1   **Common European birds are declining rapidly whilst less abundant**

2   **species' numbers are rising**

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24 **ABSTRACT**

25 Biodiversity is undergoing unprecedented global decline. Efforts to slow this rate

26 have focused foremost on rarer species, which are at most risk of extinction.

27 Less interest has been paid to more common species, despite their greater

28 importance in terms of ecosystem function and service provision. How rates of

29 decline are partitioned between common and less abundant species remains

30 unclear. Using a 30-year dataset of 144 bird species we examined Europe-wide

31 trends in avian abundance and biomass. Overall avian abundance and biomass

32 are both declining with most of this decline being attributed to more common

33 species, whilst less abundant species showed an overall increase in both

34 abundance and biomass. If overall avian declines are mainly due to reductions in

35 a small number of common species, conservation efforts targeted at rarer

36 species must be better matched with efforts to increase overall bird numbers, if

37 ecological impacts of birds are to be maintained.

38

39 **INTRODUCTION**

40 That a relatively small number of species are common whilst a far greater

41 number are less abundant has been termed a 'law' of ecology as it has been

42 observed in all communities that have been studied (Gaston 1994; McGill et al.

43 2007; Henderson & Magurran 2010). Global biodiversity is undergoing

44 unprecedented decline (Butchart et al. 2010) and conservation efforts to reverse

45 or at least slow the rate have focused foremost on the less abundant species,

46 which by definition face the greatest extinction threats (Baillie et al. 2004;

47   Caughley & Gunn 1995; Gaston 2010). Considerably less attention has been

48   given to declines in more common species, which is troubling because these are

49   important in the delivery of absolute levels of ecosystem function and of

50   ecosystem goods and services (Grime 1998; Geider et al. 2001; Gaston 2008,

51   2011). Indeed, although they may constitute a small proportion of the species

52   richness, common species often define the structure, character and dynamics of

53   ecosystems (Ellison et al. 2005; Gaston 2010). Even relatively small proportional

54   declines in the abundances of common species will often result in the loss of

55   large numbers of individuals and substantial amounts of biomass, with dramatic

56   ecosystem consequences (Ellison et al. 2005; Gaston 2010). This suggests that

57   a key issue in the strategic allocation of inevitably limited conservation resources

58   is how directional change in population sizes is distributed amongst common and

59   rare species, and particularly whether there are any systematic patterns of

60   variation.

61   Birds provide an excellent opportunity to investigate possible asymmetries in

62   population changes between common and less abundant species as they vary

63   widely in abundance and have been the subject of intensive monitoring

64   programmes for a number of decades, thus providing geographically wide-

65   ranging, robust, long term datasets (Gregory et al 2005; Gregory & van Strien

66   2010). Potential declines in common birds are also important as a growing body

67   of evidence suggests that birds play vital roles in the structuring and functioning

68   of ecosystems and that declines in their numbers will likely reduce key

69   ecosystem processes and services including decomposition, pest control,

70   pollination and seed dispersal (Sekercioglu et al. 2004; Whelan et al 2008;

71   Wenny et al. 2011; Gangoso et al. 2013). In this study we utilise data from the

72   Pan-European Common Bird Monitoring Scheme (PECBMS) to construct a 30-

73   year dataset across 25 countries (Supplementary materials Fig. S1), for 144 bird

74   species, and examine how population trajectories (both in terms of abundance

75   and biomass) differ between species based on their abundance.

76

77   **MATERIALS AND METHODS**

78   **Bird Abundance Estimates.**

79   Two data sources, population estimates from Birdlife International and European

80   population indices from The Pan-European Common Bird Monitoring Scheme

81   (PECBMS), were used to calculate bird abundance estimates used in the

82   analysis. Birdlife International (2004) provides estimated numbers of breeding

83   pairs for 520 species in 52 European countries and regions. Estimates for 144

84   species and 25 countries covered by PECBMS were extracted. These are based

85   on survey data with a mean starting year of 1997 and a mean end year of 2000

86   hence we assume that the population estimates reflect the population size in the

87   year 2000. The population estimates consist of a minimum and maximum

88   population size, in breeding pairs, for each country, of which a geometric mean

89   was taken and multiplied by two to give an abundance estimate for each species

90   and country. As these estimates are based on the number of breeding pairs they

91   do not take into account the non-breeding population, although we assume the

92   breeding population reflects the size of the actual population. A single abundance

4

93 estimate was then produced for each species by summing population estimates

94 across all countries.   PECBMS collects survey data from all participating

95 countries and incorporates these data into a single supranational European index

96 for each species for the period 1980-2009. The number of countries contributing

97 to the scheme, and the number of years covered by the data has been increasing

98 since its inception, meaning that in the earlier years a smaller number of

99 countries were used to produce the indices. Missing data were estimated using

100 existing data from another countries within the same region that share

101 socioeconomic, environment and environmental pressures. The European Bird

102 Census Council website (http://www.ebcc.info/index.php?ID=509) provides full

103 details of the methods used to calculate indices and their associated caveats.

104 These indices were then applied to the population estimates calculated from the

105 Birdlife international data to produce abundance estimates each for species from

106 1980-2009. Biomass estimates were calculated using body mass data (a mean of

107 male and female masses) were taken from Snow & Perrins (1998), Dunning

108 (2007) and Birdlife International (2012). Both data sets are publically available

109 and our derived dataset is available on request.

110 For 28 species we did not have indices of change for some of the earlier years

111 (ranging from 8 to 19 years (mean=14.07, SD=4.25), see Supplementary Material

112 Table S1). In these cases we calculated the population estimates for the missing

113 years based on the abundances for the years for which indices of change were

114 available. Three methods were utilised, taking the geometric mean of the

115 available abundance and using this value for the missing years, and linear

116   regression / exponential regression of the available abundances then using the

117   predictions from the regression to fill the missing years. Additionally we repeated

118   the analysis with the interpolated data removed.   Finally, to reduce the noise

119   associated with annual fluctuations, the data were smoothed using a generalised

120   additive model with degrees of freedom 0.3 times the number of years in the

121   dataset (Fewster et al. 2000). The effects of interpolation method and of

122   smoothing the data were examined by calculating R^2 values and parameter

123   estimates for the different data manipulations (Table S2). After the data had been

124   smoothed the best model fit was achieved using data where linear regression

125   had been used to interpolate the data for missing years and hence these data

126   were used in all subsequent analysis.

127   **Factors affecting species population trajectories**

128   To detect differences in directional changes in population sizes between common

129   and less common species we assigned all species of bird to a quartile based on

130   their abundance, with the least abundant species occupying quartile one and the

131   most abundant in quartile four (from here termed Q1, Q2, Q3 & Q4). Species

132   were assigned to both variable and fixed quartiles. For variable quartiles

133   assignment was performed on a yearly basis allowing species to move between

134   quartiles as their abundance changed, hence the species composition of the

135   quartiles was dynamic. Full details of assignment to, and movement between,

136   quartiles are available (Supplementary Materials Table S3). For fixed quartiles,

137   species were assigned to quartiles based on abundance in year one of the study.

138 For each bird species we also identified three additional factors likely to affect

139 their population trajectories: major feeding guild, habitat, and body size. Feeding

140 guild was based on feeding preferences used for the majority of the year, not

141 including seasonal variation (taken from Snow & Perrins 1998; Handbook of the

142 Birds of the World Alive 2013): aerial insectivore (n=9), carnivore (n=5), granivore

143 (n=32), herbivore (n=6), insectivore (n=79) & omnivore (n=13). Habitat type was

144 taken from the PECBMS: farmland (n=36), forest (n=32), inland water (n=8) and

145 other habitat (n=68).

146 To investigate the role of different variables in determining changes in abundance

147 of species within the study we used general linear mixed effects models with a

148 Gaussian error structure. All models were fitted with the R (v3.0.2) language and

149 environment (R core team 2012), using the package 'lme4' (Bates et al. 2013).

150 Abundance was used as the dependent variable in the model, with one data

151 point for each species (n=144) per year (n=30). As absolute rank is formulated

152 from the absolute abundance they are obviously correlated. In order to minimise

153 this correlation we z-transformed each species' abundance independently using

154 species-specific means and standard deviations, the resulting standardised

155 abundances approximated a Gaussian distribution and were used in subsequent

156 analysis. Fixed factors included in the maximal models were time (year,

157 continuous integer variable) major feeding guild (six-level categorical variable),

158 habitat (four-level categorical variable), and body mass (continuous variable). All

159 fixed effects were also standardised using the 'arm' package (Gelman et al.

160 2009) to ensure they were on a common scale, which increases the

161   interpretability of the parameter estimates particularly when interactions are

162   involved (Schielzeth 2010). In all cases models with variable quartiles were found

163   to be better in terms of parsimony (based on AIC) and variance explained (see

164   below), hence this method was used for all the subsequent mixed effect models.

165   The fixed effects structure included two-way interactions of year with each other

166   variable. Species was modelled with a random slope (by time) and intercept.

167   To evaluate the variance explained we calculated R^2 values of the global model,

168   i.e. the model containing all the parameters of interest, using the methods of

169   Nakagawa and Schielzeth (2013). We calculated $R^2_{GLMM(m)}$, the marginal R^2

170   which describes the variance explained by the fixed factors, and $R^2_{GLMM(c)}$, the

171   conditional R^2 which is concerned with the variance explained by both the fixed

172   and random factors (Nakagawa and Schielzeth 2013).

173   Model simplification and selection were performed using a multi-model inference

174   approach based on the methods and recommendations of Burnham and

175   Anderson (2002) and Grueber et al. (2011). We used the package 'MuMIn'

176   (Bartoń 2011) to produce all subsets of models based on the global model and

177   rank them based on AIC_c Following Richards (2008), and to be 95% sure that the

178   most parsimonious models were maintained within the best supported model set,

179   we retained all models where Δ AIC <6. When multiple equally feasible models

180   were found in the candidate model set we used model averaging to produce the

181   averaged parameter estimates and relative importance of each parameter

182   (Burnham and Anderson 2002).

183   Two sets of sensitivity analyses were carried out to explore the robustness of the

184 models. First, to examine how sensitive the models were to the composition of

185 species within the analysis, species were randomly removed from the dataset,

186 the global model was re-run and the $R^2_{GLMM(m)}$ was calculated for 100 iterations.

187 This process was repeated with between 1 and 50 species being removed (a

188 total of 5000 model runs). Second, our abundance data are based on population

189 estimates, with associated variation and uncertainty which are unknown, thus

190 excluding the calculation of confidence intervals around the data. Therefore, to

191 simulate the effects of variation in the dataset we randomly altered each

192 abundance estimate, re-ran the models and calculated the $R^2_{GLMM(m)}$ for 100

193 iterations (a total of 3000 model runs). The magnitude of the alteration was

194 chosen randomly from a uniform distribution from between 1 and up to 30% of

195 the estimated abundance for each species and year (See Supplementary

196 Materials, Sensitivity analysis methods and R code for full details). Abundance

197 and biomass estimates calculated within the simulations were used to provide

198 variability around the mean estimates.

199 To determine whether there were differences in the number of species

200 demonstrating significant population declines or increases between abundance

201 quartiles we produced linear regression models (abundance against year) for

202 each species individually as we were unable to determine significance for the

203 species-specific slopes from the mixed effects model. General additive models

204 used to illustrate the trends on plots were carried out using package 'gam'. F and

205 p values were calculated using Satterthwaite (1946) approximations to determine

206 denominator degrees of freedom in package 'lmerTest' (Kuznetsova et al. 2013).

207   **Results**

208   ***Overall trends***

209   Summing all species, we found a negative trend in total estimated bird

210   abundance between 1980 and 2009, resulting in a decrease of 421 million

211   individuals (Table 1, Figure 1a). Generalised linear models highlight steep

212   declines during the first half of the study (1980-1994) followed by a period of

213   greater stability during the second half (Figure 1a). When these estimated

214   abundances were converted to biomass there was a total decrease of over 7000

215   tonnes (Table 2; Figure 2b). Similar to the abundance data, avian biomass

216   declined during the first 20 years (1980-1999) of the study but showed recovery

217   in the final ten years. See supplementary materials Fig. S2 for individual species

218   abundance plots.

219

220   ***Factors affecting population trajectories***

221   The global model explained around 82% of the variation in the data ($R^2_{GLMM(c)}$ =

222   0.817) of which around 30% was explained by the fixed factors, and their

223   interactions ($R^2_{GLMM(m)}$ = 0.299). We produced a candidate model set consisting

224   of all simplified versions of the global model and compared them based on their

225   AIC_c. The 11 models with ΔAIC_c <6 (Table S4) were used to produce model

226   averaged parameter estimates.

227

228   *Relative importance of parameters.* Abundance quartile, time, and body mass

229   were all retained in each model within the candidate model set having a relative

230   importance (RI) of 1 in the final average model. Feeding guild was retained in

231   82% of top models with a RI of 0.97. Habitat, however, was only retained in 46%

232   of the top models with a RI of 0.18. The interaction of time and the other main

233   effects was used to determine how abundance changed with time in relation to

234   these factors. The interaction of abundance quartile with time was retained in all

235   models with a relative importance of 1, whilst the interaction of feeding guild and

236   time was found in 36% of the models (RI=0.43), and the interaction of body mass

237   and time was also retained in 56% of the models but with a RI of 0.46. Finally,

238   the interaction between habitat and time was retained in 9% of the candidate

239   model set (RI=0.01). These results suggest that abundance quartile is a better

240   predictor of population trajectory than major feeding guild, habitat type or body

241   mass.

242

243   *Model averaged parameter estimates.* The model averaged parameter estimates

244   also highlight how changes in abundance with time are strongly affected by

245   abundance quartile (Table S5; Quartile and time interaction), with the steepest

246   declines being in Q4 (β = -1.56, SE=0.24) followed by Q3 (β = -0.761, SE=0.222)

247   and Q2 (β = -0.505, SE=0.191) (Q1 as the base level), whilst species within Q1

248   showed an increase in abundance with time (β=0.718, SE=0.139, Q2 as base

249   level). All quartile interactions with time were significant (at α = 0.001), and reflect

250   the patterns in the actual data (Figure 2) with declines within Q2, Q3 & Q4 and

251   increases in Q1 when variable quartiles were used. When considered by feeding

252   guild, whilst we found considerable decreases in granivores we found no

253 statistically significant changes in abundance with time (Table S5; Figure S3). In

254 terms of habitat type, we found not significant changes in abundance with time

255 (Table S5; Figure S4).

256

257 *Sensitivity analysis***.** The models proved to be very robust to both the species

258 composition used within the analysis and random changes in the abundance

259 estimates used in the models. Removing up to 50 species reduced the $R^2_{GLMM(m)}$

260 from 0.299 (SD=0.0006) to 0.282 (SD=0.075) (Figure S5, Table S6). Altering all

261 of the abundance estimates between 1 and up to a maximum of 30% (the

262 change in abundance was chosen randomly between 1 & the maximum at each

263 of 100 iterations) reduced $R^2_{GLMM(m)}$ from 0.299 (SD=0.0006) to 0.210 (SD=0.006,

264 max % abundance change =26) (Figure S6, Table S7).

265 *Changes by quartile.* When quartile was assigned on a yearly basis (Method one)

266 69 species stayed in the same quartile, 67 species occupied 2 quartiles and 8

267 species occupied three quartiles, over the 30 year study period. Of those that did

268 move between quartiles, 41 species were in the same quartile in the final year as

269 at the start of the study. 21 species moved into a more abundant quartile and 16

270 species moved into a less abundant quartile. When considered by abundance

271 quartile and as predicted by our model there were considerable asymmetries in

272 population trajectories between the different abundance quartiles.

273 The vast majority of the changes in abundance and biomass were driven by

274 changes in the most common, Q4, species, accounting for 83% of the total

275 abundance decline when the species composition was variable (method one,

276   Table 1. a, Fig 2. I. d). When species were fixed to their year one quartile, Q4

277   changes accounted for 92% of the total change in abundance (Table 1b, Fig.

278   2.IId). Of the 36 most common species 24 were decreasing (22 statistically

279   significantly α = 0.05) and 12 showed increases (10 significantly, Table 1. C).

280   Species belonging to Q3, representing the second most abundant group, also

281   demonstrated an overall decline, although these changes represent only a small

282   fraction of the overall decline (Table 1. a & c, Fig. 2. I & II c). When quartile

283   composition was flexible, Q2 species also showed declines (Table 2. a, Fig. 2. I.

284   b). When however species assigned to Q2 in 1980 were considered they showed

285   a modest increase in abundance (Table 1. b, Fig 2. II. B). Similarly, and in

286   contrast to the most common species, Q1 species demonstrated an overall

287   increase in abundance with either variable or fixed species composition (Table 1.

288   a & b, Fig. 2 I & II a). Of these least abundant species, 24 were found to be

289   increasing (17 significantly) and 12 were decreasing (8 significantly, Table 1. c).

290

291   ***Biomass***

292   When calculated in terms of biomass the patterns largely reflected those for

293   abundance (Table 2, Fig 3), although while both were declining this was steeper

294   when considered in terms of abundance rather than biomass. This can be

295   partially explained by the fact that the most abundant birds tended to be smaller

296   (there is a negative correlation between body mass and abundance, rs = -0.4077,

297   p < 0.001, Supplementary material Figure S8). Hence reductions in abundance in

298   lighter birds were not reflected in terms of biomass. Moreover when biomass for

299   the most common Q4 species was calculated allowing for a variable species

300   composition we actually found only a modest decrease in biomass (Fig. 3 I d).

301   This is largely due to the most common species in year one of the study (mean

302   biomass =138.4g SD=146) being replaced by heavier species (mean biomass

303   =173.6g SD=164.2) by the end (Supplementary materials Fig. S9).

304

305   **Discussion**

306   European birds are declining at an alarming rate, and much of this decline has

307   been attributed to decreases in the number of farmland birds caused by

308   agricultural intensification (Donald, Green & Heath 2001). In addition there have

309   been a number of well publicised declines of very common European birds such

310   as the House Sparrow (Delaet & Summers-Smith 2007) and Common Starling

311   (Smith, Ryegard & Svensson 2012). At the same time a number of the rare

312   species have shown dramatic increases in recent years, probably due to the

313   impacts of direct conservation action (Gregory et al. 2003; Holling 2011). It has,

314   however, remained unclear as to whether being common in itself is a factor

315   affecting population trajectory. This work demonstrates for the first time how

316   more common birds are generally declining faster than less abundant species

317   while accounting for other factors which have been postulated as being

318   responsible for avian population declines. This is particularly worrying as by

319   definition the commonest birds are the most numerous and hence declines in

320   these species have a much greater impact in terms of the ecosystem function

321   and services which they provide. Our results are based on the outcomes of many

322   thousands of individual surveys of breeding birds throughout Europe, each with

323   associated variation and uncertainty and hence we emphasise the point that our

324   results are abundance and biomass estimates. That the data used has

325   undergone considerable verification and quality control and that our conclusions

326   remain unaffected by high levels of added random variation gives us confidence

327   in the patterns we describe.

328   In addition to changes in avian abundance we also provide evidence for a shift in

329   the body mass distribution within European birds, with a general trend for smaller

330   birds to decline faster than larger birds and for larger birds to be increasing in

331   abundance, which is likely to be the main reason why avian biomass has not

332   declined as rapidly as has abundance. These changes in body mass distribution

333   will also likely have impacts in terms of the ecosystem services provided by birds

334   as the levels of many of these services are linked to consumption rates (e.g. pest

335   control, scavenging services), which are driven by metabolic rates, which are in

336   turn a function of body mass. As the mean power-law scaling exponent of field

337   metabolic rate and body mass relationship has been estimated at 0.64 for birds

338   (Hudson et al. 2013), a reduction in abundance of lower body mass species will

339   lead to a disproportionate loss in ecosystem services even if this loss is, to a

340   certain extent offset by increases in abundance of species with greater body

341   mass. Our results confirm trends for a number of species of farmland bird

342   species, many of which are common and have shown steep declines in a number

343   of European countries in recent years (Chamberlain et al 2000; Fox 2004;

344 Wretenberg et al. 2006). A proportion of the patterns we present may be

345 attributed to changes previously described such as the declines in farmland bird

346 species and the associated declines in granivorous birds (Moorcroft et al. 2002),

347 indeed Q4 contains a greater proportion of farmland granivores than other

348 quartiles, although there are more insectivores and birds utilising habitats other

349 than farmland within this quartile. We did not however find any significant

350 interactions between feeding guild and time or habitat and time.

351 Whilst conservation policy aims to identify declines in as wide a range of species

352 as possible, including the most common species, it is almost inevitable, given

353 limited resources, that conservation action has a long history of focusing on rarity

354 and this approach has had some notable successes (Male & Bean 2005; Donald

355 et al. 2007; Hoffman et al. 2010). Being common however does not provide

356 immunity from future decline and possible extinction. Indeed the literature

357 provides numerous examples of once common species that have been driven to

358 extinction, or have ceased to be common, in relatively short periods (Gaston &

359 Fuller 2007; Lindenmayer et al. 2011). In this study, we have demonstrated that

360 the vast majority of the decline in European birds is explained by considerable

361 losses in number of relatively few common bird species. Conversely, less

362 abundant species are generally increasing in number. Whilst our results do not

363 contain data on species considered especially rare in Europe (<1500 breeding

364 pairs; Holling & Rare Breeding Birds Panel 2011), those for Q1 reflect the

365 population trends that have been reported regionally for such species, with a UK

rare species indicator for example demonstrating a 260% increase between 1973

and 1998 (Gregory et al. 2003), with much of that increase being due to targeted

conservation action.

One possible clue to the declines in the most abundant species is that, almost by

definition, common species are widespread and their numbers are linked to the

deterioration of the quality of the environment on a landscape scale (Gaston &

Fuller 2007). Conservation management tends to be targeted locally to increase

the abundance of rare species, often through the establishment and maintenance

of protected areas. Such management plans however offer little protection for

more common and widespread species (Hoffman et al. 2010). Whilst protected

areas are vital to conserving rare and endangered species, we suggest an

increasing proportion of conservation funding and effort be afforded to wider

scale environmental improvement programs, such as effective agri-environment

and urban green space schemes.

401

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582 different patterns of agricultural intensification. *J. Appl. Ecol.*, 43, 1110–1120.

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585   **Figure Legends**

586   Figure 1. Total changes in abundance and biomass of birds considered by the

587   PECBMS. Each point represents the totalled abundance estimates of 144

588   species from 1980 to 2009. Lines represent the fitted values from a general

589   additive model (red - degrees of freedom = 10, blue - degrees of freedom =3).

590   Linear regression reveals a significant decrease of both abundance (β = -9.89 x

591   10^6, t = - 6.127, p < 0.0001) and biomass (β = -133.51, t = - 2.074, p = 0.0474)

592   over the 30 year study period. Box and whisker plots represent the variation

593   generated by randomly altering each abundance estimate +/- 1 & 20% for 100

594   iterations.

595

596   Figure 2. Total estimates of abundance separated into quartiles. I.) Quartiles

597   based on abundance on a yearly basis hence quartiles have a variable species

598   composition II). Quartiles based on abundance in year one of the study (1980)

599   hence quartiles have a fixed species composition. Lines represent the fitted

600   values from a general additive model (red - degrees of freedom = 10, blue -

601   degrees of freedom =3). Species representing each quartile are; Q1 Grey Heron

602   (*Ardea cinerea*), Q2 Reed Warbler (*Acrocephalus scirpaceus*), Q3 Jackdaw

603   (*Corvus monedula*) & Q4 House Sparrow (*Passer domesticus*). Box and whisker

604   plots represent the variation generated by randomly altering each abundance

605   estimate +/- 1 & 20% for 100 iterations.

606

607 Figure 3. Total estimates of biomass separated into quartiles. I.) Quartiles based

608 on abundance on a yearly basis hence quartiles have a variable species

609 composition II). Quartiles based on abundance in year one of the study (1980)

610 hence quartiles have a fixed species composition. Lines represent the fitted

611 values from a general additive model (red - degrees of freedom = 10, blue -

612 degrees of freedom =3). Box and whisker plots represent the variation generated

613 by randomly altering each abundance estimate +/- 1 & 20% for 100 iterations.

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618 **Table Legends**

619 Table 1. Changes in estimated avian abundance (number of individuals) within

620 Europe between 1980 and 2009. a) Total changes and changes by quartile when

621 species composition of each quartile is allowed to vary with time. b) Changes by

622 quartile when species composition of each quartile is fixed in year one. c)

623 Number of species increasing or decreasing and the number of species for which

624 these changes were statistically significant ($\alpha = 0.05$).

625

626 Table 2. Changes in estimated avian biomass (Tonnes) within Europe between

627 1980 and 2009 a) Total changes and changes by quartile when species

628 composition of each quartile is allowed to vary with time. b) Changes by quartile

629 when species composition of each quartile is fixed in year one.

630

Tables

Table 1.

a)

Quartile	Year 1	Year 30	Change	Proportion of total change
All	2063173982	1641329711	-421844271	
Q1	13576444	13597987	21543	0.000
Q2	88694609	79127422	-9567187	0.023
Q3	293659205	232800545	-60858660	0.144
Q4	1667243724	1315803757	-351439967	0.833

b)

Quartile	Year 1	Year 30	Change	Proportion of total change
Q1	13576444	18390981	4814537	0.011
Q2	88694609	91421345	2726736	0.006
Q3	293659205	266209319	-27449886	0.063
Q4	1667243724	1265308066	-401935658	0.920

c)

	Increase	Decrease	Significant increase	Significant decrease
Total	74	70	55	62
Q1	24	12	17	8
Q2	21	15	17	14
Q3	17	19	11	18
Q4	12	24	10	22

653   Table 2.

654   a)

Quartile	Year 1 (Tonnes)	Year 30 (Tonnes)	Change (Tonnes)	Proportion of change
Total	93084	86037	-7047	
Q1	3476	4274	798	0.092
Q2	9225	7637	-1588	0.184
Q3	18223	13141	-5082	0.588
Q4	62159	60986	-1174	0.136

655

656   b)

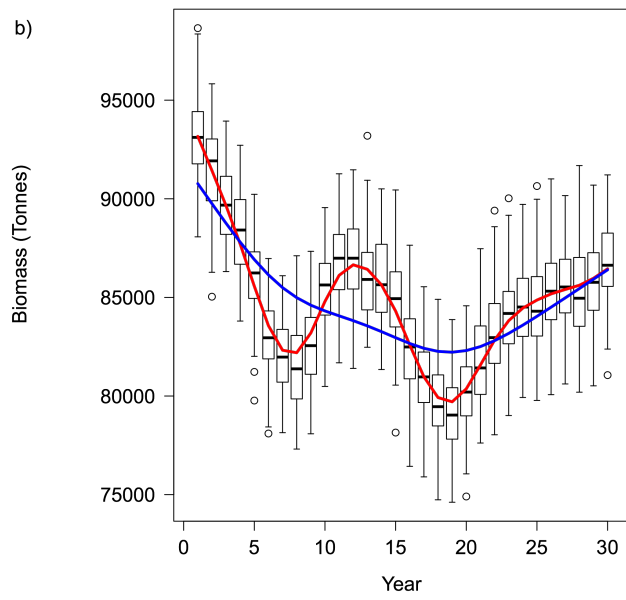| Quartile	Year 1 (Tonnes)	Year 30 (Tonnes)	Change (Tonnes)	Proportion of change
Q1	3476	5298	1823	0.102
Q2	9225	11066	1841	0.103
Q3	18223	19988	1765	0.099
Q4	62159	49685	-12475	0.697

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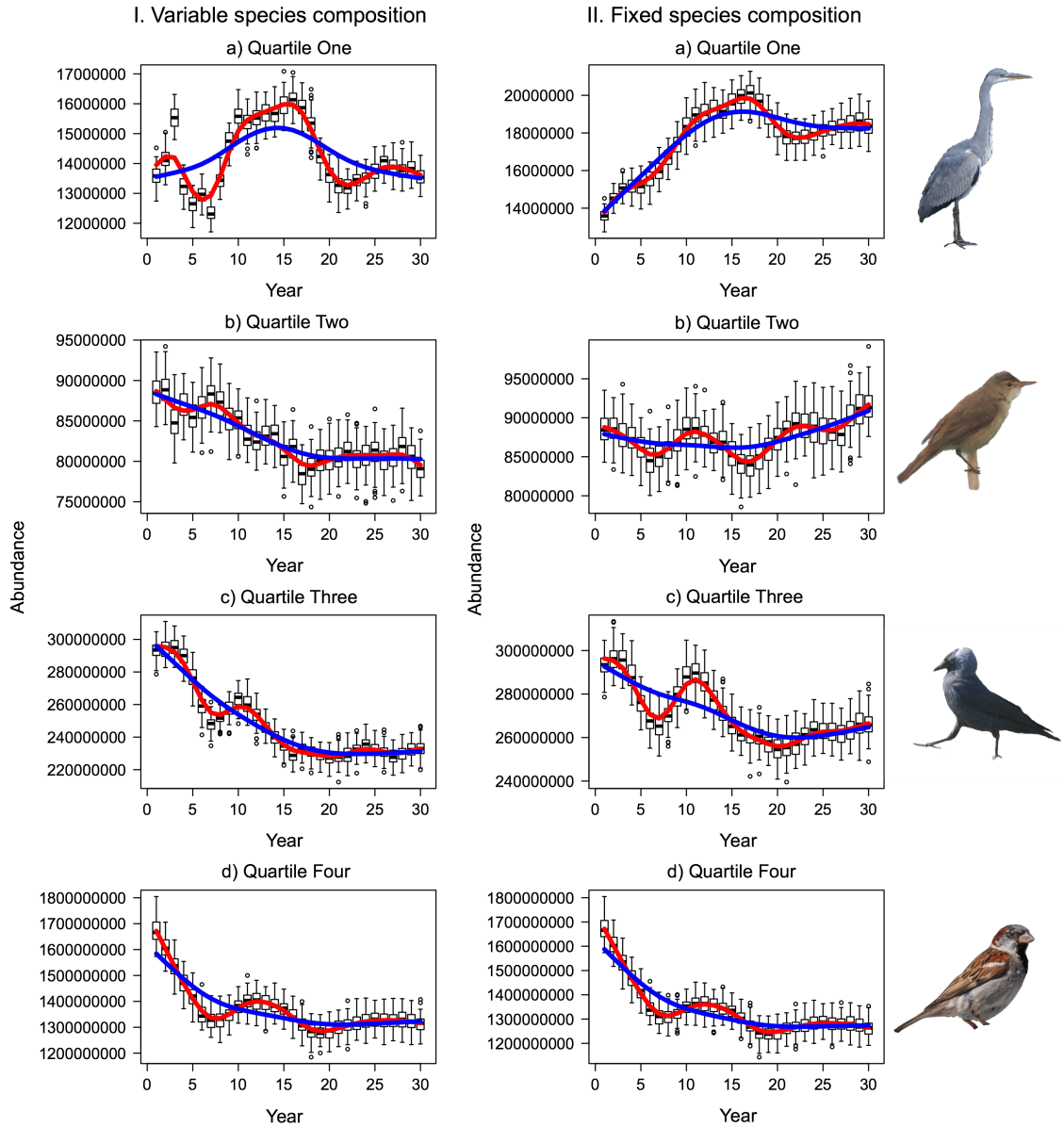
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669 **Figures**

670 Figure 1.
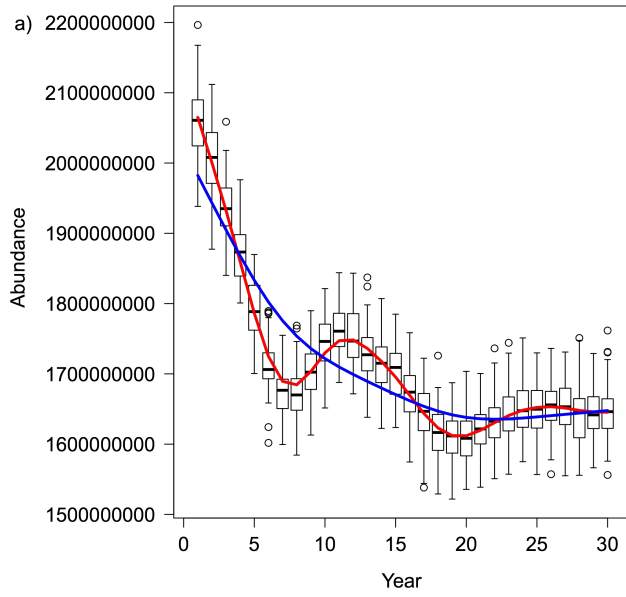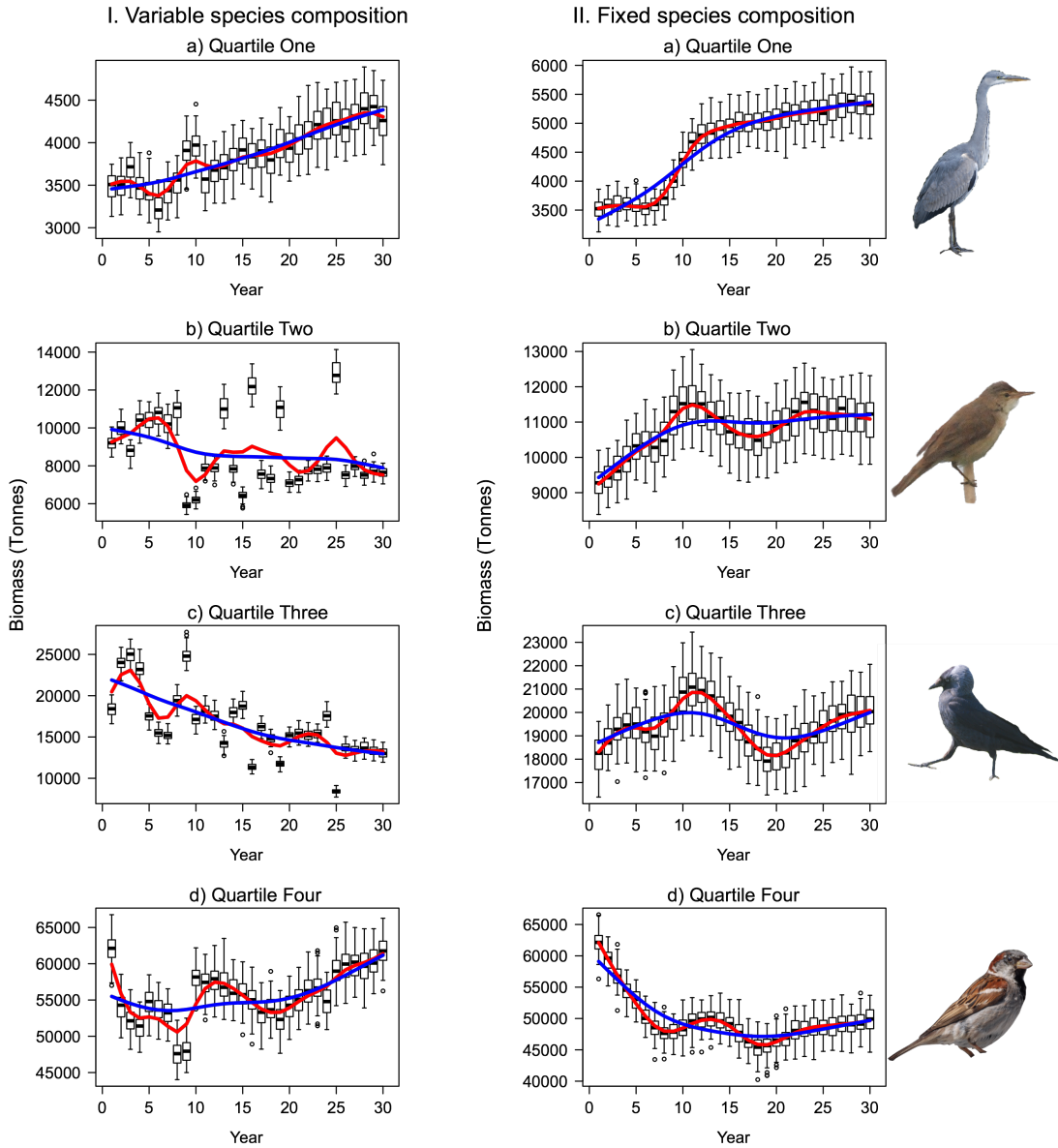

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677   Figure 2.

683   Figure 3.

I. Variable species composition   II. Fixed species composition

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