	NA	NA	75.1	19.3
Chestnut-cheeked Starling	NA	NA	6.9	5.0
Total (mean)	**26.9**	**10.4**	**60.9**	**40.3**

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513 **Table 5:** Effects of data type, season and range size on the probability of our validation locations to

514 fall within the predicted ranges using GLMMs. Significant effects are highlighted in bold.

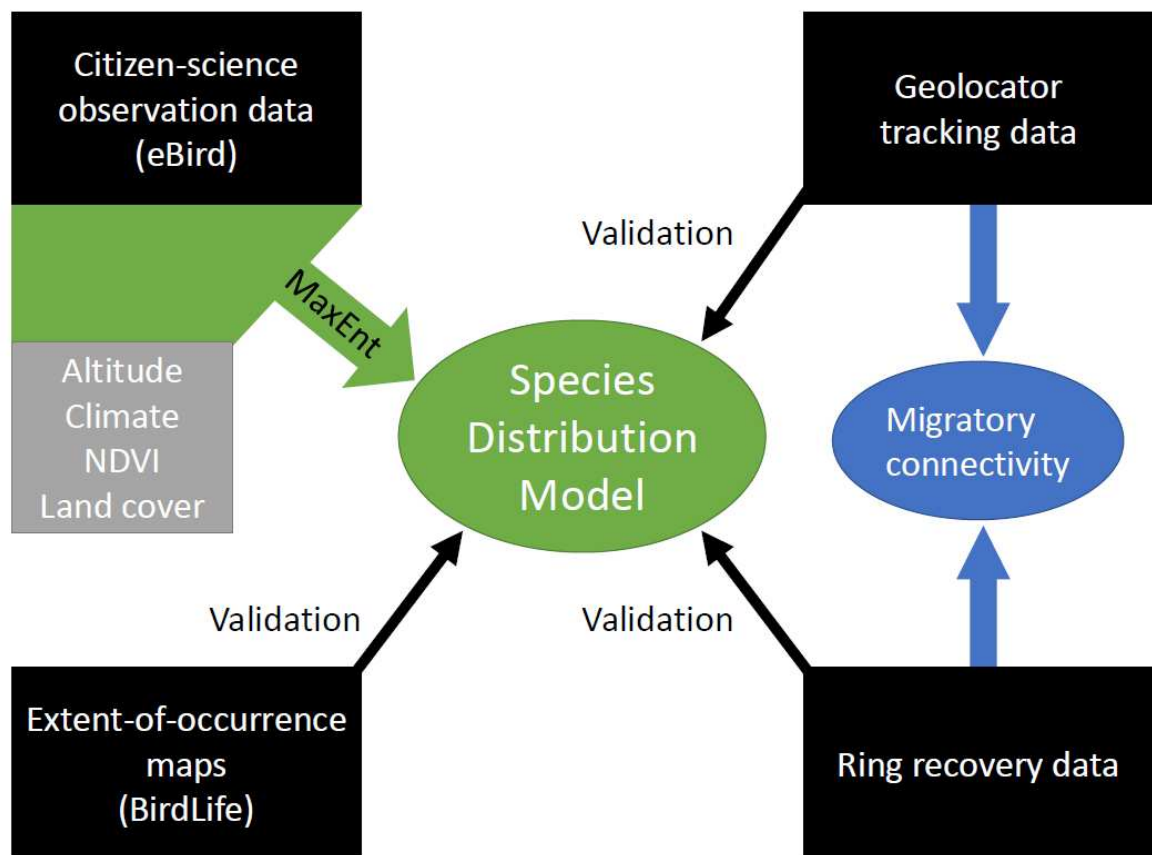| Model	Data type	Season	Range size	R^2
1 (point data)	$Chi^2 = 0.456$	$Chi^2 = 7.700$	$Chi^2 = 10.497$	$R_{cond} = 0.03$
	p = 0.500	p = **0.021**	p = **0.001**	$R_{marg} = 0.03$
2 (polygons)	$Chi^2 = 26.767$	$Chi^2 = 4.093$	$Chi^2 = 4.700$	$R_{cond} = 0.05$
	p < **0.001**	p = 0.129	p = **0.030**	$R_{marg} = 0.05$

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519 **Figures**

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521 **Figure 1**: Overview on the data sources used for fitting our seasonal species distribution models, for

522 the validation of these models and for analyzing migratory connectivity.

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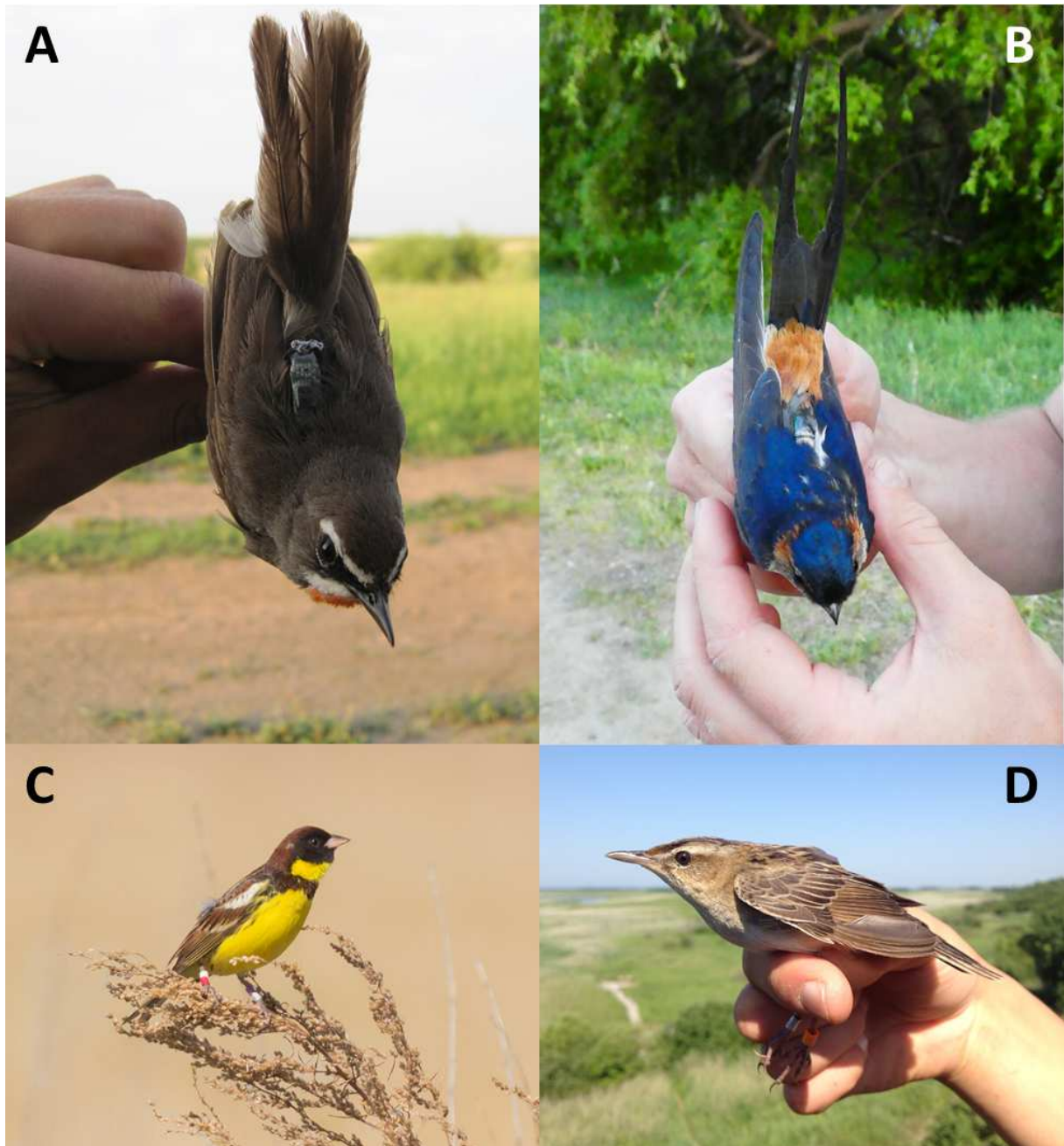
Figure 2: Light-level geolocators mounted with leg-loop harnesses on the back of A) Siberian Rubythroat, B) Red-rumped Swallow, C) Yellow-breasted Bunting and D) Pallas´s Grasshopper Warbler. Note that the devices are well visible from above (A-B) but are hardly visible in more natural postures (C-D). Color-ring combinations were used to identify individual birds in the field (C-D). Photographs by R. J. Heim, L. Fuhse, A. Heim and W. Heim (from A to D).

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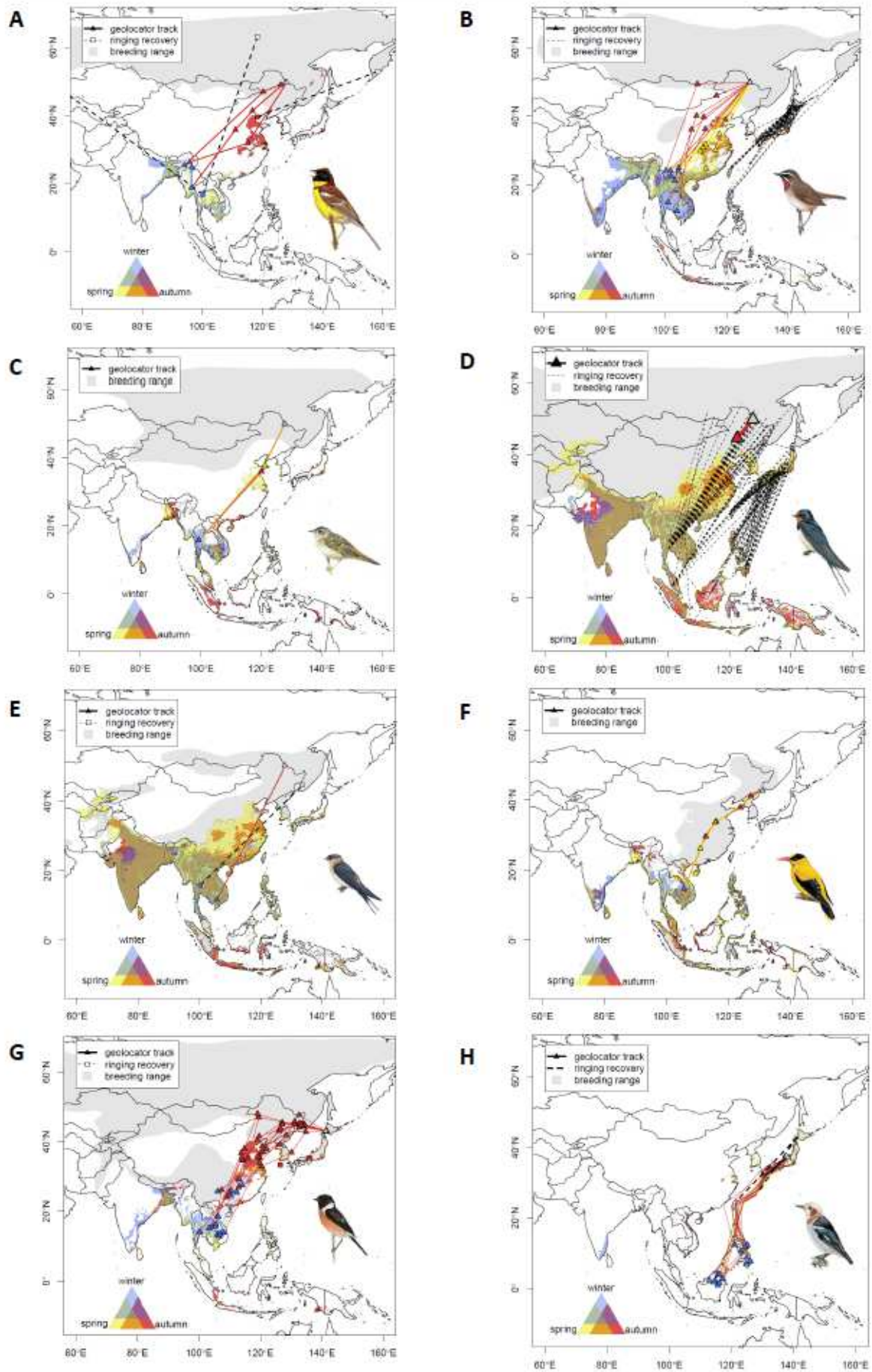
532   **Figure 3:** Predicted ranges in autumn, winter and spring, geolocator positions and ring recoveries for

533   A) Yellow-breasted Bunting, B) Siberian Rubythroat, C) Pallas´s Grasshopper Warbler, D) Barn

534   Swallow, E) Red-rumped Swallow, F) Black-naped Oriole, G) Stejneger´s Stonechat and H) Chestnut-

535   cheeked Starling. The species´ breeding ranges (following BirdLife 2019) are shaded grey. Note that

536   only winter positions are depicted for Chestnut-cheeked Starling. Bird pictograms reproduced with

537   permission of Lynx Edicions.

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554   **Competing interests**

555   The authors declare that they have no competing interests.

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557   **Data availability statement**

558   All observation data are available from eBird (www.ebird.org). All location data (ringing recoveries

559   and geolocation positions) are available in the electronic supplement of this article.

560

561   **References**

562   Amano T, Yamaura Y. 2007. Ecological and life-history traits related to range contractions among

563   breeding birds in Japan. Biological Conservation **137**:271–282.

564   Ambrosini R, Møller AP, Saino N. 2009. A quantitative measure of migratory connectivity. Journal of

565   Theoretical Biology **257**:203–211. Elsevier.

566   Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and

567   S4. R package version **1**:1–23.

568   Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, Stuart-Smith RD, Wotherspoon S,

569   Krkosek M, Stuart-Smith JF. 2014. Statistical solutions for error and bias in global citizen science

570   datasets. Biological Conservation **173**:144–154.

571   BirdLife International. 2019. IUCN Red List for birds.

572   Bivand R, Keitt T, Rowlingson B, Pebesma E, Sumner M, Hijmans R. 2015. rgdal: Bindings for the

573   Geospatial Data Abstraction Library 2017. R package version 0.8-13.

574   Bivand R, Rundel C, Pebesma E, Stuetz R, Hufthammer KO. 2016. rgeos: interface to geometry

575   engine-open source (GEOS). URL https://CRAN. R-project. org/package= rgeos. R package

576   version 0.3-26.[p 410].

577   Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K, Mace GM. 2010. Distorted

578   views of biodiversity: spatial and temporal bias in species occurrence data. PLoS Biology

579   **8**:e1000385.

580   Bonter DN, Cooper CB. 2012. Data validation in citizen science: a case study from Project

581   FeederWatch. Frontiers in Ecology and the Environment **10**:305–307. Wiley Online Library.

582   Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson

583   WD. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory

584   birds. BioScience **61**:689–698.

585   Brooks TM, Pimm SL, Kapos V, Ravilious C. 1999. Threat from deforestation to montane and lowland

586   birds and mammals in insular South-east Asia. Journal of Animal Ecology **68**:1061–1078.

587   Callaghan CT, Slater M, Major RE, Morrison M, Martin JM, Kingsford RT. 2018. Travelling birds

588   generate eco-travellers: The economic potential of vagrant birdwatching. Human Dimensions of

589   Wildlife **23**:71–82. Taylor & Francis.

590   Cantú-Salazar L, Gaston KJ. 2013. Species richness and representation in protected areas of the W

591   estern hemisphere: discrepancies between checklists and range maps. Diversity and

592   Distributions **19**:782–793. Wiley Online Library.

593   Chen J, Liao A, Chen J, Peng S, Chen L, Zhang H. 2017. 30-Meter Global Land Cover Data Product–

594   Globe Land30. Geomatics World **24**:1–8.

595   Cherel Y, Hobson KA, Guinet C, Vanpe C. 2007. Stable isotopes document seasonal changes in trophic

596   niches and winter foraging individual specialization in diving predators from the Southern

597   Ocean. Journal of Animal Ecology **76**:826–836. Wiley Online Library.

598   Cherel Y, Kernaléguen L, Richard P, Guinet C. 2009. Whisker isotopic signature depicts migration

599   patterns and multi-year intra-and inter-individual foraging strategies in fur seals. Biology letters

600   **5**:830–832. The Royal Society.

601   Clark JA, Thorup K, Stroud DA. 2009. Quantifying the movement patterns of birds from ring

602   recoveries. Ringing & Migration **24**:180–188. Taylor & Francis.

603   Combreau O, Riou S, Judas J, Lawrence M, Launay F. 2011. Migratory pathways and connectivity in

604   Asian houbara bustards: evidence from 15 years of satellite tracking. PLoS One **6**:e20570. Public

605   Library of Science.

606   Conrad CC, Hilchey KG. 2011. A review of citizen science and community-based environmental

607   monitoring: issues and opportunities. Environmental Monitoring and Assessment **176**:273–291.

608   Devictor V, Whittaker RJ, Beltrame C. 2010. Beyond scarcity: citizen science programmes as useful

609   tools for conservation biogeography. Diversity and Distributions **16**:354–362.

610   Didan K. 2015. MOD13Q1 MODIS/Terra vegetation indices 16-day L3 global 250m SIN grid V006.

611   NASA EOSDIS Land Processes DAAC.

612   Dray S, Dufour A-B. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal

613   of statistical software **22**:1–20.

614   Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for

615   ecologists. Diversity and distributions **17**:43–57. Wiley Online Library.

616   Eng ML, Stutchbury BJM, Morrissey CA. 2019. A neonicotinoid insecticide reduces fueling and delays

617   migration in songbirds. Science **365**:1177–1180.

618   Engler JO, Rödder D, Stiels D, Förschler MI. 2014. Suitable, reachable but not colonised: Seasonal

619   niche duality in an endemic mountainous songbird. Journal of Ornithology **155**:657–669.

620   Estoque RC, Ooba M, Avitabile V, Hijioka Y, DasGupta R, Togawa T, Murayama Y. 2019. The future of

621   Southeast Asia's forests. Nature communications **10**:1829. Nature Publishing Group.

622   Fick SE, Hijmans RJ. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land

623   areas. International journal of climatology **37**:4302–4315. Wiley Online Library.

624 Finch T, J. Butler S, M. A. Franco A, Cresswell W, Chapman J. 2017. Low migratory connectivity is

625   common in long-distance migrant birds. Journal of Animal Ecology.

626 Fink D, Auer T, Johnston A, Ruiz-Gutierrez V, Hochachka WM, Kelling S. 2020. Modeling avian full

627   annual cycle distribution and population trends with citizen science data. Ecological

628   Applications **30**:e02056. Wiley Online Library.

629 Forseth T, Nesje TF, Jonsson B, Hårsaker K. 1999. Juvenile migration in brown trout: a consequence of

630   energetic state. Journal of Animal Ecology **68**:783–793. Wiley Online Library.

631 Freitag A, Meyer R, Whiteman L. 2016. Strategies employed by citizen science programs to increase

632   the credibility of their data. Citizen Science: Theory and Practice **1**. Ubiquity Press.

633 Fudickar AM, Wikelski M, Partecke J. 2012. Tracking migratory songbirds: accuracy of light-level

634   loggers (geolocators) in forest habitats. Methods in Ecology and Evolution **3**:47–52.

635 Gavrilov EI, Gavrilov AE, Kovshar VA. 2002. Long-term dynamics of numbers of Swallows (Hirundo

636   rustica L.) on seasonal migrations in the foothills of West Tien Shan (South Kazakhstan). Avian

637   Ecol. Behav:1–22.

638 Gilbert M, Sokha C, Joyner PH, Thomson RL, Poole C. 2012. Characterizing the trade of wild birds for

639   merit release in Phnom Penh, Cambodia and associated risks to health and ecology. Biological

640   Conservation **153**:10–16.

641 Graham CH, Hijmans RJ. 2006. A comparison of methods for mapping species ranges and species

642   richness. Global Ecology and biogeography **15**:578–587. Wiley Online Library.

643 Gschweng M, Kalko EK V, Berthold P, Fiedler W, Fahr J. 2012. Multi-temporal distribution modelling

644   with satellite tracking data: predicting responses of a long-distance migrant to changing

645   environmental conditions. Journal of Applied Ecology **49**:803–813.

646 Guillera-Arroita G. 2017. Modelling of species distributions, range dynamics and communities under

647   imperfect detection: advances, challenges and opportunities. Ecography **40**:281–295.

648   Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models.

649   Ecology letters **8**:993–1009.

650   Han L-X, Huang S-L, Yuan Y-C, Qiu Y-L. 2007. Fall Migration Dynamics of Birds on Fenghuang

651   Mountain, Yunnan Province, China. Zoological Research **28**:35–40.

652   Hartig F. 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models.

653   R package.

654   Heim W, Pedersen L, Heim R, Kamp J, Smirenski SM, Thomas A, Tøttrup AP, Thorup K. 2018. Full

655   annual cycle tracking of a small songbird, the Siberian Rubythroat Calliope calliope, along the

656   East Asian flyway. Journal of ornithology **159**:893–899.

657   Higuchi H, Morishita E. 1999. Population declines of Tropical Migratory Birds in Japan. Actinia **12**:51–

658   59.

659   Hijmans RJ, Etten J van, Cheng J, Mattiuzzi M, Sumner M, Greenberg JA, Lamigueiro OP, Bevan A,

660   Racine EB, Shortridge A. 2016a. raster: Geographic Data Analysis and Modeling.

661   Hijmans RJ, Phillips SJ, Leathwick JR, Elith J. 2016b. dismo: species distribution modeling. R package

662   ver. 1.0-15.

663   Hochachka WM, Fink D, Hutchinson RA, Sheldon D, Wong W-K, Kelling S. 2012. Data-intensive

664   science applied to broad-scale citizen science. Trends in Ecology & Evolution **27**:130–137.

665   Hurlbert AH, Jetz W. 2007. Species richness, hotspots, and the scale dependence of range maps in

666   ecology and conservation. Proceedings of the National Academy of Sciences **104**:13384–13389.

667   National Acad Sciences.

668   Hurlbert AH, Liang Z. 2012. Spatiotemporal variation in avian migration phenology: citizen science

669   reveals effects of climate change. PLoS ONE **7**:e31662.

670   Isaac NJB, van Strien AJ, August TA, de Zeeuw MP, Roy DB. 2014. Statistics for citizen science:

671   extracting signals of change from noisy ecological data. Methods in Ecology and Evolution

672   **5**:1052–1060.

673   Jarvis A, Reuter HI, Nelson A, Guevara E. 2008. Hole-filled SRTM for the globe Version 4. available

674   from the CGIAR-CSI SRTM 90m Database (http://srtm. csi. cgiar. org) **15**:25–54.

675   Jiguet F, Barbet-Massin M, Chevallier D. 2011. Predictive distribution models applied to satellite

676   tracks: modelling the western African winter range of European migrant Black Storks Ciconia

677   nigra. Journal of Ornithology **152**:111–118.

678   Jiménez-Valverde A, Lobo JM. 2007. Threshold criteria for conversion of probability of species

679   presence to either–or presence–absence. Acta oecologica **31**:361–369. Elsevier.

680   Johnston A, Fink D, Hochachka WM, Kelling S. 2018. Estimates of observer expertise improve species

681   distributions from citizen science data. Methods in Ecology and Evolution **9**:88–97.

682   Johnston A, Moran N, Musgrove A, Fink D, Baillie SR. 2020. Estimating species distributions from

683   spatially biased citizen science data. Ecological Modelling **422**:108927. Elsevier.

684   Kamp J et al. 2015. Global population collapse in a superabundant migratory bird and illegal trapping

685   in China. Conservation Biology **29**:1684–1694.

686   Kamp J, Oppel S, Heldbjerg H, Nyegaard T, Donald PF. 2016. Unstructured citizen science data fail to

687   detect long-term population declines of common birds in Denmark. Diversity and Distributions

688   **22**:1024–1035.

689   Kehoe L, Romero-Muñoz A, Polaina E, Estes L, Kreft H, Kuemmerle T. 2017. Biodiversity at risk under

690   future cropland expansion and intensification. Nature ecology & evolution **1**:1129.

691   Kéry M, Gardner B, Monnerat C. 2010. Predicting species distributions from checklist data using site-

692   occupancy models. Journal of Biogeography **37**:1851–1862. Wiley Online Library.

693   Koike S, Hijikata N, Higuchi H. 2016. Migration and Wintering of Chestnut-Cheeked Starlings Agropsar

694   philippensis. Ornithological Science **15**:63–74.

695   Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, Stillfried M,

696   Heckmann I, Scharf AK, Augeri DM. 2013. The importance of correcting for sampling bias in

697   MaxEnt species distribution models. Diversity and Distributions **19**:1366–1379. Wiley Online

698   Library.

699   La Sorte FA, Somveille M. 2019. Survey completeness of a global citizen-science database of bird

700   occurrence. Ecography **42**:1–10. Wiley Online Library.

701   Laughlin AJ, Taylor CM, Bradley DW, Leclair D, Clark RC, Dawson RD, Dunn PO, Horn A, Leonard M,

702   Sheldon DR. 2013. Integrating information from geolocators, weather radar, and citizen science

703   to uncover a key stopover area of an aerial insectivore. The Auk **130**:230–239. Oxford University

704   Press.

705   Lei J, Jia Y, Zuo A, Zeng Q, Shi L, Zhou Y, Zhang H, Lu C, Lei G, Wen L. 2019. Bird Satellite Tracking

706   Revealed Critical Protection Gaps in East Asian–Australasian Flyway. International journal of

707   environmental research and public health **16**:1147. Multidisciplinary Digital Publishing Institute.

708   Lesiv M, Schepaschenko D, Moltchanova E, Bun R, Dürauer M, Prishchepov A V, Schierhorn F, Estel S,

709   Kuemmerle T, Alcántara C. 2018. Spatial distribution of arable and abandoned land across

710   former Soviet Union countries. Scientific data **5**:180056. Nature Publishing Group.

711   Lisovski S, Hahn S. 2012. GeoLight- processing and analysing light-based geolocator data in R.

712   Methods in Ecology and Evolution **3**:1055–1059.

713   Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S. 2012.

714   Geolocation by light: accuracy and precision affected by environmental factors. Methods in

715   Ecology and Evolution **3**:603–612.

716   Loiselle BA, Howell CA, Graham CH, Goerck JM, Brooks T, Smith KG, Williams PH. 2003. Avoiding

717   pitfalls of using species distribution models in conservation planning. Conservation biology

718   **17**:1591–1600. Wiley Online Library.

719   Lotz A, Allen CR. 2007. Observer bias in anuran call surveys. The Journal of wildlife management

720   **71**:675–679. Wiley Online Library.

721   Manel S, Williams HC, Ormerod SJ. 2001. Evaluating presence–absence models in ecology: the need

722   to account for prevalence. Journal of applied Ecology **38**:921–931. Wiley Online Library.

723   Marra PP, Hunter D, Perrault AM. 2011. Migratory connectivity and the conservation of migratory

724   animals. Environmental Law:317–354. JSTOR.

725   Martínez-Meyer E, Peterson AT, Navarro-Sigüenza AG. 2004. Evolution of seasonal ecological niches

726   in the Passerina buntings (Aves : Cardinalidae). Proceedings of the Royal Society B: Biological

727   Sciences **271**:1151–1157.

728   McClure HE. 1974. Migration and Survival of the Birds of Asia. SEATO, Bangkok, Thailand.

729   McKinnon EA, Love OP. 2018. Ten years tracking the migrations of small landbirds: Lessons learned in

730   the golden age of bio-logging. The Auk: Ornithological Advances **135**:834–856.

731   Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized

732   linear mixed-effects models. Methods in ecology and evolution **4**:133–142. Wiley Online

733   Library.

734   Nakazawa Y, Peterson AT, Martínez-Meyer E, Navarro-Sigüenza AG. 2004. Seasonal niches of

735   Nearctic-Neotropical migratory birds: implications for the evolution of migration. The Auk

736   **121**:610–618.

737   Palm EC, Newman SH, Prosser DJ, Xiao X, Ze L, Batbayar N, Balachandran S, Takekawa JY. 2015.

738   Mapping migratory flyways in Asia using dynamic Brownian bridge movement models.

739   Movement Ecology **3**:3.

740   Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic

741   distributions. Ecological modelling **190**:231–259. Elsevier.

742   Rahbek C, Graves GR. 2001. Multiscale assessment of patterns of avian species richness. Proceedings

743 of the National Academy of Sciences **98**:4534–4539. National Acad Sciences.

744 Rakhimberdiev E, Senner NR, Verhoeven MA, Winkler DW, Bouten W, Piersma T. 2016. Comparing

745 inferences of solar geolocation data against high-precision GPS data : annual movements of a

746 double-tagged black-tailed godwit:1–8.

747 Ravkin ES, Ravkin YS. 2005. Birds of north Eurasian plains: numbers, distribution and spatial

748 organization of communities. Nauka, Novosibirsk, Russia. SHORT COMMUNICATIONS **815**:303–

749 308.

750 Robson C. 2008. Field guide to the birds of South-East Asia. Bloomsbury Publishing, London.

751 Robson D, Barriocanal C. 2011. Ecological conditions in wintering and passage areas as determinants

752 of timing of spring migration in trans-Saharan migratory birds. Journal of Animal Ecology

753 **80**:320–331. Wiley Online Library.

754 Shepherd CR, Nijman V, Krishnasamy K, Eaton JA, Chng SCL. 2016. Illegal trade pushing the Critically

755 Endangered Black-winged Myna Acridotheres melanopterus towards imminent extinction. Bird

756 conservation international **26**:147–153. Cambridge University Press.

757 Suárez-Seoane S, de la Morena ELG, Prieto MBM, Osborne PE, de Juana E. 2008. Maximum entropy

758 niche-based modelling of seasonal changes in little bustard (Tetrax tetrax) distribution.

759 ecological modelling **219**:17–29. Elsevier.

760 Sukhbaatar T. 2019. Report of Dariganga bird ringing station-2018. Available from

761 https://www.researchgate.net/publication/330761624_Report_of_Dariganga_bird_ringing_stat

762 ion-2018.

763 Sullivan BL, Aycrigg JL, Barry JH, Bonney RE, Bruns N, Cooper CB, Damoulas T, Dhondt AA, Dietterich

764 T, Farnsworth A. 2014. The eBird enterprise: an integrated approach to development and

765 application of citizen science. Biological Conservation **169**:31–40.

766 Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: A citizen-based bird

767   observation network in the biological sciences. Biological Conservation **142**:2282–2292.

768   Elsevier.

769   Supp SR, Sorte FA La, Cormier TA, Lim MCW, Powers DR, Wethington SM, Goetz S, Graham CH. 2015.

770   Citizen-science data provides new insight into annual and seasonal variation in migration

771   patterns. Ecosphere **6**:1–19.

772   Thorup K, Conn PB. 2009. Estimating the seasonal distribution of migrant bird species: Can standard

773   ringing data be used? Pages 1107–1117 Modeling demographic processes in marked

774   populations. Springer.

775   Thorup K, Korner-Nievergelt F, Cohen EB, Baillie SR. 2014. Large-scale spatial analysis of ringing and

776   re-encounter data to infer movement patterns: A review including methodological perspectives.

777   Methods in Ecology and Evolution **5**:1337–1350. Wiley Online Library.

778   Thorup K, Tøttrup AP, Willemoes M, Klaassen RHG, Strandberg R, Vega ML, Dasari HP, Araújo MB,

779   Wikelski M, Rahbek C. 2017. Resource tracking within and across continents in long-distance

780   bird migrants. Science Advances **3**:e1601360.

781   Thuiller W, Araujo MB, Lavorel S. 2004. Do we need land-cover data to model species distributions in

782   Europe? Journal of Biogeography **31**:353–361. Wiley Online Library.

783   Trierweiler C, Klaassen RHG, Drent RH, Exo K-M, Komdeur J, Bairlein F, Koks BJ. 2014. Migratory

784   connectivity and population-specific migration routes in a long-distance migratory bird.

785   Proceedings of the Royal Society B: Biological Sciences **281**:20132897. The Royal Society.

786   Tye CA, McCleery RA, Fletcher Jr RJ, Greene DU, Butryn RS. 2017. Evaluating citizen vs. professional

787   data for modelling distributions of a rare squirrel. Journal of applied ecology **54**:628–637. Wiley

788   Online Library.

789   Urbanek S. 2009. rJava: Low-level R to Java interface. R package version 0.8-1.

790   van Strien AJ, van Swaay CAM, Termaat T. 2013. Opportunistic citizen science data of animal species

791   produce reliable estimates of distribution trends if analysed with occupancy models. Journal of

792   Applied Ecology **50**:1450–1458. Wiley Online Library.

793   Warren CC, Veech JA, Weckerly FW, O'Donnell L, Ott JR. 2013. Detection heterogeneity and

794   abundance estimation in populations of Golden-cheeked Warblers (Setophaga chrysoparia).

795   The Auk **130**:677–688. Oxford University Press.

796   Weng KC, Castilho PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, Schallert RJ, Goldman KJ,

797   Block BA. 2005. Satellite tagging and cardiac physiology reveal niche expansion in salmon

798   sharks. Science **310**:104–106. American Association for the Advancement of Science.

799   Wilcove DS, Giam X, Edwards DP, Fisher B, Koh LP. 2013. Navjot's nightmare revisited: logging,

800   agriculture, and biodiversity in Southeast Asia. Trends in ecology & evolution **28**:531–540.

801   Elsevier.

802   Williams HM, Willemoes M, Thorup K. 2017. A temporally explicit species distribution model for a

803   long distance avian migrant, the common cuckoo. Journal of Avian Biology **48**:1624–1636.

804   Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A, Group NPSDW. 2008. Effects of sample

805   size on the performance of species distribution models. Diversity and distributions **14**:763–773.

806   Wiley Online Library.

807   Yamaura Y, Schmaljohann H, Lisovski S, Senzaki M, Kawamura K, Fujimaki Y, Nakamura F. 2017.

808   Tracking the Stejneger's stonechat Saxicola stejnegeri along the East Asian–Australian Flyway

809   from Japan via China to southeast Asia. Journal of Avian Biology **48**:197–202.

810   Yong DL, Liu Y, Low BW, Española CP, Choi C-Y, Kawakami K. 2015. Migratory songbirds in the East

811   Asian-Australasian Flyway: a review from a conservation perspective. Bird Conservation

812   International **25**:1–37.

813   Zhao S, Peng C, Jiang H, Tian D, Lei X, Zhou X. 2006. Land use change in Asia and the ecological

814   consequences. Ecological Research **21**:890–896.

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822 **Supporting information**

823 Supplied as separate files.

824 Supplement 1: AUC and kappa values for MaxEnt models using different thresholds, and

825 with/without bias grid.

826 Supplement 2: Details about the geolocation data analysis and field work.

827 Supplement 3: Geolocation positions for all geolocator-tracked individuals.

828 Supplement 4: Seasonal predicted range sizes for all study species.

829 Supplement 5: Validation of seasonal species distribution models by calculating overlap with A) mean

830 geolocation positions, B) mean geolocation positions plus standard deviation, C) ringing and recovery

831 sites and D) BirdLife range maps.
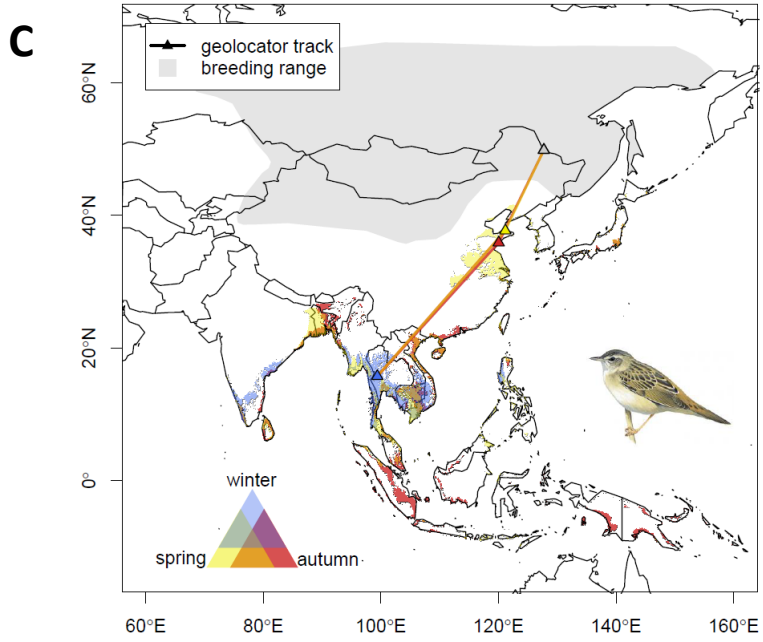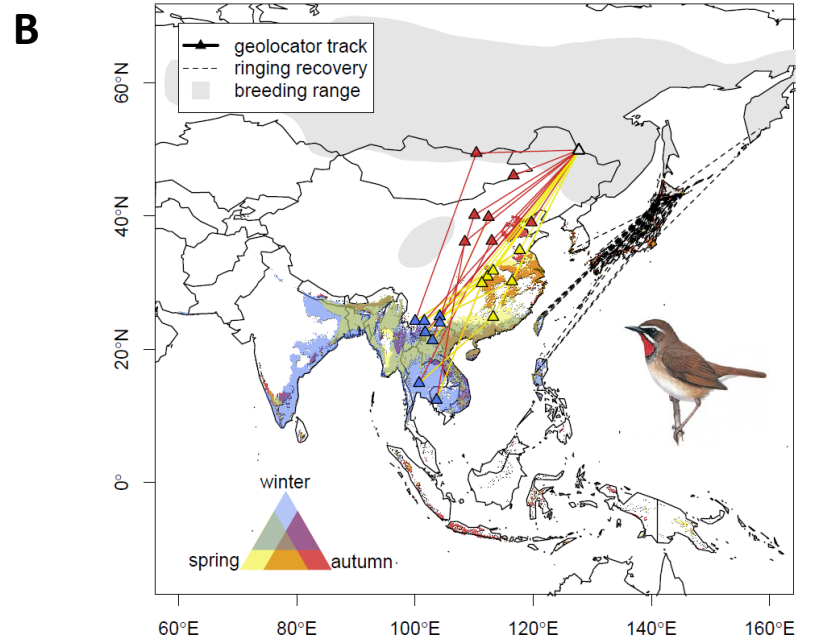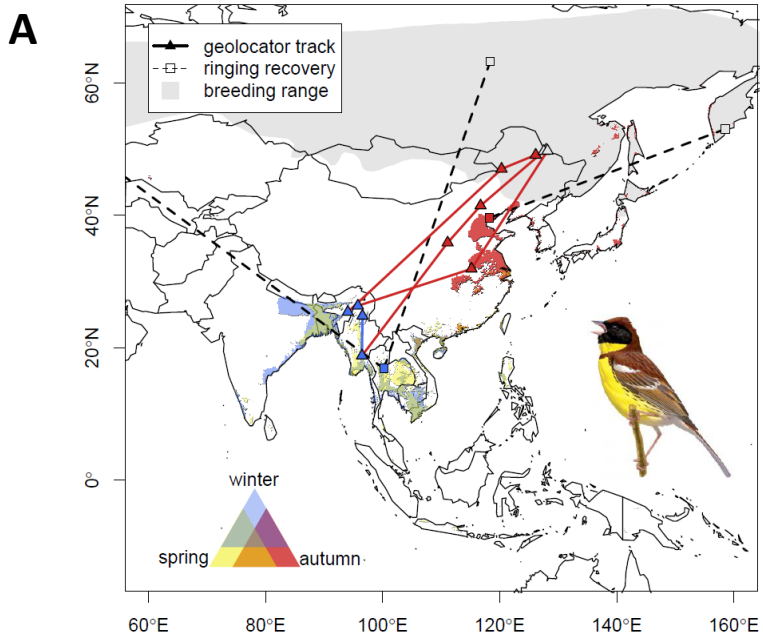
832
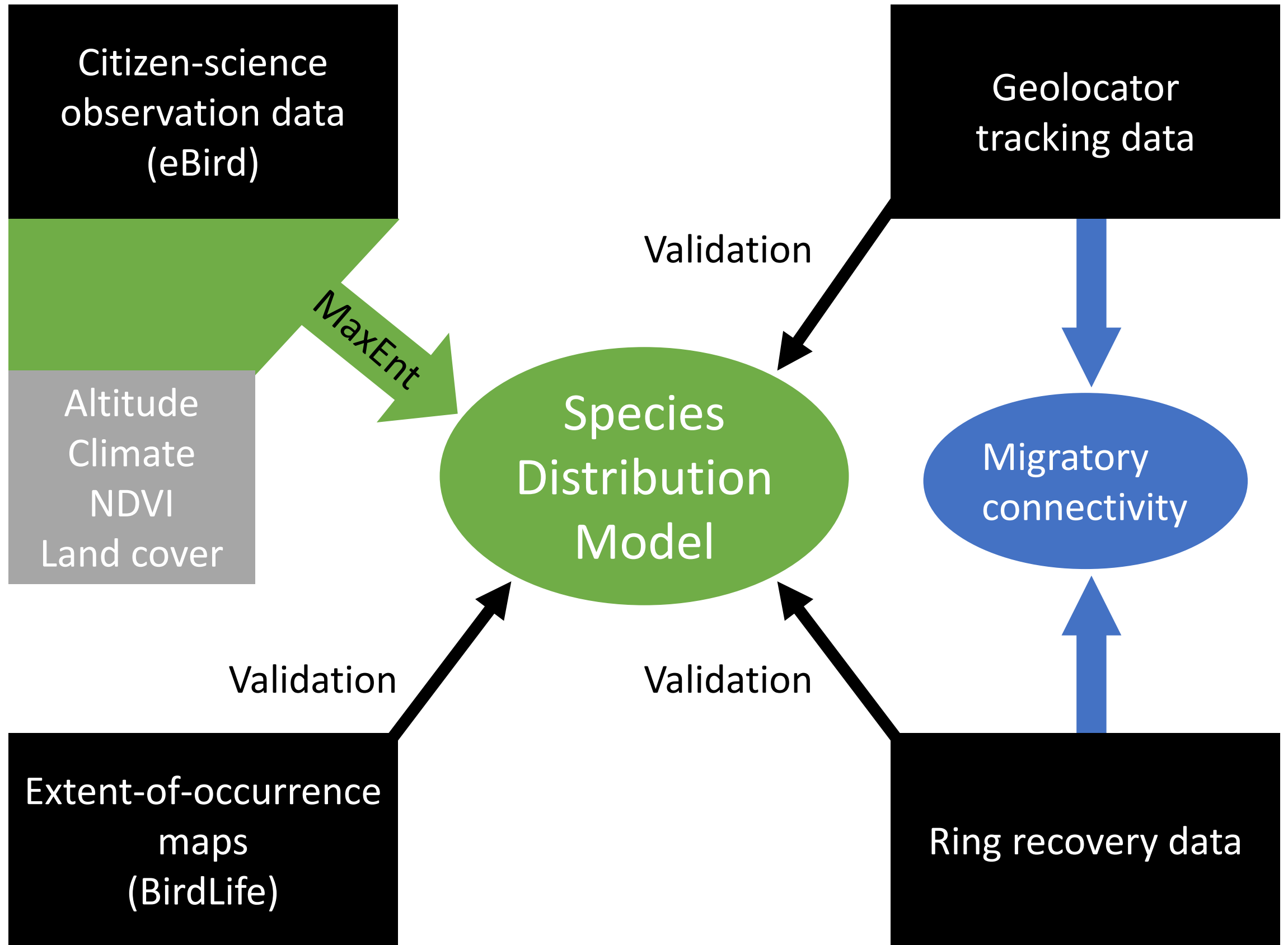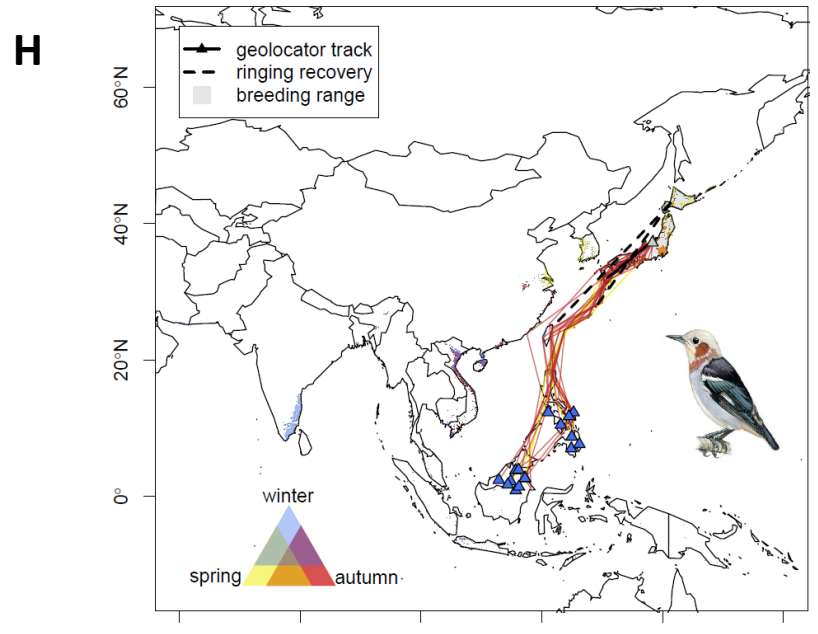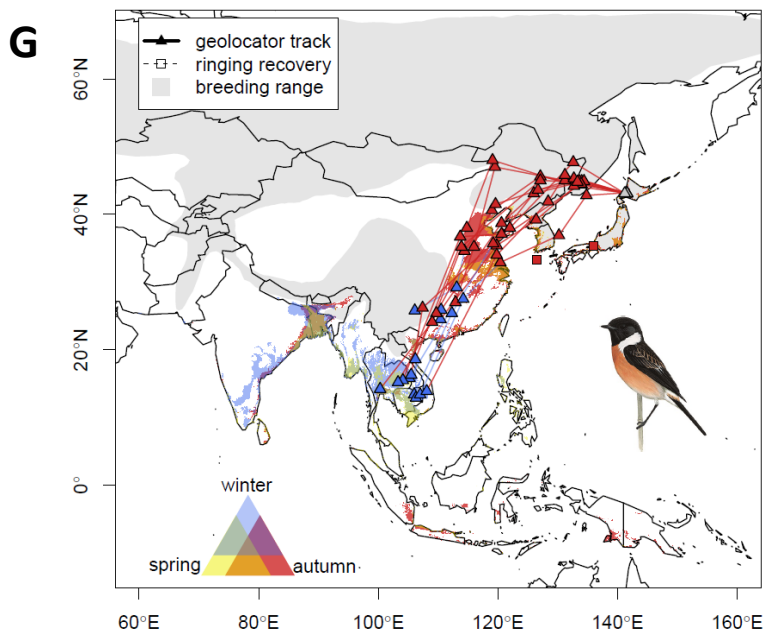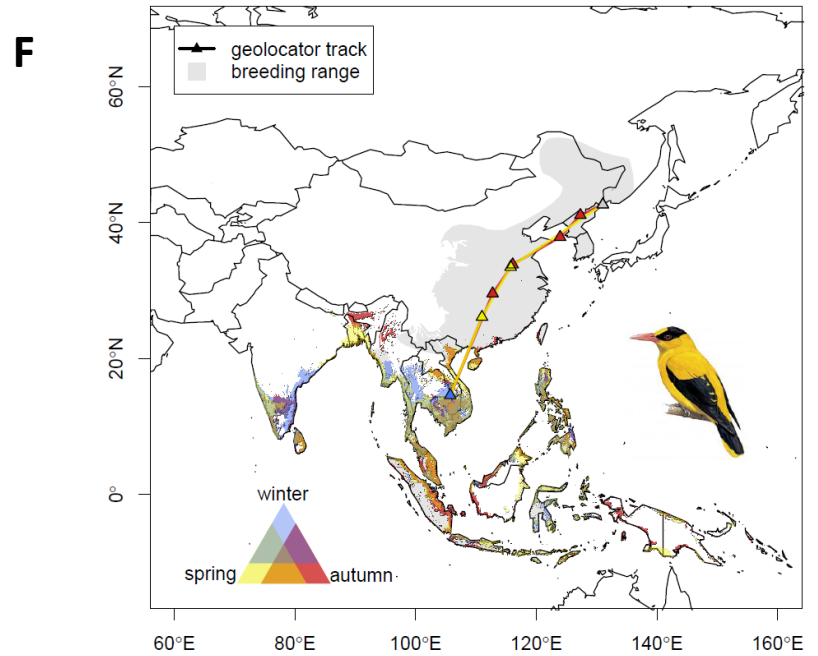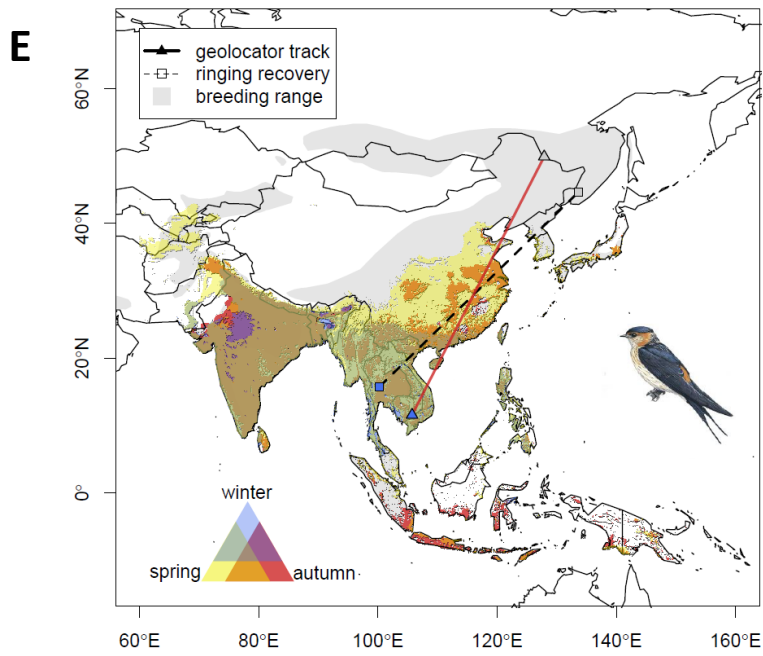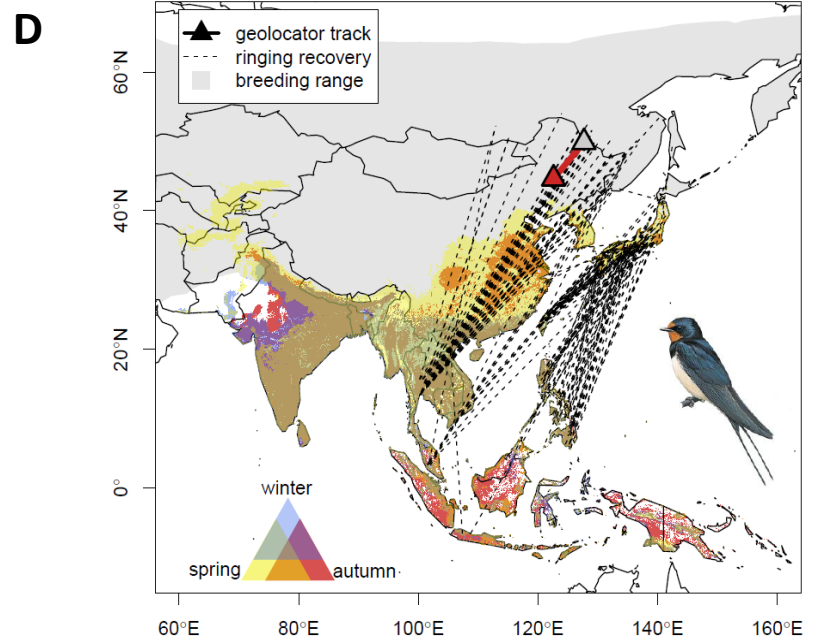
Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Nothing to declare.

Wieland Heim, on behalf of the authors

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