Author(s): Reino, Luís; Triviño, María; Beja, Pedro; Araújo, Miguel B.; Figueira, Rui; Segurado, Pedro

Title: Modelling landscape constraints on farmland bird species range shifts under climate change

Year: 2018

Version: Accepted version (Final draft)

Modelling landscape constraints on farmland bird species range shifts under climate change

Luís Reino[1,2,3], María Triviño[4,5], Pedro Beja[1,3], Miguel B. Araújo[2,4,6], Rui Figueira [1,3] and Pedro Segurado[7]

[1] CIBIO/InBIO-Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, nº9, 4485-661 Vairão, Portugal

[2] CIBIO/InBIO-Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade de Évora, 7004-516 Évora, Portugal

[3] CEABN/InBIO-Centro de Estudos Ambientais 'Prof. Baeta Neves', Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

[4] University of Jyvaskyla, Department of Biological and Environmental Sciences, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

[5] Museo de Nacional de Ciencias Naturales, CSIC, Calle José Gutiérrez Abascal, 2, 28006 Madrid, Spain

[6] Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen, Denmark

[7] CEF - Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

Running title: Landscape constraints on species range shifts

Word count: 4809

1

Abstract

Several studies estimating the effects of global environmental change on biodiversity are focused on climate change. Yet, non-climatic factors such as changes in land cover can also be of paramount importance. This may be particularly important for habitat specialists associated with human-dominated landscapes, where land cover and climate changes may be largely decoupled. Here, we tested this idea by modelling the influence of climate, landscape composition and pattern, on the predicted future (2021-2050) distributions of 21 farmland bird species in the Iberian Peninsula, using boosted regression trees and 10-km resolution presence/absence data. We also evaluated whether habitat specialist species were more affected by landscape factors than generalist species. Overall, this study showed that the contribution of current landscape composition and pattern to the performance of species distribution models (SDMs) was relatively low. However, SDMs built using either climate or climate plus landscape variables yielded very different predictions of future species range shifts and, hence, of the geographical patterns of change in species richness. Our results indicate that open habitat specialist species tend to expand their range, whereas habitat generalist species tend to retract under climate change scenarios. The effect of incorporating landscape factors were particularly marked on open habitat specialists of conservation concern, for which the expected expansion under climate change seems to be severely constrained by land cover change. Overall, results suggest that particular attention should be given to landscape change in addition to climate when modelling the impacts of environmental changes for both farmland specialist and generalist bird distributions.

Introduction

58   Many studies have attempted to estimate the future effects of global environmental

59   changes on biodiversity (e.g., Thuiller *et al.*, 2005; Araújo *et al.*, 2006; Garcia *et al.*, 2011).

60   Many of these studies examine the effect of climate change alone, leaving aside the effects

61   of non-climatic drivers (e.g., Harfoot *et al.*, 2014, Morelli & Tryjanowsky, 2015, Titeux et al.,

62   2016). However, the effects of climate change on biodiversity can be influenced by

63   interactions with other components of global change (e.g., Clavero *et al.*, 2011; Hof *et al.*,

64   2012, Maxwell *et al.*, 2016), particularly with land use changes and related effects on other

65   pressures such as water regime (e.g., Jetz *et al.*, 2007; Rosenzweig et al., 2008; Thuiller *et

66   al.*, 2014a; Newbold *et al.*, 2016).

67   Both climate and land cover changes are considered major drivers of global biodiversity

68   change (Sala *et al.*, 2000; Jetz *et al.*, 2007; de Chazal & Rounsevell, 2009). However, climate

69   is often regarded as the most important driver at large spatial extents and coarse spatial

70   resolutions (e.g., Thuiller *et al.*, 2004a; Luoto *et al.*, 2007; Triviño *et al.*, 2011). The relative

71   contribution of climate and land cover on future species range shift projections remain

72   poorly explored (Pearce-Higgins and Green, 2014; but see studies from Table 1, Suppl.

73   Mat.). Previous studies have found that land cover can be correlated with climate and that

74   including land cover variables did not improve the accuracy of species distribution models,

75   as expected (e.g., Seoane *et al.*, 2003; Thuiller *et al.*, 2004a; Triviño *et al.*, 2011; Reino *et

76   al.*, 2013). Although climate and land cover are generally correlated, however, climate does

77   not necessarily fully control land cover, which may be affected by a number of additional

78   factors such as soil type, topography, socio-economic contexts and policies (Veldkamp &

79   Lambin, 2001; Ribeiro *et al.*, 2014, 2016). In addition, because climate and land cover often

80   play key roles at different spatial scales (Pearson *et al.*, 2004), they are likely to show

81   different geographical patterns of change and hence may affect different regions in a

82 distinct way. Moreover, climate and landscape drivers may interact in their effect on

83 species geographical range, because the two drivers may have different effects on different

84 groups of species (Opdam & Wascher, 2004; Sohl, 2014; Jarzyna *et al.*, 2015).

85 Most studies modelling the consequences of changes in the structural component of

86 landscape have ignored potentially important processes related to landscape

87 fragmentation (e.g., Vallecillo *et al.*, 2009; Triviño *et al.*, 2011), although they have been

88 shown to be determinant for some species (Jarzyna *et al.*, 2015). This is the case, for

89 instance, of some farmland bird specialists that were shown to be very sensitive to habitat

90 fragmentation at several spatial scales (Reino *et al.*, 2009, Reino *et al.*, 2013). There is a

91 well-established idea that generalist species tend to cope better with environmental

92 changes than specialist species (Gilman *et al.*, 2010, Clavel *et al.*, 2011, Davey *et al.*; 2012,

93 Lurgi *et al.*; 2012; Case *et al.*, 2015). However, at the same time, some studies point to an

94 idiosyncratic nature of species responses to climate change, making it difficult to draw

95 generalizations (e.g., Mair *et al.*, 2012; Moritz & Agudo, 2013; Sohl, 2014). For example, in

96 a recent study, Princé *et al.* (2015) found that the relative sensitivity of farmland bird

97 specialists and generalists to climate and land cover changes varied among the different

98 global change scenarios that were considered (Princé *et al.*, 2015).

99 Here we model the relative importance of changes at the landscape level on range shifts

100 predictions under future environmental change scenarios, aiming at bringing new insights

101 on the interplay of three component of the environment: biosphere, atmosphere and

102 anthroposphere. We focused on farmland birds in the Iberian Peninsula, considering both

103 climate change and changes in land cover and landscape structure, mainly as the result of

104 land abandonment and changes in agricultural practices, associated with three

105 socioeconomic scenarios for the period of 2021 to 2050. We hypothesize that taking into

106 account changes in landscape composition and structure will potentially strongly affect

107 predictions of farmland bird geographical ranges under climate change scenarios. We also

108   expect that the potential impacts of landscape changes on farmland bird geographical

109   ranges is dependent on the degree of habitat specialization (Clavel *et al.*, 2011), namely the

110   association to farmland landscapes. The overarching goal of this study is thus to examine

111   the proposition that landscape changes should be accounted for when forecasting the

112   effects of environmental changes on the distribution of species highly sensitive to

113   landscape structure.

114

115   **Material and Methods**

116   *Data*

117   We used distributional records for 21 Iberian farmland bird species (Table 1), obtained from

118   the most recent breeding bird atlas from Spain (Martí & Moral, 2003) and Portugal (Equipa

119   Atlas, 2008), reporting the occurrence of bird species in 5923 10×10 km resolution UTM

120   cells. These are the highest-resolution bird distribution data available for Iberia. Farmland

121   birds selected for this study include species with different degrees of habitat specialization

122   to open habitats, because these seem to be those most at risk from ongoing changes in

123   agricultural land cover. Some of the species are highly specialized to open grassland

124   habitats (e.g., Calandra lark *Melanocorypha calandra*), whereas others can tolerate

125   different degrees of habitat fragmentation (e.g., Little bustard *Tetrax tetrax*), or are often

126   considered habitat generalists (e.g., Corn bunting *Emberiza calandra*). Nonetheless, most

127   of the farmland species considered may tolerate a wide range of habitats, though we

128   excluded species which are often associated with tree-cover habitats (e.g., red-legged

129   partridge *Alectoris rufa*). For each species, the mean landscape Shannon diversity index in

130   the occurrence cells, based on the forty-four land cover classes from CORINE (EEA, 2000),

131   was computed and the resulting values, after rescaling between 0 and 1, were inverted. We

132   used the resulting index, here referred to as Landscape Specialization Index (LSI), as a

133   surrogate of habitat specialization (see Table 1). A significant negative relationship between

134   bird's habitat specialization and landscape fragmentation derived from CORINE land cover

135   maps was shown elsewhere (Devictor *et al.*, 2008).

136   We used three climatic variables that synthetize two factors – energy and water – that

137   determine biological diversity distribution worldwide (Hawkins et al., 2003): average

138   minimum temperature of the coldest month, average mean maximum temperature of the

139   hottest month and average total annual precipitation. A fourth selected climatic variable -

140   standard deviation of monthly means of minimum temperature – reflected seasonality of

141   climate. The baseline climatic data was obtained from the Portuguese and Spanish

142   meteorological agencies (IM and AEMET, respectively), interpolated to a UTM 10×10 km

143   grid (Araújo *et al.*, 2012).

144   The future climate was based on the scenarios developed in the ALARM project

145   (http://www.alarmproject.net/alarm, Assessing Large-scale Environmental Risks for

146   biodiversity with tested Methods; Settele et al. (2005)), resampled at a 10-min resolution

147   (~16 km at the latitude of the study). Future scenarios of climate and land cover for the

148   period 2021-2050 were based on the three alternative storylines developed in the ALARM

149   project: 1) "Business As Might Be Usual" (BAMBU based on the A2 scenario from the IPCC),

150   2) "Growth Applied Strategy" (GRAS based on the A1F1 scenario from IPCC) and 3)

151   "Sustainable European Development Goal" (SEDG based on the B1 scenario from IPCC).

152   These scenarios covered a broad range of potential socio-economic, political, technological

153   and geobiosphere changes, and were developed to describe alternative future pathways of

154   key driving factors affecting biodiversity (Araújo *et al.*, 2008; Dendoncker *et al.*, 2006;

155   Rounsevell *et al.*, 2006; Spangenberg *et al.*, 2007, 2012). The future land cover change

156   scenarios were based on the Coordination of Information on the Environment (CORINE

157   Land Cover; EEA, 2002, see Rounsevell *et al.*, (2006) and Dendoncker *et al.*, (2007) for

158   methodology details). The forty-four land cover classes from CORINE were aggregated into

159   six classes for these scenarios: *Urban*, *Cropland*, *Permanent crops, Grassland*, *Forest,* and

160   *Others*. We assumed that *Cropland* was the class encompassing the most suitable habitats

161   for the selected Iberian farmland bird species. For both future scenarios and the baseline

162   period, the *Cropland* class resulted from aggregation of the following CORINE classes: 1)

163   Non-irrigated arable land; 2) Permanently irrigated land; 3) Rice fields; and 4) Complex

164   cultivation patterns. The *Grassland* class was not considered as a relevant land cover

165   aggregation for farmland bird species because it is overly abundant in Portugal due to a

166   somehow arbitrary amalgamation of several land cover types (for example, the category

167   "Land principally occupied by agriculture with significant areas of natural vegetation" was

168   included in the *Grassland* category).

169   Future climatic scenarios were downscaled to the same 10-km grid cell resolution of the

170   baseline data. For both baseline period and future land cover scenarios, we assumed that

171   the quantity of suitable habitat for farmland birds is strongly influenced by the percentage

172   of the grid cells covered with the class *Cropland*. We computed three landscape

173   fragmentation metrics on the distribution of croplands for each 10×10 km UTM grid cell of

174   Iberian Peninsula, following the approach used in a previous study (Reino *et al.*, 2013).

175   Landscape metrics comprised three variables: mean cropland patch area, number of

176   cropland patches, and edge density. We computed edge density, i.e. edges between

177   patches of different classes, using the total edge length of cropland patches at each grid

178   square. The computation of the percentage of cropland area and the three landscape

179   metrics at each 10km grid cell were based on land cover raster themes with 100m

180   resolution. We carried out the analyses in ArcGIS 9.3 (ESRI, 2006).

181   Because birds' data were restricted to the Iberian Peninsula, arguably the models may fail

182   to capture the full range of suitable conditions of each species. This may cause truncated

183   response curves at extreme conditions and, consequently, biased projections (Thuiller et

184   al., 2004b). To evaluate this potential effect, we mapped the grid cells that in the future

185   would lay outside the training conditions for each climatic variable. Only for the BAMBU

7

186   scenario and one variable (Mean Maximum Temperature), a considerable extension of the

187   Iberian Peninsula (24,7% of the grid cells) was predicted to be outside the baseline range

188   of values. For the remaining variables, extrapolation area represented less than 5% of the

189   grid cells. For the GRAS and SEDGE scenarios, the extrapolation area represented,

190   respectively, less than 2% and 1% for all climatic variables. All extrapolation areas showed

191   warmer and drier climates. Because all species occur in North Africa we can assume that

192   climate projections will not go beyond species tolerances. Nevertheless, this potential

193   problem was duly considered when interpreting our modelling results, though violation of

194   such assumption would mainly affect the high-end scenario (BAMBU). Regarding landscape

195   structure, given the high structural heterogeneity of Iberian landscape we can assume that

196   a sufficient broad gradient is covered in the baseline.

197

198   *Statistical modelling*

199   We developed boosted regression trees (BRT) (Friedman *et al.*, 2000, Hastie *et al.*, 2001) to

200   estimate the relationship between the 21 Iberian farmland birds and the climatic and

201   landscape variables for the baseline period. We then used the resulting relationships to

202   project the potential distributions under the three future climate and land cover change

203   scenarios for 2021-2050. BRT differs from the traditional classification and regression tree

204   techniques that produce a single 'best' tree, by making use of a 'boosting' technique to

205   combine large numbers of relatively simple tree models adaptively, in order to optimize

206   predictive performance (see e.g., Elith *et al.*, 2006; Leathwick *et al.*, 2006, 2008 for further

207   details). The main difference between BRT and other tree-based ensemble techniques (e.g.,

208   random forests; Prasad *et al.*, 2006) is that trees are fitted sequentially through a stagewise

209   process, i.e., at each step of model development, the trees from previous steps are left

210   unchanged as the model is enlarged (Elith *et al.*, 2008). This relative model rigidity, where

211   the overall hierarchical structure of variable effects is maintained stable, is an important

212   feature for the purpose of our study, which focuses on two very different sets of variables

213   (climate and landscape) that are expected to act hierarchically on species distributions

214   (Pearson *et al.*, 2004). Furthermore, BRT are recognized for their capabilities to reliably

215   selected meaningful variables, through automatic detection of interactions and robust

216   fitting of trends (Hastie *et al.*, 2001). BRT has also the advantage of handling different types

217   of variables, and coping with collinearity and non-linear relationships between predictors

218   (Elith *et al.*, 2008).

219   To optimize the number of trees in each BRT model, we carried out a stepwise process

220   based on 10-fold cross-validations using mean deviance on the validation data as a measure

221   of predictive performance (Elith *et al.*, 2008). Two important parameters must be defined

222   *a priori* to determine the number of trees required for optimal predictions: the learning

223   rate, which determines the contribution of each tree to the growing model, and the tree

224   complexity that controls the number of interactions among variables (i.e., the number of

225   splits of individual trees). We used three alternative values for both tree complexity and

226   learning rate to account for the uncertainties introduced by the subjectivity of the

227   previously selected parameter values. To select a range of learning rate and tree complexity

228   values ensuring that at least 1000 trees were achieved after the stepwise process (Elith *et*

229   *al.*, 2008), we first trained the data using several alternative learning rate and tree

230   complexity values. We finally set learning rate values to 0.002, 0.003 and 0.004 and tree

231   complexity values to 3, 4 and 5. Discrimination power of models was assessed by computing

232   the mean Area Under the Receiver Operational Curve (AUC; Fielding & Bell, 1997) based on

233   10-fold cross-validations. BRT were computed with the gbm (Ridgway, 2013) and dismo

234   (Hijmans *et al.*, 2012) libraries in R software version 2.15.2 (R Development Core Team,

235   2013).

236   To assess the impact of including landscape variables in the predictions of distribution

237   expansion/retraction of species, we fitted two different models per species for each

238   learning rates and tree complexity combination: a climate-only model and a

239   climate+landscape model. For each kind of model, the probabilities of occurrence from the

240   nine models resulting from the pairwise combination of learning rates and tree complexity

241   values were averaged following standard committee averaging procedures in ensemble

242   modelling (Araújo & New, 2007). The importance of each variable to the model was based

243   on the measure of relative influence described in Friedman (2001) and averaged across the

244   nine models.

245

246   *Range shifts*

247   We classified the probabilities of occurrence obtained with the BRT models into potential

248   presence/absence maps for the baseline period and for the period of 2021-2050 under the

249   three alternative scenarios hypothesis. The probability value that maximized the sum of

250   sensitivity and specificity was used as the cut-off point for discriminating predicted

251   presence and absence (Liu *et al.*, 2005).

252   Using the resulting maps of the potential species distributions we computed the net

253   variation of the geographical range for both climate-only and climate+landscape models (%

254   of variation of the predicted species prevalence relative to the baseline), between the

255   baseline and the future scenarios. We also computed the difference of the range variation

256   between climate-only and climate+landscape models to assess if the inclusion of landscape

257   variables led to a weaker/stronger range retraction or weaker/stronger range expansion.

258   We tested the correlation between the Landscape Specialization Index for each species and

259   both the variation of the geographical range area and the difference of the range area

260   variation between climate-only and climate+landscape models. We computed the number

261   of winner species (i.e. species that are currently absent but predicted to be present in the

262   future) and of loser species (i.e. species that are currently present but predicted to be

263 absent in the future) in each grid cell based on the differences between species

264 presence/absence maps for the baseline and each future scenario predictions. To test

265 differences among the three scenarios in the resulting maps, we used a modified version of

266 the t-test to assess correlation between two spatial processes (Clifford *et al.*, 1989)

267 implemented in the SpatialPack R package (Osorio *et al.*, 2012).

268

269 **Results**

270 *Model performance*

271 The incorporation of landscape variables in the climate-based models consistently

272 improved model's discrimination ability, as measured with mean cross-validation AUC

273 values (Wilcoxon signed rank test, P<0.001). However, the contribution of landscape

274 variables did not increase substantially the discrimination ability of models, with percent

275 (%) of improvements varying from 0.06% for *Calandrella rufescens* to 4.68% for *Circus*

276 *pygargus* (Table 1). The species Landscape Specialization Index was positively correlated

277 with AUC values of both the climate-only (Pearson r=0.49, p<0.05) and climate+landscape

278 models (Pearson r=0.51, p<0.02). However, habitat specialization was not correlated with

279 the percentage increase of discrimination ability (Pearson r=-0.08, p=0.74).

280

281 *Variable importance*

282 The climatic variables with the highest relative influence in the models were the average

283 minimum temperature of the coldest month and the average mean maximum temperature

284 of the warmest month (Table 2). The importance of these two variables showed no

285 significant correlations with the species Landscape Specialization Index (mean maximum

286 temperature, Pearson r=0.06, p-value=0.80; mean maximum temperature, Pearson r= -

287 0.16, p-value=0.48). Among the landscape variables, the mean cropland patch area

288 followed by the edge density were found to be the most influential for all the species,

289 independently of their degree of specialization.

290

291 *Range shifts*

292 The direction of projected range shifts for 17 out of 21 farmland bird species were

293 consistent among the three socio-economic scenarios. Among these, range expansion was

294 predicted for 10 species and range contraction was predicted for 7 species (Table 3).

295 Overall, the strongest influence of landscape variables in range shifts, were found for

296 species predicted either to show stronger retraction or weaker expansion of their

297 geographical range (Table 3). The maximum variation in the percentage of range shift

298 change was found for *Otis tarda* (e.g., -158.8% for the GRAS scenario) and *Pterocles alchata*

299 (e.g., 151.0% for the GRAS scenario). For the three scenarios, no significant correlations

300 were found between the percentage of increase in the discrimination ability of models and

301 the percentage of predicted range shift changes after considering landscape variables

302 (Pearson's correlation, $r<1$ and $p>0.6$ for all scenarios).

303 When the outputs of climate+landscape models were related with the species' degree of

304 habitat specialization, as given by the Landscape Specialization Index (LSI), some general

305 trends on the predicted range shifts emerged. The relationship between predicted range

306 shifts and LSI indicates a tendency from range retractions to range expansions for increasing

307 species' habitat specialization (Fig. 1). This positive correlation was significant (Pearson's

308 correlation, $p < 0.05$) for all scenarios in the case of climate-only models. In the case of

309 climate+landscape models, the correlation was significant for the GRAS scenario, whereas

310 for the BAMBU and SEDGE scenarios the relationships were only marginally significant (Fig.

311 1).

312   A significant negative relationship between LSI and the variation of range shift percent

313   change after including landscape variables in the models (i.e. the difference between the

314   percent change of range shift in the climate-only model and the percent change of range

315   shift in the climate + landscape model), was found for the three scenarios (Pearson's

316   correlation, $p < 0.05$; Fig. 2). For increasing LSI values, a tendency for the percentages of

317   change to be more negative was found, i.e., as the degree of species habitat specialization

318   increases, climate-only models tended to be more over-optimistic in comparison to

319   climate+landscape models.

320

321   *Species richness*

322   The mean number of farmland bird species per 10x10 km UTM grid cell was forecasted to

323   be significantly higher in the future under any of the three socioeconomic scenarios than

324   at present (Wilcoxon signed rank test, $p < 0.001$). However, the average absolute increase

325   in local species richness was significantly lower using the climate+landscape model than the

326   climate-only model under the BAMBU (0.48 species ± 3.16 SD *vs*. 1.43 species ± 3.74 SD),

327   GRAS (0.20 species ± 3.34 SD *vs*. 1.31 species ± 3.83 SD) and SEDGE (0.59 species ± 3.21 SD

328   *vs*. 1.68 species ± 3.65 SD) scenarios. There were also differences between models in the

329   spatial pattern of absolute variation in local species richness. Generally, climate-only

330   models tended to predict larger areas of richness increase in both central and southern

331   Iberia, while climate+landscape models tended to predict larger areas of richness increase

332   in Northern Iberia (Fig. 3). Consistent increases in species richness were predicted to occur

333   irrespective of model type in central and southern Iberia.

334

335   *Losers and winners*

336   The geographical patterns of loser and winner species per 10 km grid square were also

337   largely dependent on whether landscape variables were included or not in the models (Fig.

338   4). Significant correlations among the three climate change scenarios were found for both

339   winners and losers maps, even after accounting for spatial autocorrelation (modified t-test,

340    $p < 0.001$). Climate-only models predicted a larger area with high numbers of winner species

341   (Fig. 4, left maps, yellow areas), mainly in the centre, southern Iberian mountain ranges and

342   the eastern coast. Contrarily, climate+landscape models predicted a larger area showing

343   high numbers of loser species, mainly in the southern plains (Fig. 4, right maps, blue areas).

344

345

346   **Discussion**

347   Our results confirm the hypothesis that the inclusion of landscape variables in species

348   distribution models strongly affect range shift predictions of Iberian farmland birds, despite

349   a generally low contribution to models' performance. Overall, the resulting species

350   distribution models predict that habitat specialists will tend to expand their range, whereas

351   generalists will tend to retract under climate change scenarios. However, in many cases,

352   the inclusion of landscape variables in the models leads to an attenuation of the projected

353   range expansion of specialist species under scenarios of both climate and landscape

354   changes.

355

356   *Impacts of landscape variables on predicted range shifts*

357   Our results are in agreement with other studies that also show a relatively small

358   contribution of landscape related covariates in relation to climate when modelling

359   distributions at coarse spatial resolutions (e.g., Thuiller *et al.*, 2004a; Luoto *et al.*, 2007;

360   Triviño *et al.*, 2011). These findings have supported the view that, for many species,

361   variables such as land cover could sometimes be disregarded from predictive distribution

362   models at wide spatial scales and coarse resolutions (Pearson *et al.*, 2004; Thuiller *et al.*,

14

363   2004a; Triviño *et al.*, 2011). Furthermore, the often-found correlation between climate and

364   land cover variables has supported this view (e.g., Thuiller *et al.*, 2004a).

365

366   Despite the small explanatory power of landscape metrics, we found that they were

367   associated to major changes on species range shifts under global environmental change. In

368   fact, the addition of landscape variables in the models resulted in deviations up to 150% of

369   the range shift predictions of models using climate alone (Table 3). Landscape changes may

370   occur at a higher pace and magnitude compared to climatic changes and consequently even

371   small contributions to models might result in a noticeable impact on predictions. The

372   significant impact of land use on predictions is also partially in accordance with recent

373   studies that predict large-scale changes in biodiversity (Thuiller *et al.*, 2014a; Princé *et al.*,

374   2015, Estrada *et al.*, 2016).

375

376   Finally, despite their low contribution to models' accuracy, the inclusion of landscape

377   variables also extensively affected predictions of the geographical patterns of richness and

378   of species gains and losses in relation to the climate-only based models. Joint models

379   (climate/landscape) predicted globally more "loser species" and less "winner species" per

380   grid-square than the climate-only models, resulting in an overall lower predicted mean

381   richness per grid-square. In fact, it has been shown that population changes in farmland

382   birds are often closely related to changes in the intensity of agricultural management rather

383   than to be driven by climatic changes alone (e.g., Pearce-Higgins & Green, 2014). These may

384   implicitly suggest that for the majority of farmland species, recent climate change could still

385   be considered of secondary importance, when compared to changes in agricultural

386   management, which is generally leading worldwide to the intensification of agriculture

387   (e.g., Eglington & Pearce-Higgins, 2012). Even if climatic variables are more determinant

388   according to models of farmland bird distribution, their change in the recent past has been

389   much more subtle than land use changes, which might explain the aforementioned trend.

390

391   *The importance of landscape variables along the habitat specialization gradient*

392   The trend found in the projected range shifts along the species' habitat specialization

393   gradient contrasts with the generally accepted idea that generalist species cope better with

394   environmental changes than specialist species (e.g., Clavel *et al.*, 2011). The latter species

395   also appear to have a narrower thermal tolerance, for instance, when compared with more

396   generalist species. This means that habitat change unrelated to climate change may affect

397   species community composition (e.g., Clavero et al. 2011). Nevertheless, the general results

398   of this study are in line with a recent study that found a tendency of generalist bird species

399   occurring in farmlands to be often more affected by climate and land cover changes than

400   specialist farmland birds (Princé *et al.*, 2015). However, strict generalizations can hardly be

401   drawn from our results, which supports the idiosyncratic nature of species responses to

402   climate change (Moritz & Agudo, 2013). In the case of Iberian farmland birds, specialist

403   species are most often adapted to higher temperatures, which might explain the frequent

404   geographic range expansions predicted for these species. However, because habitat

405   specialists are often more dependent of specific habitat conditions this may halt their

406   expansion to other areas with suitable habitat conditions due to habitat and land cover

407   change, for instance.

408   A major effect of incorporating landscape variables in the models was a less optimistic

409   future for specialist species, mainly with a lower range expansion or, in some cases, a

410   stronger range contraction than predicted by climate-only models. A possible explanation

411   is that, since specialist species tend to be more constrained by both landscape changes and

412   the level of intensity of agricultural management (see Eglington & Pearce-Higgins, 2012), a

413   decrease in landscape favourability in the new expansion areas will counteract with the

414   climatic favourability, resulting in an antagonistic effect between climate and landscape.

415   This is a relevant result for conservation purposes because very often specialist species

416   have an important conservation status and therefore it is crucial to produce more realistic

417   predictions when accounting for the potential effects of climate change (Eglington &

418   Pearce-Higgins, 2012).

419   Lower expansions after including landscape variables in the models were projected for six

420   non-passerine species (out of nine) and two passerine species. This outcome suggests that

421   for a considerable number of species, including some of the most relevant farmland species

422   of European conservation concern (e.g., little and great bustards and lesser kestrel), future

423   projections based on climatic variables alone might lead to overestimating the expected

424   expansion. Stronger contractions after accounting for landscape changes were predicted

425   only for four species, including three non-passerine species, of which two are of European

426   conservation concern (Black-bellied Sandgrouse and Pin-tailed Sandgrouse), and a

427   passerine species (Corn Bunting). On the contrary, for some species, including some with a

428   relevant conservation status, the incorporation of landscape variables reduced the

429   possibility of a strong range contraction or lead to an increase of the predicted geographical

430   ranges. The set of species in this group included both lark species (crested and Thekla's

431   larks) and two species of European conservation concern (Black-eared wheatear and

432   Dupont's lark). For two Iberian widespread species (skylark and Linnet), at least partially,

433   lower impacts on species range are also expected when landscape variables are included in

434   the models. After accounting for landscape changes, a future range increase was predicted

435   for a few generalist and ecotone-related species. This seems to be the case of the woodlark,

436   which is an open-habitat species associated with more fragmented farmland landscapes,

437   but also of other farmland species like short-toed lark, which is frequent in more

438   fragmented and convoluted landscapes (Reino *et al.*, 2009).

439

440

Conclusions

442 This study underpins the need to consider landscape composition and structure when

443 modelling species range shifts under future climate scenarios. This is particularly the case

444 for habitat specialists, which are strongly constrained by habitat availability and

445 configuration. In addition, our models show that specialist species (many with relevant

446 European conservation concern, Table S2) produce less optimistic predictions when

447 landscape changes are also accounted for. The interplay between climate and landscape

448 variables has important implications for an adequate mitigation strategy under climate

449 change. Because farmlands are one of the most extensively modified landscapes and very

450 dependent on management practices and regional policies, the rate, magnitude and

451 direction of alteration is probably more decoupled from climate change than other less

452 altered landscapes. For example, Princé *et al.*, (2015) recently reported that including

453 farmland cover variables could potentially compensate the negative effect of climate

454 change on some species. This means that one needs to be aware when attributing some of

455 the forecasted changes specifically to climate warming (Eglington & Pearce-Higgins, 2012).

456 On the other hand, it also means there is more margin to put into practice management

457 actions that may counteract the negative effects of climate change on bird communities.

458 Our results confirm this idea by showing that more optimistic predictions under climate

459 change for the future are possible when land cover changes are also taken into account.

460 This might suggest that, by implementing right mitigation measures at the landscape level,

461 it would be possible to produce more optimistic predictions for the future, i.e., enlarged

462 range expansions and reduced range contractions.

463

464

18

477

478   **References**

479   Araújo, M.B., New, M. (2007) Ensemble forecasting of species distributions. *Trends in*

480   *Ecology and Evolution*, **22**, 42-47.

481   Araújo, MB, Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate

482   impact models under climate change. *Global Change Biology*, **11**, 1504-1513.

483   Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modelling.

484   *Ecology*, **93**, 1527-1539.

485   Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of

486   amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712–1728.

487   Araújo, M.B., Guilhaumon, F., Neto, D.R., Pozo, I. & Calmaestra, R. (2012) Biodiversidade e

488   Alterações Climáticas /Biodiversidad y Alteraciones Climáticas. Ministério do

489   Ambiente e Ordenamento do Território & Ministerio de Medio Ambiente y Medio

490   Rural y Marino, Lisboa/Madrid.

491 Araújo, M.B., Nogués-Bravo, D., Reginster, I., Rounsevell, M. & Whittaker, R.J. (2008)

492   Exposure of European biodiversity to changes in human-induced pressures.

493   *Environmental Science and Policy*, **11**, 38-45.

494 Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2012) The fate of European breeding birds

495   under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881-890.

496 Bomhard, B., Richardson, D.M., Donaldson, J.S., Hughes, G.O., Midgley, G.F., Raimondo,

497   D.C. & Thuiller, W. (2005) Potential impacts of future land use and climate change on

498   the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Global*

499   *Change Biology*, **11**, 1452-1468.

500 Bota, G., Morales, M.B., Mañosa, S. & Camprodon, J. (Eds) (2005) Ecology and conservation

501   of steppe-land birds. Lynx Edicions & Centre Tecnològic Forestal de Catalunya,

502   Barcelona.

503 Brotons, L. & Jiguet, F. (2010) Bird communities and climate change. In Effects of Climate

504   Change on Birds (eds. A. P. Møller, W. Fiedler & P. Berthold), pp. 275–294. Oxford

505   University Press, Oxford, U.K.

506 Case, M.J., Lawler, J.J. & Tomasevic, J.A. (2015) Relative sensitivity to climate change of

507   species in northwestern North America. *Biological Conservation*, **187**,127–133.

508 Clavel, J., Julliard, R. & Devictor, V. (2011) Worldwide decline of specialist species: toward

509   a global functional homogenization? *Frontiers in Ecology and the Environment*, **9**,

510   222–228.

511 Clavero, M., Villero, D. & Brotons, L. (2011) Climate change or land-use dynamics: Do we

512   know what climate change indicators indicate? *PLoS ONE*, **6**, e18581.

513 de Chazal, J. & Rounsevell, M.D.A. (2009) Land-use and climate change within assessments

514   of biodiversity change: A review. *Global Environmental Change-Human and Policy*

515   *Dimensions*, **19**, 306-315.

516   Clifford, P., Richardson, S. & Hemon, D. (1989) Assessing the significance of the correlation

517   between two spatial processes. *Biometrics*, **45**, 123–134.

518   Davey, C.M., Chamberlain, D.E., Newson, S.E., Noble, D.G. & Johnston, A. (2012). Rise of the

519   generalists: evidence for climate driven homogenization in avian communities: Avian

520   diversity, homogenization and warming climate. *Global Ecology and Biogeography*,

521   **21**, 568–578.

522   Dendoncker, N., Bogaert, P. & Rounsevell, M. (2006) A statistical method to downscale

523   aggregated land-use data and scenarios. *Journal of Land-use Science*, **1**, 63–82.

524   Dendoncker, N., Rounsevell, M. & Bogaert, P. (2007) Spatial analysis and modeling of land-

525   use distributions in Belgium. *Computers Environment and Urban Systems*, **31**, 188–

526   205.

527   Devictor, V., Julliard, R., Jiguet, F. (2008) Distribution of specialist and generalist species

528   along spatial gradients of habitat disturbance and fragmentation. *Oikos*, **117,** 507-

529   514.

530   Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse

531   of Europe's farmland bird populations. *Proceedings of the Royal Society of London.*

532   *Series B: Biological Sciences*, **268,** 25-29.

533   Donald, P.F., Sanderson, F.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Further evidence of

534   continent-wide impacts of agricultural intensification on European farmland birds,

535   1990–2000. *Agriculture, Ecosystems & Environment*, **116**, 189-196.

536   Eglington, S.M. Pearce-Higgins, J.W. (2012) Disentangling the relative importance of

537   changes in climate and land-use intensity in driving recent bird population trends.

538   PLoS ONE 7: e30407.

539   Equipa Atlas (2008) Atlas das aves nidificantes em Portugal (1999-2005). Assírio & Alvim,

540   Lisboa.

541   Estrada, A., Delgado, M.P., Arroyo, B., Traba, J. and Morales, M.B., 2016. Forecasting large-

542   scale habitat suitability of European Bustards under climate change: the role of

543   environmental and geographic variables. *PloS one*, 11(3), p.e0149810.

544   European Environmental Agency (2000) CORINE Land Cover. European Environmental

545   Agency, Luxembourg.

546   ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research

547   Institute.

548   Friedman, J.H., Hastie, T. & Tibshirani, R. (2000) Additive logistic regression: a statistical

549   view of boosting. *Annals of Statistics*, **28**, 337–374.

550   Friedman, J.H. (2001) Greedy Function Approximation: A Gradient Boosting Machine,

551   *Annals of Statistics*, **29**, 1189-1232.

552   Fronzek, S., Carter, T.R. & Jylhä, K. (2012) Representing two centuries of past and future

553   climate for assessing risks to biodiversity in Europe. *Global Ecology and*

554   *Biogeography*, **21**, 19-35.

555   Garcia, R.A., Burgess, N.D., Cabeza, M., Rahbek, C. & Araújo, M.B. (2011) African vertebrate

556   species under warming climates: sources of uncertainty from ensemble forecasting.

557   *Global Change Biology*, **18**, 1253-1269.

558   Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A Framework

559   for Community Interactions under Climate Change. *Trends in Ecology & Evolution*, **25**,

560   325–31.

561   Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V., Smith,

562   M.J., Scharlemann, J.P.W. & Purves, D.W. (2014) Emergent global patterns of

563   ecosystem structure and function from a mechanistic general ecosystem model. *PLoS*

564   *Biol*, **12**, e1001841.

565   Hastie, T., Tibshirani, R. & Friedman, J.H. (2001) The elements of statistical learning: data

566   mining, inference, and prediction. Springer-Verlag, New York, US.

567 Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D. M., Kerr, J.T.,

568 Mittelbach, G. ., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003).

569 Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**,

570 3105–3117.

571 Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. & Hijmans, M.R.J. (2012) Package 'dismo'.

572 The Comprehensive R Archive Network Web Site, http://cran.r-

573 project.org/web/packages/dismo/dismo.pdf; accessed January 2013.

574 Hof, C., Araújo, M.B., Jetz, W. & Rahbek, C. (2011) Climate change, pathogens and land use

575 change additively threat amphibian diversity. *Nature*, **480**, 516-519.

576 Jarzyna, M.A., Porter, W.F., Maurer, B.A., Zuckerberg, B. & Finley, A.O. (2015) Landscape

577 fragmentation affects responses of avian communities to climate change. *Global

578 Change Biology*, **21 21**, 2942-53.

579 Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use

580 change on the global diversity of birds. *PLoS Biology*, **5**, 1211-1219.

581 Lambin, E.F., Turner, B.L., Geist, H.J., Agbola, S.B., Angelsen, A., Bruce J.W., Coomes, O.T.,

582 Dirzo R., Fische,r G., Folke, C., George, P.S., Homewood, K., Imbernon, J., Leemans,

583 R., Li X., Moran EF, Mortimore, M., Ramakrishnan, P.S., Richards, J.F., Skånes, H.,

584 Steffen, W., Stone, G.D., Svedin, U., Veldkamp, T.A., Vogel, C. & Xu, J. (2001) The

585 causes of land-use and land-cover change: moving beyond the myths. *Global

586 Environmental Change*, **11**, 261-269.

587 Lemoine, N., Schaefer, H.C. & Bohning-Gaese, K. (2007) Species richness of migratory birds

588 is influenced by global climate change. *Global Ecology and Biogeography*, **16**, 55-64.

589 Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence

590 in the prediction of species distributions. *Ecography*, **28**, 385–393.

591 Luoto, M., Virkkala, R. & Heikkinen, R.K. (2007) The role of land cover in bioclimatic models

592 depends on spatial resolution. *Global Ecology and Biogeography*, **16**, 34-42.

593   Lurgi, M., Lopez, B.C., Montoya JM, (2012) Novel communities from climate change.

594   Philosophical Transactions of the Royal Society B: Biological Sciences, 367, 2913–

595   2922.

596   Mair, L., Thomas, C.D., Anderson, B.J., Fox, R., Botham, M. & Hill, J.K. (2012) Temporal

597   variation in responses of species to four decades of climate warming. *Global Change*

598   *Biology*, **18**, 2439–2447.

599   Martí, R. & Moral, J.C. (2003). Atlas de las aves reproductoras de España. Dirección General

600   de Conservación de la Naturaleza, Sociedad Española de Ornithología, Madrid

601   Martin, Y., Van Dyck, H., Dendoncker, N. & Titeux, N. (2013) Testing instead of assuming

602   the importance of land use change scenarios to model species distributions under

603   climate change. *Global Ecology and Biogeography*, **22**, 1204-1216.

604   Maxwell, S.L., Fuller, R.A., Brooks, T.M. & Watson, J.E. (2016) Biodiversity: The ravages of

605   guns, nets and bulldozers. *Nature*, 536(7615), 143-145.

606   Morelli, F. & Tryjanowski, P. (2015) No species is an island: testing the effects of biotic

607   interactions on models of avian niche occupation. Ecology and evolution, 5(3), 759-

608   768.

609   Moritz, C. & Agudo, R. (2013) The Future of Species Under Climate Change: Resilience or

610   Decline? *Science*, **341**, 504–508.

611   Mücher, C., Steinnocher, K,, Kressler, F. & Heunks, C. (2000) Land cover characterization

612   and change detection for environmental monitoring of pan-Europe. *International*

613   *Journal of Remote Sensing*, **21**, 1159–1181.

614   Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L., Hoskins,

615   A.J., Lysenko, I., Phillips, H.R. & Burton, V.J. (2016) Has land use pushed terrestrial

616   biodiversity beyond the planetary boundary? A global assessment. *Science*,

617   353(6296), pp.288-291.

618   Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking

619   landscape and biogeographical scale levels in research and conservation. *Biological*

620   *Conservation*, **117**, 285–297.

621   Osorio, F., Vallejos, R., Cuevas, F. (2012) SpatialPack: Package for analysis of spatial data. R

622   package version 0.2.

623   Pain, D.J. & Pienkowsky, M.W. (Eds) (1997) Farming and Birds in Europe: The Common

624   Agricultural Policy and Its Implications for Bird Conservation. Academic Press,

625   London.

626   Pearce-Higgins, J.W., Green, R.E. (2014) Birds and Climate Change: Impacts and

627   Conservation Responses. Cambridge University Press, Cambridge.

628   Pearson, R.G., Dawson, T.P., Berry, P.M. & Harrison, P.A. (2002) Species: A spatial evaluation

629   of climate impact on the envelope of species. *Ecological Modelling*, **154**, 289-300.

630   Pearson, R.G., Dawson, T.P. & Liu, C. (2004) Modelling species distribution in Britain: a

631   hierarchical integration of climate and land cover data. *Ecography*, **27**, 285–298.

632   Pielke, R.A., Marland, G., Betts, R.A., Chase, T.N., Eastman, J.L., Niles, J.O., Niyogi, D.d.S. &

633   Running, S.W. (2002) The influence of land-use change and landscape dynamics on

634   the climate system: relevance to climate-change policy beyond the radiative effect

635   of greenhouse gases. *Philosophical Transactions of the Royal Society of London.*

636   *Series A: Mathematical, Physical and Engineering Sciences*, **360**, 1705-1719.

637   Pompe, S., Hanspach, J., Badeck, F., Klotz, S., Thuiller, W., *et al*. (2008) Climate and land-use

638   change impacts on plant distributions in Germany. *Biology Letters*, **4**, 64–567.

639   Prasad, A.M., Iverson, L.R. & Liaw, A. (2006) Newer classification and regression tree

640   techniques: bagging and random forests for ecological prediction. *Ecosystems*, **9**,

641   181–199.

642 Princé, K., Lorrillière, R., Barbet-Massin, M. & Jiguet, F. (2013) Predicting the fate of French

643 bird communities under agriculture and climate change scenarios. *Environmental*

644 *Science & Policy*, **33**, 120-132.

645 Princé, K., Lorrillière, R., Barbet-Massin, M., Léger, F. & Jiguet, F. (2015) Forecasting the

646 Effects of Land Use Scenarios on Farmland Birds Reveal a Potential Mitigation of

647 Climate Change Impacts. *PloS one*, **10**(2), e0117850.

648 R Development Core Team (2013) R: A Language and Environment for Statistical

649 Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at:

650 http://www.R-project.org (accessed 1st January 2013).

651 Ribeiro, P.F., Santos, J.L., Bugalho, M.N., Santana, J., Reino, L., Beja, P., & Moreira, F. (2014)

652 Modelling farming system dynamics in High Nature Value Farmland under policy

653 change. *Agriculture, Ecosystems & Environment*, **183**, 138-144.

654 Ribeiro, P.F., Santos, J.L., Santana, J., Reino, L., Leitão, P.J., Beja, P., Moreira, F. (2016)

655 Landscape makers and landscape takers: links between farming systems and

656 landscape patterns along an intensification gradient. *Landscape Ecology*, **31**, 791-

657 803.

658 Ridgeway, G. (2013) A guide to the gbm package. The Comprehensive R Archive Network

659 Web Site, http://cran.r-project.org/web/packages/gbm/index.html; accessed

660 January 2013.

661 Reino, L., Beja, P., Osborne, P.E., Morgado, R., Fabião, A. & Rotenberry, J.T. (2009) Distance

662 to edges, edge contrast and landscape fragmentation: Interactions affecting

663 farmland birds around forest plantations. *Biological Conservation*, **142**, 824–838.

664 Reino, L. Beja, P. Araújo, M.B., Dray, S. & Segurado, P. (2013) Does local habitat

665 fragmentation affect large-scale distributions? The case of a specialist grassland bird.

666 *Diversity and Distributions*, **19**, 423-432.

667   Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root,

668   T.L., Estrella, N., Seguin, B., Tryjanowski, P. (2008) Attributing physical and biological

669   impacts to anthropogenic climate change. *Nature*, **453**(7193),

670   Rounsevell, M.D.A., Reginste, I., Araújo, M.B., Carter, T.R., Dendoncker, N., et al. (2006) A

671   coherent set of future land-use change scenarios for Europe. *Agriculture, Ecosystems*

672   *& Environment*, **114**, 57–68.

673   Sala, O.E., Chapin, F.S., Armesto, J.J. & et al. (2000) Biodiversity - Global biodiversity

674   scenarios for the year 2100. *Science*, **287**, 1770–1774.

675   Seoane, J., Viñuela, J., Díaz-Delgado, R. & Bustamante, J. (2003) The effects of land use and

676   climate on red kite distribution in the Iberian peninsula. *Biological Conservation*, **111**,

677   401-414.

678   Settele, J., Hammen, V., Hulme, P., Karlson, U., Klotz, S., Kotarac, M. & Kühn, I. (2005)

679   ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested

680   Methods. *Gaia-Ecological Perspectives for Science and Society*, **14**, 69-72.

681   Sohl, T.R. (2014) The Relative Impacts of Climate and Land-Use Change on Conterminous

682   United States Bird Species from 2001 to 2075. *PLoS ONE*, **9**, e112251.

683   Spangenberg, J.H. (2007) Integrated scenarios for assessing biodiversity risks. *Sustainable*

684   *Development*, **15**, 343–356.

685   Spangenberg, J.H., Bondeau, A., Carter, T.R., Fronzek, S., Jäger, J., Jylhä, K., Kühn, I., Omann,

686   I., Paul, A., Reginster, I., Rounsevell, M., Stocker, A., Sykes, M.T. & Settele J. (2012)

687   Scenarios for investigating risks to biodiversity. *Global Ecology and Biogeography*, **21**,

688   5–18.

689   Titeux, N., Henle, K., Mihoub, J.B., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H.

690   & Brotons, L. (2016) Biodiversity scenarios neglect future land‑use changes. *Global*

691   *Change Biology*, **22**, 2505-2515.

692   Titeux, N., Maes, D., Marmion, M., Luoto, M. & Heikkinen, R.K. (2009) Inclusion of soil data

693   improves the performance of bioclimatic envelope models for insect species

694   distributions in temperate Europe. *Journal of Biogeography*, **36**, 1459-1473.

695   Thuiller, W., Araújo, M.B. & Lavorel, S. (2004a) Do we need land-cover data to model

696   species distributions in Europe? *Journal of Biogeography*, **31**, 353-361.

697   Thuiller W., Brotons L., Araújo M.B., & Lavorel S. (2004b) Effects of restricting

698   environmental range of data to project current and future species distributions.

699   Ecography, 27, 165–172.

700   Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change

701   threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*

702   *of the United States of America*, **102**, 8245-8250.

703   Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B. & Araújo, M.B. (2011)

704   Consequences of climate change on the Tree of Life in Europe. *Nature*, **470**, 531-534.

705   Thuiller, W., Pironon, S., Psomas, A., Barbet-Massin, M., Jiguet, F., Lavergne, S., Pearmn,

706   P.B., Renaud, J., Zupan, L. & Zimmermann, N.E. (2014) The European functional tree

707   of bird life in the face of global change. *Nature communications*, *5*: 3118. doi:

708   10.1038/ncomms4118

709   Triviño, M., Thuiller, W., Cabeza, M., Hickler, T. & Araújo, M.B. (2011) The contribution of

710   vegetation and landscape configuration for predicting environmental change impacts

711   on Iberian birds. *PLoS ONE*, **6**, e29373.

712   Vallecillo, S., Brotons, L. & Thuiller, W. (2009) Dangers of predicting bird species

713   distributions in response to land-cover changes. *Ecological Applications*, **19**, 538–

714   549.

715   Veldkamp, A. & Lambin, E.F. (2001) Predicting land-use change. *Agriculture, Ecosystems &*

716   *Environment*, **85**, 1–6.

717

Table 1 – Discrimination power as measured by the mean cross-validation
AUC among the nine combinations of BRT settings, and respective
standard deviation, of distribution models developed for each farmland bird
species using either climate variables and both climate and landscape
variables. In each case we indicate the percent variation of mean AUC for
climate + landscape models in relation to climate only models.

Species	Climate	Climate + Landscape	% AUC variation
Falco naumanni	0.878 (0.0005)	0.888 (0.0005)	1.16
Circus pygargus	0.820 (0.0017)	0.859 (0.001)	4.68
Tetrax tetrax	0.852 (0.0014)	0.882 (0.0007)	3.42
Otis tarda	0.867 (0.0015)	0.889 (0.0011)	2.53
Coturnix coturnix	0.774 (0.0023)	0.804 (0.0013)	3.89
Pterocles alchata	0.933 (0.0011)	0.941 (0.0007)	0.89
Pterocles orientalis	0.859 (0.0008)	0.884 (0.0009)	2.93
Burhinus oedicnemus	0.852 (0.0011)	0.876 (0.0012)	2.82
Coracias garrulus	0.846 (0.0011)	0.856 (0.001)	1.21
Alauda arvensis	0.868 (0.0003)	0.871 (0.0004)	0.28
Anthus campestris	0.846 (0.0006)	0.851 (0.0008)	0.60
Lullula arborea	0.839 (0.0005)	0.851 (0.0004)	1.49
Melanocorypha calandra	0.885 (0.0006)	0.909 (0.0004)	2.69
Calandrella brachydactyla	0.824 (0.0005)	0.842 (0.0007)	2.11
Calandrella rufescens	0.947 (0.0009)	0.947 (0.0007)	0.06
Galerida cristata	0.908 (0.0006)	0.925 (0.0004)	1.86
Galerida theklae	0.869 (0.0012)	0.877 (0.0012)	0.90
Chersophilus duponti	0.919 (0.0009)	0.928 (0.0007)	0.87
Oenanthe hispanica	0.856 (0.0006)	0.861 (0.0009)	0.55
Carduelis cannabina	0.793 (0.0015)	0.801 (0.0017)	0.97
Emberiza calandra	0.892 (0.0007)	0.913 (0.0006)	2.29

734

Table 2 – Mean importance of variables in the climate+landscape BRT model (grey intensity reflects variable importance). Crop – presence/absence of cropland; Edge - edge density; MPA - mean cropland patch area; NUMP - number of cropland patches; Prec - average total annual precipitation; Tmax - average mean maximum temperature; Tmin - average minimum temperature of the coldest month; Tmin SD - minimum temperature standard deviation.

742

| Species	Crop	Edge	MPA	NUMP	Prec	Tmax	Tmin	Tmin SD
F. naumanni	0.01	6.07	25.99	2.11	9.42	36.63	6.95	12.83
C. pygargus	0.02	8.96	9.51	3.20	12.55	21.66	30.92	13.19
T. tetrax	0.00	7.29	7.64	2.25	13.03	17.18	38.40	14.22
O. tarda	0.00	7.28	14.45	2.29	10.25	43.23	8.57	13.92
C. coturnix	0.11	9.05	13.04	2.85	15.51	18.99	23.19	17.26
P. alchata	0.00	7.33	22.84	2.85	12.89	28.47	7.72	17.89
P. orientalis	0.00	8.23	21.08	2.76	10.16	36.25	8.39	13.13
B. oedicnemus	0.01	6.68	7.22	2.71	9.87	22.31	40.24	10.97
C. garrulus	0.00	6.58	9.76	2.06	12.82	20.12	30.43	18.24
A. arvensis	0.05	3.47	3.85	1.87	11.79	18.48	48.09	12.39
A. campestris	0.01	5.20	6.31	2.16	13.65	23.29	34.99	14.38
L. arborea	0.04	4.13	11.91	2.96	13.68	24.34	24.89	18.05
M. calandra	0.00	4.47	8.25	1.55	9.18	31.46	34.58	10.51
C. brachydactyla	0.01	6.61	7.58	2.34	8.28	17.38	47.51	10.30
C. rufescens	0.00	7.17	8.22	5.24	9.84	15.52	43.01	11.00
G. cristata	0.02	4.55	6.53	1.06	7.08	8.41	64.70	7.65
G. theklae	0.01	4.34	5.69	1.51	10.05	19.26	46.36	12.78
C. duponti	0.00	9.64	12.21	7.45	13.41	18.58	23.26	15.45
O. hispanica	0.01	3.73	5.64	3.23	8.68	18.94	46.28	13.49
C. cannabina	0.05	7.99	21.67	3.11	12.69	25.17	12.00	17.32
E. calandra	0.09	5.06	13.40	1.87	10.57	49.40	8.73	10.89

743
744
745
746

747
748
Table 3. Differences between the range shifts predicted by species distribution models based on climate alone and on climate + landscape for the three future ALARM storyline scenarios. Values indicate the additional percentage of change introduced when landscape variables are also considered in the models. Symbols denote the direction of the range change of the climate/landscape and whether the model based on climate/landscape predicts stronger or lower changes than model based on climate alone. ▽ - weaker retraction; ▼- stronger retraction; △ - weaker expansion; ▲ - stronger expansion.

758

| Species	Additional % change		
	BAMBU	**GRAS**	**SEDGE**
Falco naumanni	-21.2 △	-8.0 △	-33.0 △
Circus pygargus	-14.4 △	-17.7 △	-12.7 △
Tetrax tetrax	-20.6 △	-25.0 △	-21.0 △
Otis tarda	-132.6 △	-158.8 △	-138.7 △
Coturnix coturnix	-40.8 ▼	-44.8 ▼	-42.7 ▼
Pterocles alchata	-121.5 ▼	-151.0 △	-132.6 ▼
Pterocles orientalis	-58.1 ▼	-73.3 ▼	-74.5 ▼
Burhinus oedicnemus	-28.2 △	-29.7 △	-28.4 △
Coracias garrulus	14.6 ▲	23.6 ▲	7.5 ▲
Alauda arvensis	1.9 ▽	3.9 ▽	-0.9 ▼
Anthus campestris	-21.2 ▼	-33.7 ▼	-22.6 ▼
Lullula arborea	37.1 ▲	44.9 ▲	40.6 ▲
Melanocorypha calandra	-9.1 △	-3.9 △	-16.5 △
Calandrella brachydactyla	10.7 ▲	13.4 ▲	8.0 ▲
Calandrella rufescens	-45.4 △	-29.5 △	-58.0 △
Galerida cristata	7.3 ▽	1.3 ▽	12.9 ▽
Galerida theklae	20.3 ▽	21.2 ▽	22.5 ▽
Chersophilus duponti	-0.8 ▼	2.7 ▽	1.2 ▽
Oenanthe hispanica	10.1 ▽	9.7 ▽	19.4 ▽
Carduelis cannabina	2.4 ▲	4.2 ▽	-1.0 △
Emberiza calandra	-2.2 ▼	-3.3 ▼	-4.8 ▼

759

760

761

762

763

764
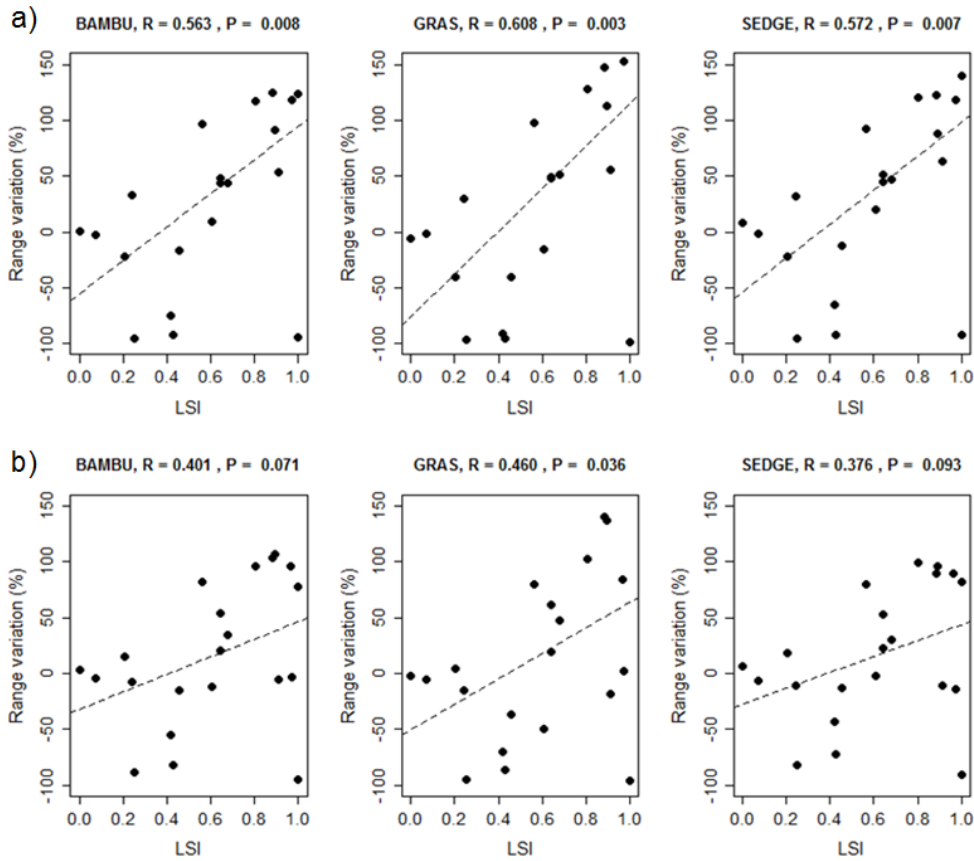
Fig. 1 – Relationship between the species Landscape Specialization Index
(LSI) in the presence cells, and the predicted species percent range variation
(future) in relation to the baseline modelled range, for the climate-only (a) and
the climate + landscape models (b). The Pearson correlation coefficient and
the respective P-level are shown.

770

771

772

773

774

775
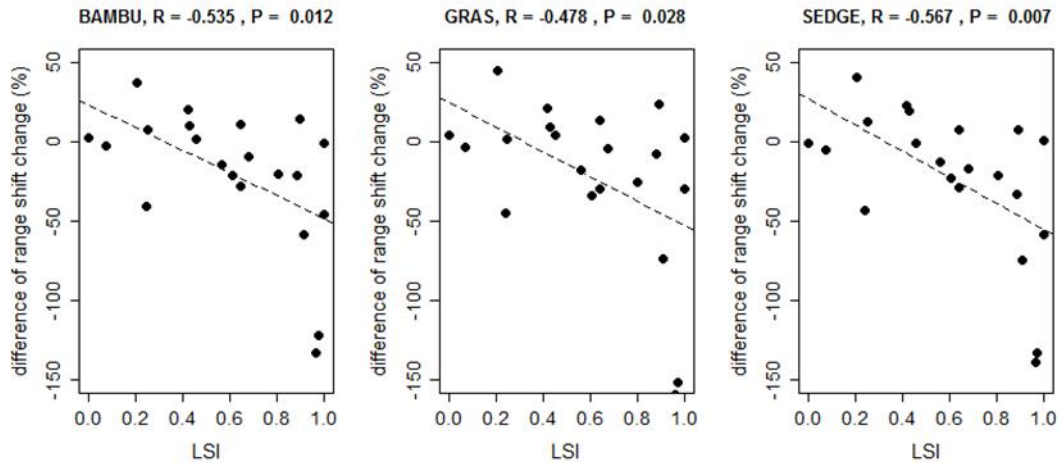
Fig. 2 – Relationship between the species Landscape Specialization Index (LSI) in the presence cells and the difference in the percent range shift change predicted by the climate + landscape models in relation to the climate-only models. The Pearson correlation coefficient and the respective *p*-level are shown.
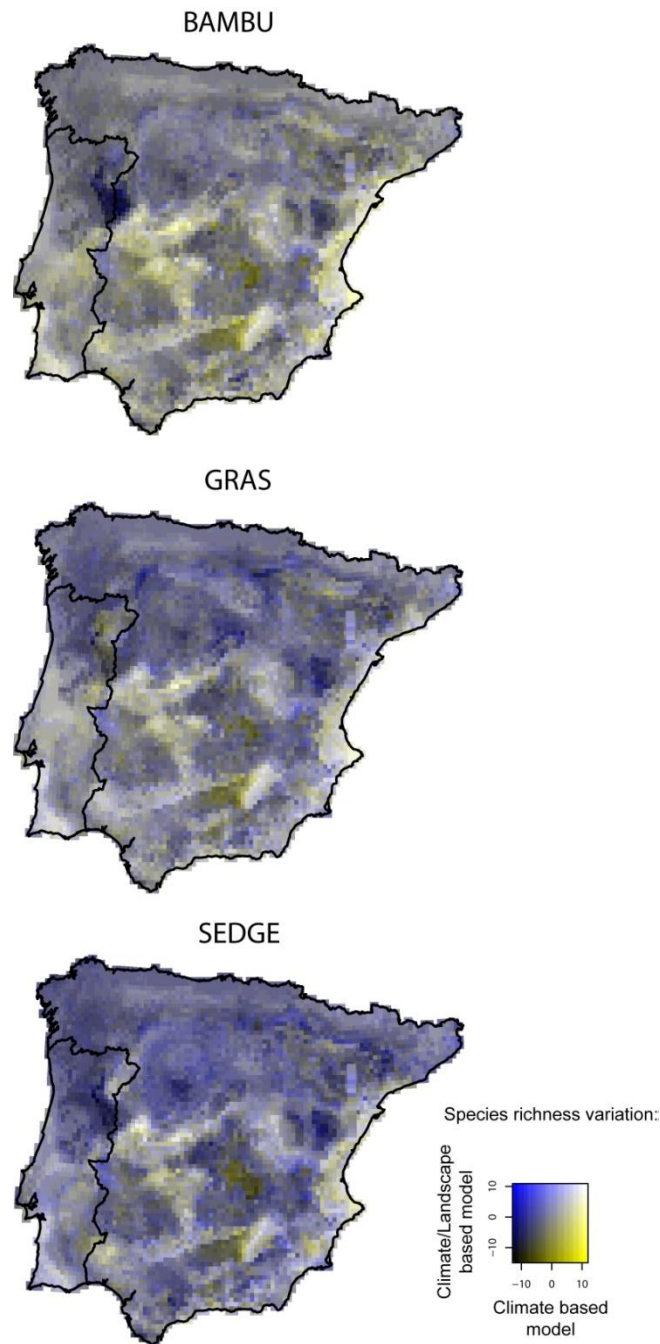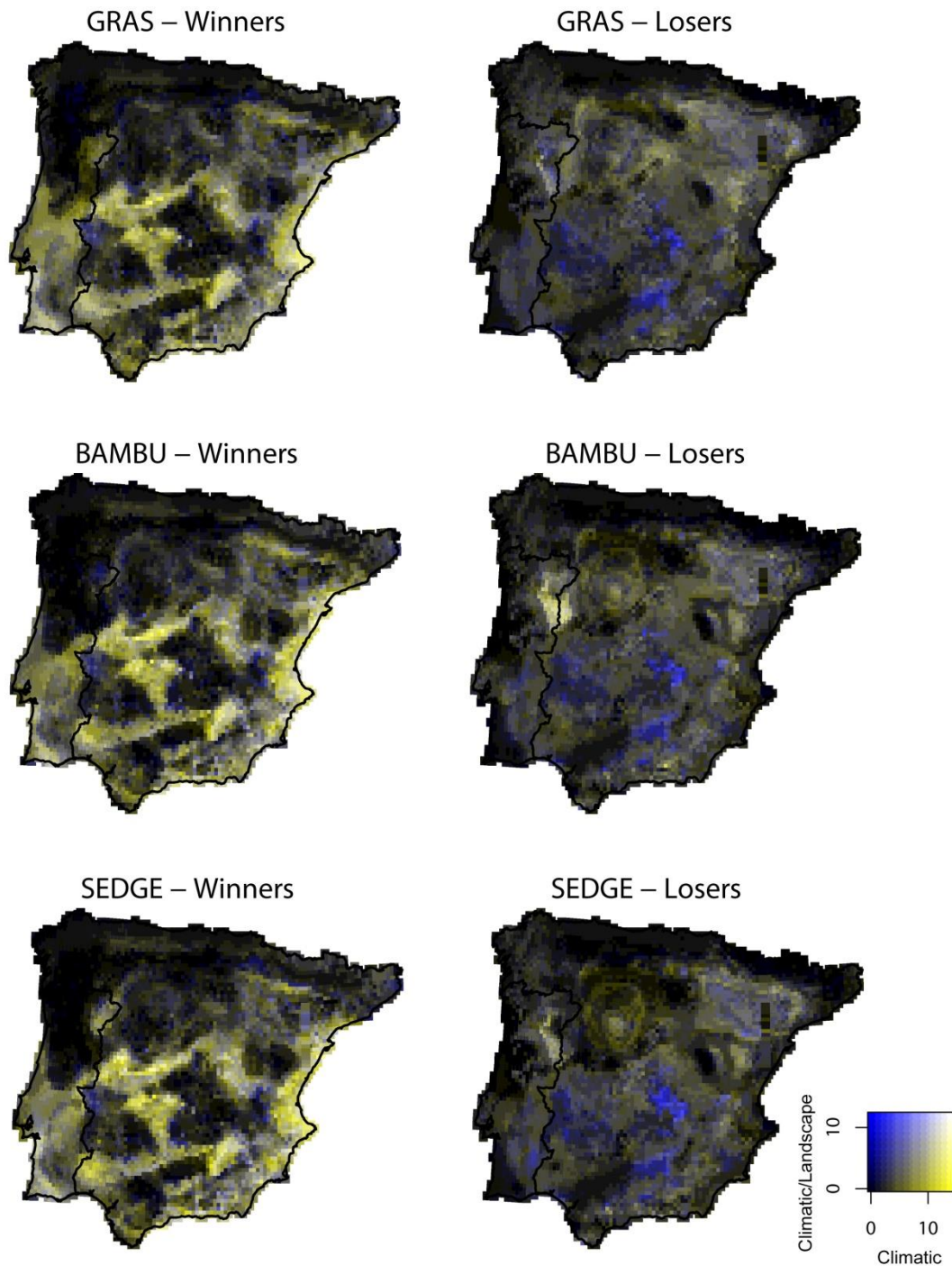
791

792

793

Fig. 3 – Bivariate map of species richness percent variation per 10-km grid squares for the three future climate change scenarios. Deviations from the grayscale gradient represent larger richness variations predicted either by climate only-based models (yellow) or by climate/landscape-based models (blue). Brighter tones represent regions with a more positive richness percent variation and darker tones represent regions with a more negative richness percent variation.

801

34

GRAS – Winners   GRAS – Losers

BAMBU – Winners   BAMBU – Losers

SEDGE – Winners   SEDGE – Losers

802

803

804   Fig. 4 – Bivariate map of the number of loser (left maps) and winner (right
805   maps) species per 10-km grid squares for the three future climate change
806   scenarios. Deviations from the grayscale gradient represent larger number of
807   losers or winners predicted either by climate only-based models (yellow) or
808   by climate/landscape-based models (blue). Brighter tones represent regions
809   with a larger number of winners or losers.

810