

# PROCEEDINGS B

## **Evolvability meets biogeography: evolutionary potential decreases at high and low environmental favourability**

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Complete List of Authors:	Martinez Padilla, Jesus; Research Unit of Biodiversity, Ecology Estrada, Alba; Universidad de Malaga Early, Regan; University of Exeter Garcia-Gonzalez, Francisco; Doñana Biological Station, Spanish Research Council CSIC,
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1 **Evolvability meets biogeography: evolutionary potential**  
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6 Martínez-Padilla, J.<sup>1\*,2,3</sup>, Estrada, A.<sup>1,4</sup>, Early, R.<sup>5</sup> and Garcia-Gonzalez, F.<sup>2,6</sup>

7

8 <sup>1</sup> Research Unit of Biodiversity, UMIB (CSIC, PA). University of Oviedo. C/Gonzalo  
9 Gutiérrez Quirós, s/n. 33600, Mieres, Asturias. Spain.

10 <sup>2</sup> Estación Biológica de Doñana. C/ Américo Vespucio, 26. 41092. Sevilla, Spain

11 <sup>3</sup> Centre d'Etudes Biologiques de Chizé (CEBC), UMR 7372 CNRS-Université de La  
12 Rochelle, Villiers-en-Bois, France

13 <sup>4</sup> Biogeography, Diversity and Conservation Research Team, Department of Animal  
14 Biology, University of Málaga, Spain

15 <sup>5</sup> Centre for Ecology and Conservation, Penryn Campus, University of Exeter, UK

16 <sup>6</sup> Centre for Evolutionary Biology, The University of Western Australia, Australia

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19 Keywords: Birds, environmental change, Europe, evolutionary ecology,  
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22 \* address for corresponding author:

23 Jesús Martínez-Padilla

24 Research Unit of Biodiversity, UMIB.

25 C/Gonzalo Gutiérrez Quirós, s/n. 33600, Mieres, Asturias. Spain.

26 Email: jmartineypadilla12@gmail.com

27

28 Short running title: Evolvability and environmental variation

29

30 **Abstract**

31 Understanding and forecasting the effects of environmental change on wild  
32 populations requires knowledge on a critical question: Do populations have the  
33 ability to evolve in response to that change? However, our knowledge on how  
34 evolution works in wild conditions under different environmental circumstances is  
35 extremely limited. We investigated how environmental variation influences the  
36 evolutionary potential of phenotypic traits. We used published data to collect or  
37 calculate 135 estimates of evolvability of morphological traits of European wild bird  
38 populations. We characterised the environmental favourability of each population  
39 throughout the species' breeding distribution. **Our results suggest that the**  
40 **evolutionary potential of morphological traits decreases as environmental**  
41 **favourability becomes high or low.** Strong environmental selection pressures and  
42 high intra-specific competition may reduce species' evolutionary potential in low  
43 and high favourability areas, respectively. This suggests that species may be least  
44 able to adapt to new climate conditions at **their** range margins and at the centre.  
45 Our results underscore the need to consider the evolutionary potential of  
46 populations when studying the drivers of species distributions, particularly when  
47 predicting the effects of environmental change. We **discuss** the utility of integrating  
48 evolutionary dynamics into a biogeographical perspective to understand how  
49 environmental variation shapes evolutionary patterns. This approach would also  
50 produce more reliable predictions about the effect of environmental change on  
51 population persistence and therefore on biodiversity.

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**56 Introduction**

57 Natural selection is the main mechanism and most powerful explanation for adaptive  
58 evolution and therefore it is essential for understanding biodiversity [1].  
59 Environmental drivers of selection are expected to shape the evolutionary dynamics  
60 of phenotypes of specific populations, as long as a fraction of the variance exhibited  
61 by these phenotypes is heritable (i.e., there are additive genetic effects determining  
62 phenotypic expression). However, the vast majority of research into species'  
63 biogeographic distributions (a key component of biodiversity) does not incorporate  
64 the role of the environment in determining species' evolutionary potential. This limits  
65 our understanding of the role of the environment in driving phenotypic change, and  
66 thus our fundamental comprehension of natural selection, but also the effects of  
67 environmental change. The degree to which populations can undergo evolutionary  
68 adaptation to new environments is one of the major uncertainties in predicting  
69 species' responses to present-day environmental changes and for making  
70 conservation decisions [2, 3]. The evolutionary potential of phenotypes in a  
71 population is an indicator of the population's capacity to respond to environmental  
72 change. However, current estimations of evolutionary potential in wild conditions are  
73 limited to a few, well-studied species, particularly of birds [4-10] and a few cases in  
74 mammals [11, 12], of which only single populations are studied. In addition, studies  
75 are typically geographically located where their environmental circumstances have  
76 not been measured [7], and if so, they do not allow comparisons among populations  
77 within species. Thus, our comprehension of the central question of how  
78 environmental conditions shape the evolution of phenotypes is rather limited.

79

80 A critical step towards deepening our understanding of the evolutionary adaptations  
81 of populations would be to consider multiple populations of multiple species covering  
82 a wide variety of environmental conditions. Taking this step requires long-term data

83 sets during which environmental conditions have changed and individuals have  
84 been monitored [12, 13], covering a sufficiently broad geographic region to contain  
85 multiple distinct populations from a variety of environments, and in which multiple  
86 species can be compared. These considerable data requirements have precluded  
87 such an analysis until now.

88

89 Linking environmental change and evolutionary dynamics is hampered by  
90 challenges in choosing metrics of both evolvability (i.e. evolutionary potential) and  
91 environmental favourability that would permit comparisons between species.  
92 Estimations of evolvability have been traditionally based on quantifying the narrow-  
93 sense heritability ( $h^2$ ) of specific phenotypes, understood as the proportion of the  
94 total phenotypic variance explained by additive genetic variance [14]. However,  $h^2$  is  
95 not an appropriate index of evolvability that can be used to compare evolvability  
96 among traits, populations or species for two reasons [15]. First, the magnitude of the  
97 variance scales with the magnitude of the trait measured. Second, additive genetic  
98 variance covaries with other sources of variance that are themselves used to  
99 calculate heritability (i.e., phenotypic variance) [15-17]. Instead, the coefficient of  
100 additive genetic variation ( $CV_A$ ) and its square ( $I_A$ ), are more suitable indexes of  
101 evolvability since they represent the additive genetic variation scaled by the mean of  
102 the phenotype [16]. Both measures are dimensionless indices that are suitable for  
103 comparisons among traits, species and populations [16].

104

105 An appropriate metric for environmental variation must integrate the multiple factors  
106 that simultaneously affect populations of a given species, but also be comparable  
107 among species [14]. The use of just one environmental variable does not summarise  
108 the ecological needs of a particular species and therefore the reliability of predicting  
109 or understanding environmental change on the adaptive potential of species is

110 extremely biased. For example, temperature is a key factor for breeding of pied  
111 flycatchers *Ficedula hypoleuca* in northern Europe, but not in southern European  
112 latitudes [18]. In fact, the relative importance of a particular environmental variable  
113 might change throughout the distribution of the species when other environmental  
114 variables are taken into account. Therefore, considering the environmental  
115 circumstances that populations experience throughout a species' geographic  
116 distribution requires the integration of multiple environmental predictors. Species  
117 distribution models (SDMs) are an excellent tool to integrate multiple environmental  
118 predictors producing a metric of environmental favourability along the species range  
119 [19]. Based on presence-absence information on the species, and environmental  
120 variables over a geographical area, models can be constructed to predict the  
121 probability of the species being present at a given site. However, the probability of  
122 occurrence is not comparable between species that differ in their prevalence within  
123 the study area [20]. The 'Favourability function' resolves this issue [19, 21] and  
124 indicates how the local probability of presence differs from that expected by chance,  
125 regardless of whether a species is rare or common. The favourability function is  
126 therefore widely used in analyses where direct comparison among species is  
127 necessary, for example, to forecast current or future environmental favourability  
128 under climate change [22, 23], to analyse inter-specific interactions [24] and to  
129 prioritise areas for conservation [25]. SDMs based on the favourability function are  
130 therefore an ideal tool to explore the association between environmental variation  
131 and evolvability ( $CV_A$  and  $I_A$ ) of phenotypes among populations and species.

132

133 Here, we explored the evolvability of morphological traits of 23 wild bird populations  
134 of 12 species found across Europe in relation to the environmental favourability  
135 experienced by each population. To do so, we carried out a comprehensive review  
136 of estimations of evolvability ( $CV_A$  and  $I_A$ ) of morphological phenotypes available in

137 the scientific literature. We focused our review on the estimations of  $CV_A$  obtained  
138 from multiple bird populations in the wild, since evolvability has been heavily studied  
139 in wild bird populations. We focused on Europe, where long-term monitoring data  
140 has led to much research on phenotypic change through time. For each population  
141 for which we obtained estimations of evolvability, we ran SDMs to obtain  
142 environmental favourability for each species and population. We tested the  
143 association between evolvability and environmental favourability at population level.  
144 As stressful conditions result in lower additive genetic variance of morphological  
145 traits in different taxa [26] including birds [27], a straightforward prediction would be  
146 a decreasing evolvability of phenotypes as environmental conditions worsen.  
147 However, our results point to a more complex relationship between evolvability and  
148 favourability.

149

## 150 **Methods**

151 In brief, our study was structured in three steps (see ESM—A, for a graphical  
152 description of the methodology): literature search; construction of SDMs using the  
153 favourability function to estimate the environmental favourability of a given area for a  
154 given species; statistical analyses of the variance of the evolutionary parameters  
155 and environmental favourability of all populations and species.

156

### 157 *Bibliographical search for estimates of evolutionary parameters*

158 We performed a bibliographical search from different sources. First, we compiled all  
159 information from published reviews that provided evolvability indices  $I_A$  or  $CV_A$  [16,  
160 28, 29]. Note that a previous review [29] also incorporated compilations of different  
161 evolutionary parameters provided by different authors [28]. Second, we widened this  
162 data set by a search in the Web of Science with the terms “*heritab*” or “*additive*

163 *genetic variation*". When one of the two indices were not provided, we calculated  $I_A$   
 164 or  $CV_A$  as follows [17]:

165

$$CV_A = \sqrt{I_A} \qquad I_A = CV_A^2$$

166

167 Original values of  $CV_A$  or  $I_A$  obtained from transformed variables were all excluded  
 168 from the analyses as transformation renders these statistics meaningless for  
 169 comparative purposes [17]. Some of the studies we inspected did not calculate  $CV_A$   
 170 or  $I_A$  but, when possible, we calculated them as follows [16]:

171

$$CV_A = \frac{\sqrt{V_A}}{\bar{x}} \qquad I_A = \frac{V_A}{\bar{x}^2}$$

172

173

174 In these cases,  $V_A$  represents additive genetic variation and  $\bar{x}$  represents the mean  
 175 of the trait. If  $V_A$  was not provided in the study, we calculated it by multiplying  $h^2$  by  
 176 total phenotypic variance ( $V_P$ ), since  $h^2 = V_A/V_P$ . Previous studies have described a  
 177 series of miscalculations when obtaining evolvability ( $CV_A$  or  $I_A$ ) in the literature [17].  
 178 Any miscalculations were corrected and if so the correct statistics were included in  
 179 the analyses. Unfortunately, standard errors for  $CV_A$  or  $I_A$  were provided only in one  
 180 case in our final data set, making not possible to consider uncertainty around  $CV_A$  or  
 181  $I_A$  values in our models.

182

183 The evolutionary parameters collected were calculated using a variety of methods,  
 184 including a large combination of parent-offspring regressions and, recently, more  
 185 complex quantitative genetic models. This heterogeneity might cause problems  
 186 when comparing evolutionary parameters between studies [29]. We accounted for



187 this effect by considering the method used to derive the calculation of the genetic  
188 parameters as a random factor in our analyses (see below –*Linking favourability*  
189 *and evolutionary potential*).

190

191 Among all studies from which  $CV_A$  or  $I_A$  were available, we selected those carried  
192 out on birds and in wild conditions. We classified phenotypic traits into five  
193 categories (morphological, physiological, life-history, sexual trait or maternal effect),  
194 but we only used morphological traits since this is the only category that provides  
195 enough evolutionary parameters for different populations and species. This category  
196 includes evolutionary parameters for body mass and body size (see ESM–*B*). Low  
197 sample size of the estimations at population level of morphological (body mass and  
198 size) traits prevented us from running species- or trait-specific models. To increase  
199 sample size, particularly for populations located in areas of low favourability, we also  
200 included unpublished  $CV_A$  and  $I_A$  estimations of morphological traits of a population  
201 of pied flycatchers in southern Europe, where environmental favourability for this  
202 species is low, using an animal model approach (see ESM–*C*). However, the  
203 exclusion of this information did not significantly change the outcome of the models  
204 (see ESM–*C*). Finally, values over 5 times the standard deviation of  $CV_A$  ( $n=1$ ) and  
205  $I_A$  ( $n = 2$ ) were considered outliers and thus excluded in our statistical models,  
206 ending up with final sample size covering 20 populations of 12 species.

207

### 208 *Species Distribution Models*

209 We used the European region covered by the Atlas of European Breeding Birds,  
210 which gives the 50x50km<sup>2</sup> UTM cells in which breeding populations of each species  
211 are found. We modelled environmental favourability for the 12 species for which we  
212 obtained  $CV_A$  or  $I_A$  of morphological traits (see ESM–*D* for further details).

213

214 We used three sets of explanatory variables to construct SDMs that model the  
215 presence/absence of breeding bird populations. 1) Geographic data, which include  
216 the longitude and latitude of the centroids of the cells in which populations were  
217 found. Geographic data were included as explanatory variables because in addition  
218 to environmental conditions, species distributions are affected by historical events  
219 such as glaciations or source-sink population dynamics [30]. Geographic variables  
220 indicate the spatial structuring of populations and allow the role of historical events  
221 to be inferred. 2) We considered altitude as a topographical predictor. 3)  
222 Temperature- and rainfall-based variables that are considered to be ‘bioclimatic  
223 predictors’ and that are likely to have an effect on the distribution of breeding birds  
224 (ESM—*E*). Raw climatic and topographical variables were obtained from WorldClim  
225 (<http://www.worldclim.org/current>) at a spatial resolution of  $1 \times 1 \text{ km}^2$ . Climatic  
226 variables were averaged values for the period 1960-1990. As breeding bird  
227 distribution was given at a spatial resolution of  $50 \times 50 \text{ km}^2$ , we obtained the mean  
228 value of each environmental variable in each  $50 \times 50 \text{ km}^2$  UTM cell. We excluded  
229 those climatic variables that had a Variance Inflation Factor (VIF) value higher than  
230 10 [31] sequentially using a stepwise procedure (ESM—*E*). We used the function  
231 “*multicol*” from the R package “*fuzzySim*” [32] to calculate VIF values. We  
232 considered linear and non-linear responses to topographical and climatic  
233 explanatory variables, including their quadratic terms. Regarding geographic  
234 variables, we included latitude and longitude, their quadratic and cubic terms, and  
235 the interactions among them [30].

236

237 SDMs for each species were constructed using explanatory variables and species  
238 distribution data at a spatial resolution of  $50 \times 50 \text{ km}^2$  with the function “*multGLM*”  
239 from “*fuzzySim*” R package [32]. We performed a forward-backward stepwise

240 logistic regression based on AIC. If models included the quadratic term of a  
241 topographical or climatic variable but not the linear term of the same variable, we  
242 removed the quadratic term.

243

244 The discrimination performance of SDMs were evaluated through the Area Under  
245 the Curve (AUC) of the Receiver Operating Characteristic; and their classification  
246 capacity using the Correct Classification Rate (CCR), the specificity, sensitivity and  
247 the True Skill Statistics (TSS) using the “*modeEVA*” package [33] in R (see ESM –  
248 *F*). For evaluation we repeated SDMs 15 times (5 times each partition), partitioning  
249 each species’ presence/absence data into training and testing datasets in three  
250 different proportions [34, see ESM – *G*]. The final models that we used for each  
251 species were those calibrated using 100% of the species distribution data as it has  
252 been shown that random removal of presence records adds a non-trivial amount of  
253 uncertainty in projections [35].

254

255 The output of the logistic regression was converted to favourability using the  
256 favourability function [19, See ESM-H]. A crucial aspect of the favourability function  
257 is that it does not give a probability output (*P-value*) but a measure of the degree to  
258 which local conditions lead to a local probability higher or lower (*F-value*) than that  
259 expected at random [19]. Therefore, whereas *P*-values for different species are not  
260 comparable because of the different prevalence of each species, *F*-values are  
261 directly equivalent. The model outputs are then levelled to the same threshold of  
262 favourability and can be compared directly, even if the model is constructed with  
263 different predictor variables. The output value of  $F=0.5$  will always correspond to the  
264 same neutral environmental threshold for all species, whatever the proportion of  
265 presences in the sample. The outcome of the favourability function provides an  
266 index of environmental favourability for a species in a given site within the

267 geographical area considered. In addition, the favourability outcome depends solely  
268 on the response to the predictors considered [21] and not on the ratio of presence  
269 and absences of the species.

270

271 The favourabilities at a spatial resolution of  $50 \times 50 \text{ km}^2$  were downscaled to  $1 \times 1 \text{ km}^2$   
272 resolution (the resolution at which all predictor variables were originally obtained) as  
273 previously described [22]. Once this was computed, we obtained the favourability  
274 value at  $1 \times 1 \text{ km}^2$  for each population and species from which we obtained a  $CV_A$  or  
275  $I_A$ .

276

### 277 *Linking favourability and evolutionary potential*

278 We assessed whether evolvability of phenotypes in different populations can be  
279 explained by the favourability values of the environments encountered by those  
280 populations. We ran Linear Mixed Models (LMM) using “*lme4*” [36] and “*lmer.test*”  
281 [37] packages in R. We run our models using  $CV_A$  and  $I_A$  as dependent variables. In  
282 the supplementary material (ESM – I), we show the outcome of our analyses using  
283 the log-transformed  $CV_A$  and  $I_A$ ; results are qualitatively equivalent to the results  
284 shown below. We tested linear and quadratic effects of favourability values. We  
285 included two more fixed factors in these models. First, we included the method used  
286 (animal model, parent-offspring regression or full-sib analyses) to obtain the  
287 evolutionary parameter. Second, we included the type of morphological trait  
288 considered, categorised as body mass or body size (see ESM–B and D). Species  
289 and location were included as random factors to avoid pseudoreplication (see ESM–  
290 B and D). We repeated the models at a spatial resolution of  $50 \times 50 \text{ km}^2$  and  $1 \times 1 \text{ km}^2$   
291 to explore potential scale-dependent patterns.

292 We further explored the change of the slope between environmental favourability  
293 and both  $CV_A$  and  $I_A$  at three different levels of environmental favourability. We

294 categorised the favourability values at three levels (“catfav” – Low, Intermediate and  
295 High favourability, corresponding to 0-0.2, 0.2-0.8, 0.8-1 respectively). These  
296 categories are split unequally due to the logistic nature of favourability [38]. Then,  
297 we used  $CV_A$  and  $I_A$  as dependent variables, and tested the interaction between  
298 environmental favourability and the three favourability categories  
299 (Favourability\*catfav). We considered the same random variables and factors  
300 described above. Factors were sequentially excluded from the analyses if  
301 associated  $p$  values were higher than 0.05. Note that these analyses exploring the  
302 association between  $CV_A$  (or  $I_A$ ) and environmental favourability in three different  
303 categories were only performed at  $1 \times 1 \text{Km}^2$  scale, since low sample sizes at the  
304  $50 \times 50 \text{Km}^2$  scale preclude such analyses.

305 In our models, we did not control for potential phylogenetic biases for three reasons.  
306 First, our study deals with the evolutionary potential of morphological traits  
307 measured at *population level*. Thus, in order to properly account for any potential  
308 phylogenetic influence, a phylogenetic tree at population level for all species  
309 considered in this study at European scale would be needed. This information is  
310 rather limited and when available in birds, a very low genetic differentiation among  
311 populations has been found [39]. Second, we looked at whether the phylogeny of  
312 the species considered in this study could influence our results. To do so, we  
313 explored whether the residuals of our model had a phylogenetic signal. We  
314 quantified the influence of phylogeny on the residuals of our models for both  $CV_A$   
315 and  $I_A$  by means of  $K$  statistics [40]. We found non-existent phylogenetic signal for  
316 neither  $CV_A$  nor  $I_A$  residuals (all  $K < 0.688$ ; all  $P > 0.409$ ), suggesting that phylogeny at  
317 species levels is highly unlikely to explain variance in our models (see ESM–J).  
318 Finally, morphological traits typically have a strong phylogenetic signal but our

319 estimates of  $CV_A$  and  $I_A$  are corrected by the mean of the trait, partially correcting for  
320 this source of error.

321

## 322 **Results**

323 Results of favourability models for each species at a European scale and their  
324 evaluation parameters are detailed in the Electronic Supplementary Material (ESM–  
325 *F* and *G*). According to the thresholds of AUC proposed by Hosmer and Lemeshow  
326 [20], our favourability models had an outstanding (72.9% of the models had  
327  $AUC \geq 0.9$ ) or excellent discrimination capacity ( $0.9 > AUC > 0.8$ ; see Methods section  
328 for full description of the models).

329

330 We obtained 136 indices of evolutionary potential for 12 species and 20 populations.  
331 We found a negative quadratic relationship between favourability and  $CV_A$  (Table 1,  
332 **Figure 1**), regardless of whether favourability was calculated at a spatial resolution  
333 of  $50 \times 50 \text{ km}^2$  or  $1 \times 1 \text{ km}^2$ . Similarly, we found a negative quadratic relationship  
334 between favourability and  $I_A$  at both scales (Table 1, **Figure 1**). When analysing only  
335 the linear relationship between evolvability (either  $CV_A$  or  $I_A$ ) and favourability at any  
336 of the two spatial resolutions considered, we did not find any statistical association  
337 (all  $p > 0.606$ ).

338 Considering  $CV_A$  as dependent variable, we found a significant interaction between  
339 environmental favourability and the categorical split of environmental favourability  
340 (interaction Favourability\*catfav;  $p = 0.005$  – **Figure 2**). We ran specific models for  
341 each category of favourability (Low, Intermediate and High). In intermediate  
342 favourability areas, there was a positive relationship between favourability and  $CV_A$   
343 (estimate:  $0.030 \pm 0.011$ ,  $p = 0.0126$ ). In high favourability areas, there was a  
344 negative relationship between favourability and  $CV_A$  (estimate =  $-0.529 \pm 0.238$ ,  $p =$

345 0.050). The association between favourability and  $CV_A$  for the low favourability  
346 category could not be computed because of small sample size.

347 Regarding  $I_A$ , we also found a significant interaction between environmental  
348 favourability and the categorical split (interaction Favourability\*catfav;  $p = 0.016$  –  
349 **Figure 2**). In intermediate favourability areas, there was a statistically significant and  
350 positive relationship between favourability and  $I_A$  (estimate =  $0.0016 \pm 0.0005$ ,  $p =$   
351  $0.004$ ). In high favourability areas, there was a statistically marginally significant and  
352 negative relationship between favourability and  $I_A$  (estimate =  $-0.529 \pm 0.238$ ,  $p =$   
353  $0.077$ ). The association between favourability and  $I_A$  for the low favourability  
354 category cannot be computed because of small sample size.

355

## 356 Discussion

357 Current scientific knowledge of the evolutionary dynamics of phenotypes in wild  
358 conditions is highly biased towards studies performed in single species and  
359 populations framed within specific environmental circumstances. This study is the  
360 first to integrate the analysis of evolutionary potential with biogeographical  
361 knowledge, and does so across many species and between populations  
362 experiencing a broad range of environmental conditions. We find that environmental  
363 favourability is associated with the evolvability of morphological traits within  
364 European populations of wild birds. Specifically, we found a negative quadratic  
365 association between environmental favourability and evolvability. The quadratic  
366 association indicated by the model may not necessarily suggests that evolvability  
367 peaks at an exact intermediate favourability value of 0.5, rather a significant  
368 negative quadratic term indicates a decreasing slope with increasing predictor  
369 values. Furthermore, the quadratic relationship suggests that the slope of the  
370 relationship between environmental favourability and evolvability changes along the  
371 gradient of environmental favourability. Contrary to our expectations, our results

372 highlight that evolvability does not increase in areas of high environmental  
373 favourability. Importantly, using a two-regression approach on the data, we  
374 confirmed that evolutionary potential decreases when environmental favourability  
375 approaches the extremes (i.e. low or high favourability), regardless of the precise  
376 value of favourability where evolvability peaks.

377

378 We hypothesised that stronger selection in areas of low favourability should erode  
379 additive genetic variance, and consequently would negatively impact on the  
380 evolvability of the traits/populations. It is, however, intriguing that evolutionary  
381 potential decreases under the best environmental conditions. Previous studies  
382 performed in single species have described a similar quadratic pattern of evolvability  
383 ( $I_A$ ) of multiple traits along a latitudinal gradient in the plants *Arabidopsis lyrata* [41]  
384 and *Triticum dicoccoides* [42], where  $I_A$  was lowest in the opposite edges of the  
385 species distribution. However, our study goes beyond latitudinal variation and  
386 quantifies environmental favourability for each population and species considered.  
387 Several non-mutually exclusive mechanisms may explain this pattern. First, we  
388 cannot rule out the possibility that the mean of the trait of populations in good  
389 environmental conditions is higher than in poor conditions, an idea previously  
390 supported in wild birds [43]. Assuming that mean of the trait can be high in better  
391 environmental conditions, higher trait means would reduce  $CV_A$  and  $I_A$ , as these  
392 statistics are standardised by the trait mean.

393

394 Alternatively, several factors related to density-dependent effects might influence the  
395 evolutionary dynamics of morphological traits. Most of the estimations of  
396 evolutionary traits carried out in highly favourable environmental conditions came  
397 from populations breeding in nest-boxes. It is common that such populations reach  
398 the carrying capacity of the habitat [44] and higher bird population density occurs in



399 areas of greater environmental favourability [45, 46]. Population sizes near to  
400 carrying capacity might lead to negative density-dependent effects and selection  
401 [47]. This hypothesis has been widely discussed since Haldane [48], who suggested  
402 local adaptation can be associated with density-dependent patterns. Interestingly,  
403 such reduced evolvability in populations at high density can be as small as in low  
404 density populations [49]. Morphological traits in populations located in highly  
405 favourable areas may be under stronger selection due to negative density-  
406 dependent effects [48, 50], or may be under stabilizing selection, which would  
407 reduce additive genetic variance [51]. Also at high densities, high predation rates  
408 [50] and parasitism [52] could explain the reduction in additive genetic variance [53].  
409 In addition, gene flow may also be a mechanism for negative density-dependent  
410 effects. In birds, high population densities reduce the rate of emigration in 67% of  
411 studies [54], along with rates of immigration [55] and recruitment [56]. Thus,  
412 reduction of immigration and emigration within high-density populations, likely  
413 associated with higher environmental favourability, is expected to increase  
414 inbreeding in the population due to reduced gene flow [57]. Therefore, we suggest  
415 that the agents of selection that dampen additive genetic variance may differ  
416 between areas of high and low environmental favourability, changing from  
417 population density to habitat-related factors respectively. Regardless of the potential  
418 underlying mechanism, our results suggest a link between species geographic  
419 distributions and **evolutionary dynamics**.

420

421 Estimations of evolvability of traits could be affected by the inclusion of non-additive  
422 sources of variance like between-year variation, or permanent or shared  
423 environmental factors. If so, estimations of additive genetic variance, and thus the  
424 evolutionary potential of the phenotype, will be lowered compared to situations  
425 where such sources of variation are not taken into account [58]. For example,

426 maternal effects have been suggested to be more prevalent under unfavourable  
427 environmental conditions [5], which decreases the estimation of additive genetic  
428 variance [59], but does not alter its statistical significance. However, given the  
429 heterogeneous ways that evolutionary parameters compiled here have been  
430 calculated, we consider that it is highly unlikely that there is a systematic bias on the  
431 calculations of  $V_A$  or any other non-additive source of variation. Taking uncertainty of  
432  $CV_A$  or  $I_A$  estimates into account would help assessing the robustness of the  
433 patterns we have uncovered here. Unfortunately, as has been previously highlighted  
434 [17], estimations of additive genetic variance, including mean-standardized  
435 measures of additive genetic variation, are typically provided without any  
436 approximation of their sampling variance.

437

438 The association between ecological and evolutionary parameters found here may  
439 have implications for population demography [50], not just within the context of  
440 density dependence of populations [60]. For example, small environmental  
441 perturbations may have consequences on the evolutionary dynamics of life-history,  
442 morphological and fitness-related traits [60, 61], influencing population growth [60-  
443 62]. Evolutionary parameters are clearly crucial for predicting the effect of  
444 environmental change on population demography [63, 64], since population growth  
445 ultimately determines species geographic distributions. SDMs are constructed  
446 based on presence/absence or presence data in given areas, but what drives the  
447 distribution of the species is the persistence of their populations, i.e. their population  
448 growth rate. Thus, integrating population dynamics and quantitative genetics [64, 65]  
449 into biogeographical research [2] will improve our understanding of the influence of  
450 environmental change on population persistence.

451

452 Our results can have profound implications for predicting or understanding the effect  
453 of environmental change on population persistence at biogeographical scales.  
454 Among all potential sources of environmental variance, climate change is a crucial  
455 one, and is a global threat to biodiversity. Climatic variables tested were accepted  
456 for in all SDMs built for our study species (See ESM–F), suggesting that climate  
457 (both temperature- and rainfall-based variables) has a strong effect on  
458 environmental favourability in our models. Based on our results, if climate becomes  
459 less suitable for populations in currently highly favourable areas, local adaptation is  
460 less likely than in some other areas (ESM – K). On the other hand,  
461 populations located in areas **at the end** of current intermediate favourability might be  
462 particularly able to evolve in response to climate change if conditions become less  
463 favourable, because these populations have a particularly high evolutionary  
464 potential (**Figures 1 and 2**; ESM – K). Evolution could prolong the period in which  
465 these populations are able to survive *in situ* as conditions worsen, or allow these  
466 populations to evade local extinction altogether. Our results also suggest that  
467 evolutionary ‘rescue’ from climate change is less likely at species’ geographic range  
468 margins, where conditions are typically less favourable than at the centre of  
469 distributions [66]. This could result in a general trend of population extinction close  
470 to species’ warm range margins. On **the other** hand, while populations located in  
471 areas of intermediate favourability might not be threatened by climate change if  
472 favourability improves, these populations’ high evolvability might mean that they  
473 undergo evolutionary adaptation to the new climate conditions regardless. This  
474 could have implications for the community the species occupy. Species ecological  
475 traits, particularly the morphological traits measured here, play a strong role in  
476 determining the outcome of biotic interactions, so evolution of these traits could  
477 impact the composition and ecosystem function of an ecological community [67, 68].

478 Thus, understanding the likelihood that evolution will occur could improve our  
479 understanding of community-level responses to climate change [67, 69].

480

481 The potential link between population persistence and evolution represents a  
482 challenge for biogeographical and macroecological studies that aim to predict the  
483 effect of environmental change [70]. By using biogeographical tools together with  
484 evolutionary parameters, we were able to describe how environmental conditions  
485 may shape the evolutionary potential of morphological traits of wild birds in Europe.  
486 Despite observations of evolutionary adaptation in response to environmental  
487 change in a diverse range of species and locations [3], difficulties in drawing general  
488 conclusions has made evolutionary potential an understudied and largely  
489 unquantified problem within biogeography [69]. Our study highlights the need to  
490 integrate evolutionary dynamics into biogeographical research, to understand how  
491 environmental variation influences evolutionary dynamics, and to produce more  
492 reliable predictions about the effect of environmental change on population  
493 persistence and therefore on biodiversity. An important general message arising  
494 from our results is that biogeographical forecasts, and particularly those based on  
495 species distribution models, would be improved by incorporating information on  
496 population-level demographic and evolutionary responses to the environment, to  
497 predict the effect of environmental change on population persistence. We require  
498 more information on the evolutionary potential of life-history and fitness-related traits  
499 of populations throughout the range of environmental conditions a species occupies,  
500 to get further insights into the mechanisms that drive evolutionary dynamics within a  
501 geographical perspective.

502

503 **Data accessibility.** Data are available from Dryad Digital Repository [DOI:  
504 [10.5061/dryad.dh98c](https://doi.org/10.5061/dryad.dh98c)].

505 **Author's contributions.** JM-P, AE and FG-G, conceived the idea and decided  
 506 methodology, RE provided information of species distribution, JM-P and AE  
 507 analyzed and modelled the data and JM-P wrote the manuscript in collaboration with  
 508 all coauthors.

509 **Competing interests.** Authors declare no competing interests exist.

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519

520

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- 726

727

728 **Table 1.** Linear Mixed Models exploring the association between environmental  
 729 favourability and evolvability at 1km<sup>2</sup> and 50x50km<sup>2</sup> resolution across Europe. Note  
 730 that we included the method (“Method”) by which  $CV_A$  and  $I_A$  were obtained and the  
 731 type of phenotypic trait considered (“Trait”) as fixed factors (see Methods for further  
 732 details). Details on the sample sizes for each measurement by population and  
 733 species are given in ESM–B and D. Bold values highlight variables with  $p < 0.05$ .  
 734 Models considering **log-transformed**  $CV_A$  and  $I_A$  are given in ESM – I.  
 735

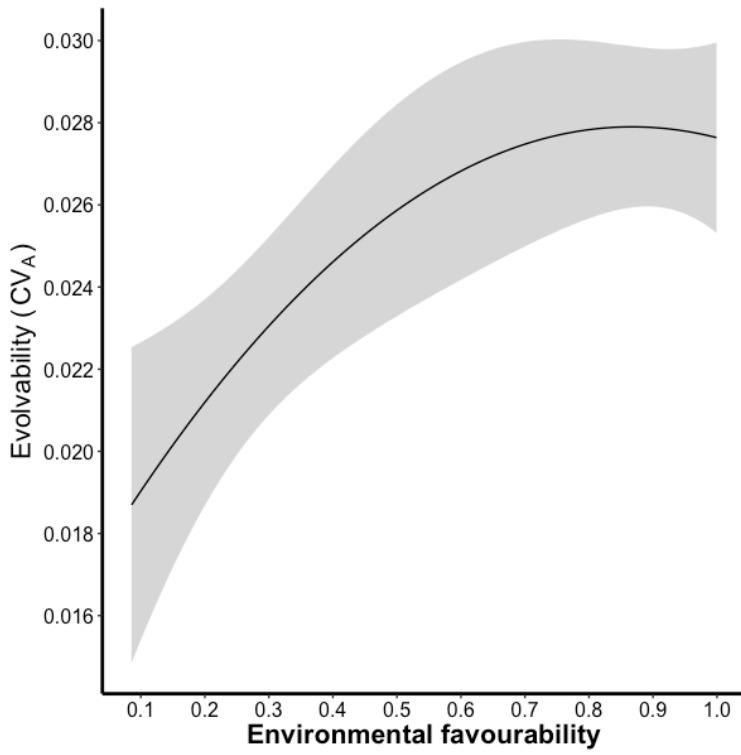
Resolution	50x50Km <sup>2</sup>			1x1Km <sup>2</sup>		
$CV_A$	Estimate (±SE)	t value	p	Estimate (±SE)	t value	p
Intercept	0.0082 (±0.0147)	0.558	0.583	0.0077 (±0.0150)	0.513	0.613
Favourability	0.1107 (±0.0539)	2.054	<b>0.050</b>	0.1109 (±0.0531)	2.089	<b>0.048</b>
Favourability <sup>2</sup>	-0.0840 (±0.0406)	-2.071	<b>0.046</b>	-0.0842 (±0.0395)	-2.133	<b>0.042</b>
Trait: size	-0.0061 (±0.0035)	-1.746	0.083	-0.0060 (±0.0035)	-1.703	0.090
Method: full-sib	-0.0016 (±0.0035)	0.235	0.815	0.0017 (±0.0069)	0.255	0.799
Method: parent-offspring	0.0018 (±0.0031)	0.599	0.549	0.0021 (±0.0031)	0.674	0.501
$I_A$	Estimate (±SE)	t value	p	Estimate (±SE)	t value	p
Intercept	0.0004 (±0.0007)	-0.586	0.563	0.0003 (±0.0007)	-0.526	0.604
Favourability	0.0067 (±0.0025)	2.661	<b>0.012</b>	0.0064 (±0.0025)	2.551	<b>0.016</b>
Favourability <sup>2</sup>	-0.0052 (±0.0018)	-2.761	<b>0.008</b>	-0.0049 (±0.0018)	-2.658	<b>0.012</b>
Trait: size	-0.0003 (±0.0001)	-2.427	<b>0.016</b>	-0.0003 (±0.0001)	-2.408	<b>0.017</b>
Method: full-sib	-0.000008 (±0.00013)	-0.001	0.999	0.000006 (±0.000197)	0.022	0.982
Method: parent-offspring	0.0001 (±0.0001)	0.771	0.442	0.0001 (±0.0001)	0.801	0.424

736

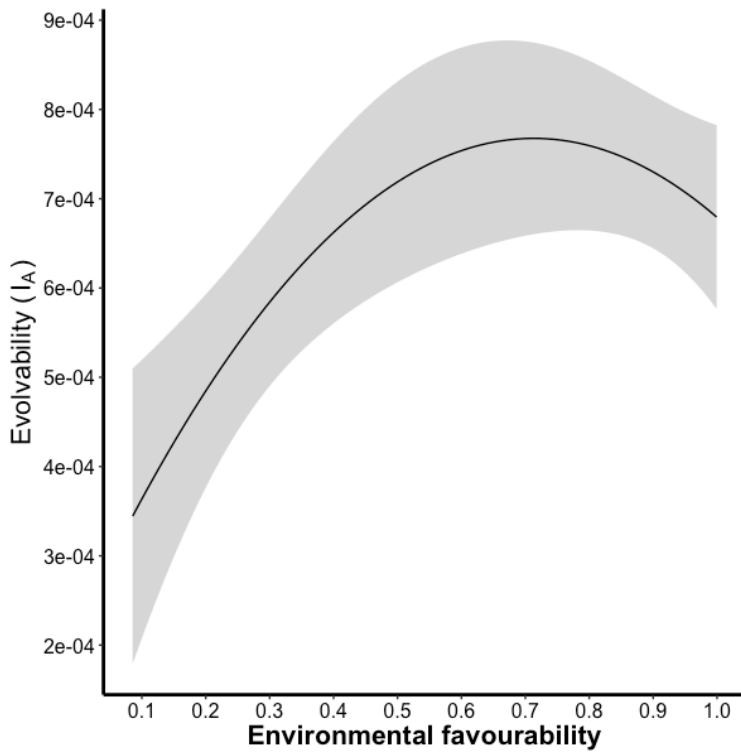
737

738

739 **Figure 1.** Estimated change in evolvability ( $CV_A$  and  $I_A$ , upper and lower panel  
740 respectively) of morphological traits in wild birds at  $1 \times 1 \text{ km}^2$  scale with 95%  
741 confidence interval against a gradient of environmental favourability from Linear  
742 Mixed Models (see Methods for further details). Y-axis represent the predicted  
743 values obtained for **untransformed**  $CV_A$  and  $I_A$  from the models described in the  
744 main text. The function that defines the curve represented for the association  
745 between predicted values of  $CV_A$  and environmental favourability ("Fav") is  $CV_A = -$   
746  **$0.01506 \cdot \text{Fav}^2 + 0.02612 \cdot \text{Fav} + 0.01657$** . Similarly, the function that defines the  
747 curve represented for the association between predicted values of  $I_A$  and  
748 environmental favourability is  **$I_A = -0.00107 \cdot \text{Fav}^2 + 0.001532 \cdot \text{Fav} + 0.00022$** .  
749 These populations belong to the following species: great reed warbler  
750 (*Acrocephalus arundinaceus*), common house martins (*Delichon urbica*), common  
751 kestrel (*Falco tinnunculus*), collared flycatcher (*Ficedula albicollis*), pied flycatcher  
752 (*Ficedula hypoleuca*), barn swallow (*Hirundo rustica*), common gull (*Larus canus*),  
753 blue tit (*Parus caeruleus*), great tit (*Parus major*), house sparrow (*Passer*  
754 *domesticus*), Siberian jay (*Perisoreus infaustus*) and magpie (*Pica pica*). All  
755 references containing the raw values of  $CV_A$ ,  $I_A$  or the data used to calculate them  
756 are listed in ESM–D.



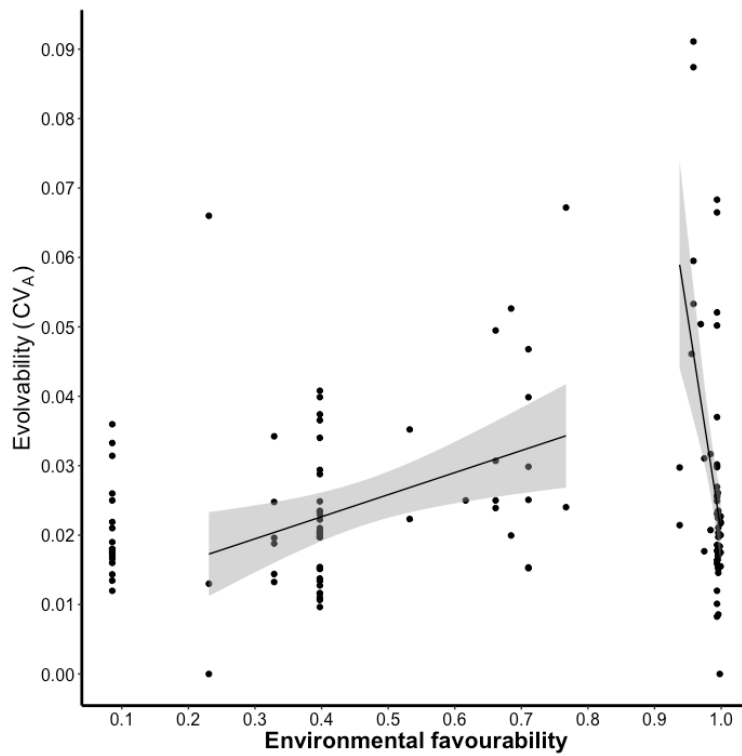
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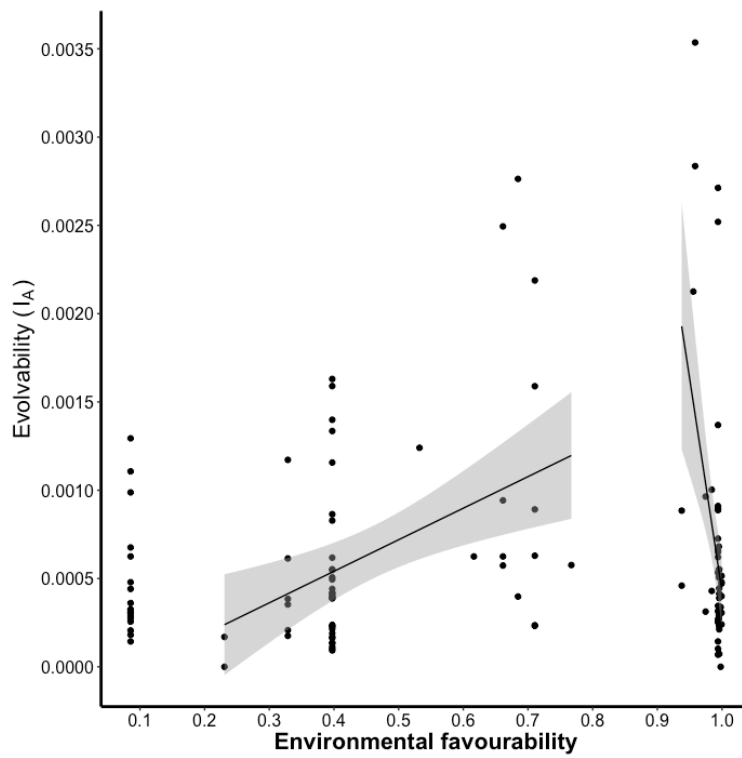
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759

760 **Figure 2.** Association between environmental favourability and untransformed  
761 values of  $CV_A$  (a) or  $I_A$  (b), split for categories of low, intermediated and high  
762 environmental favourability.



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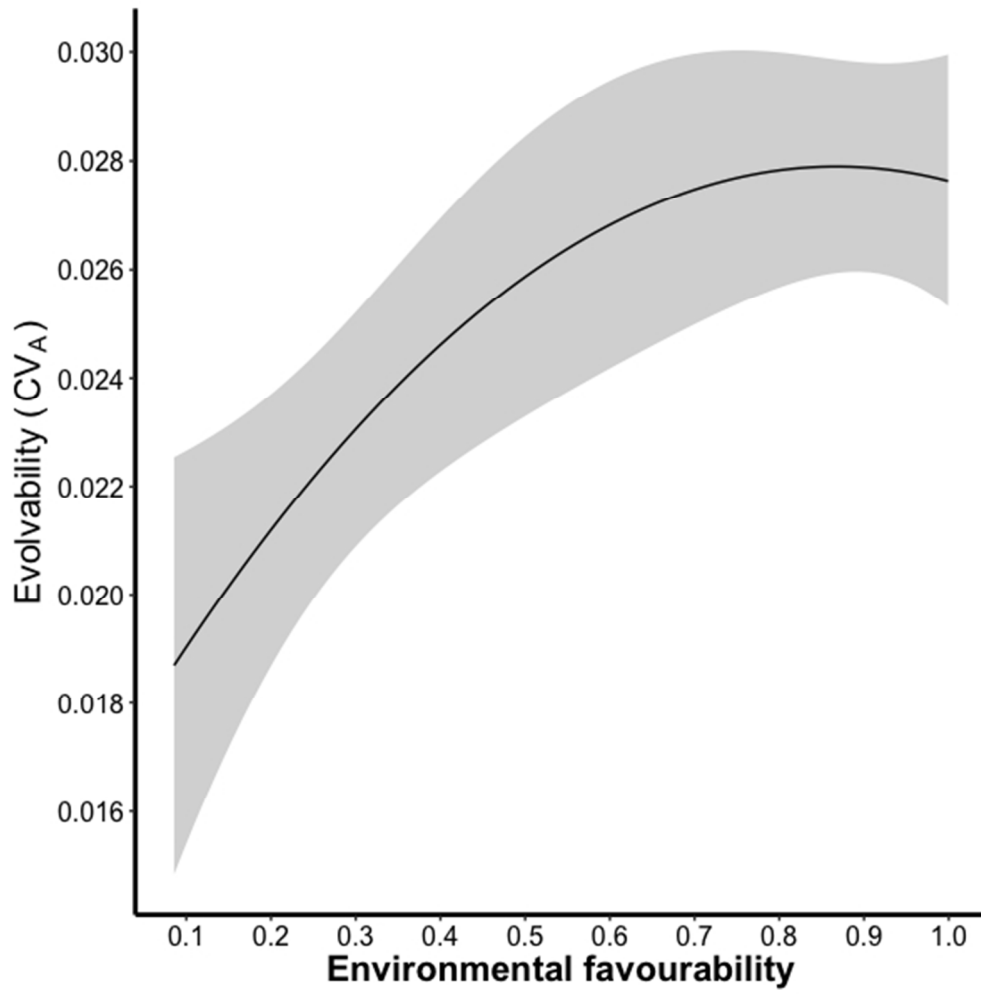
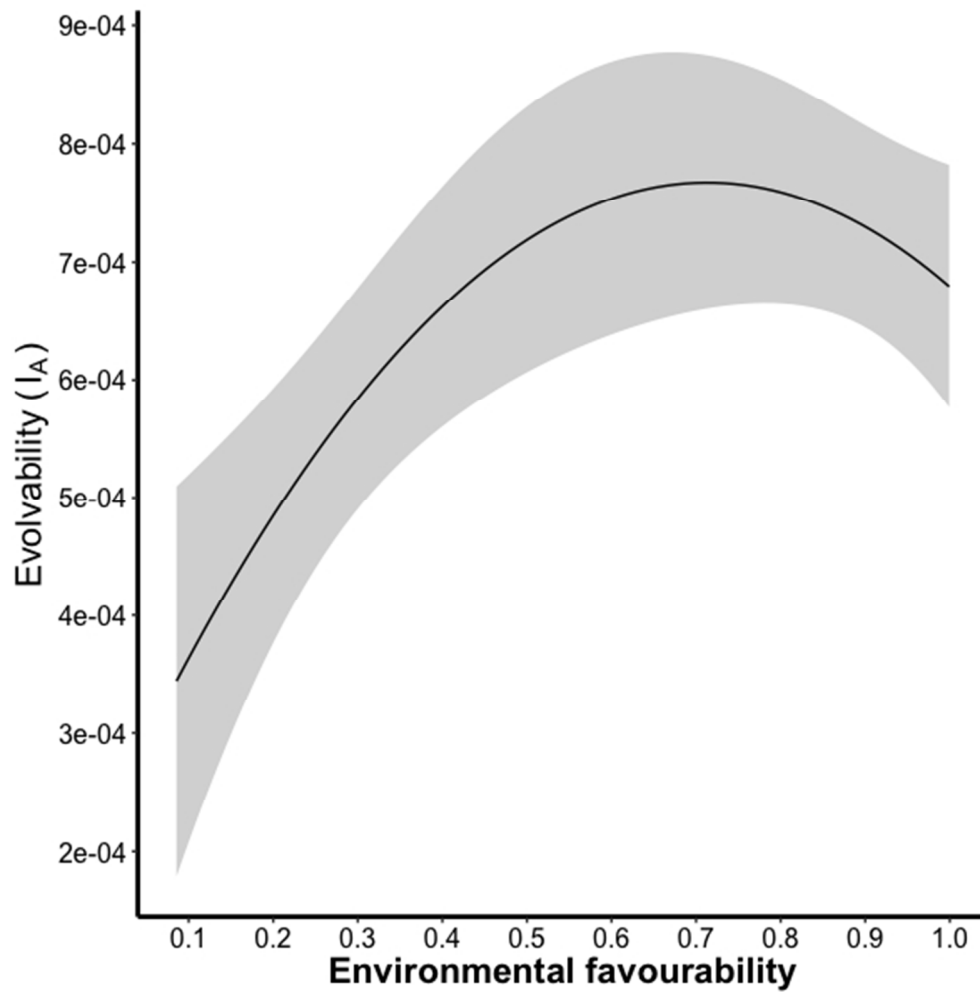


Figure 1a - CV<sub>A</sub> and favourability

211x211mm (72 x 72 DPI)

Figure 1b -  $I_A$  and favourability

211x211mm (72 x 72 DPI)

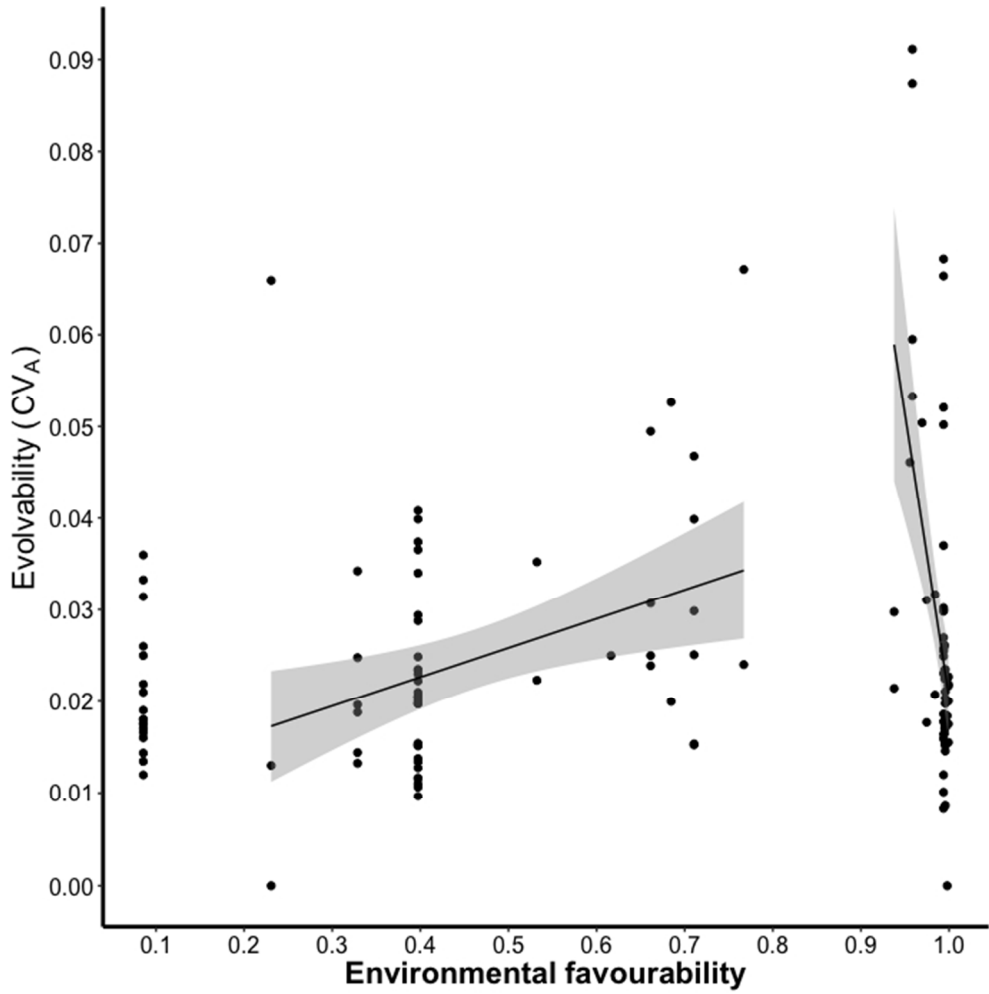
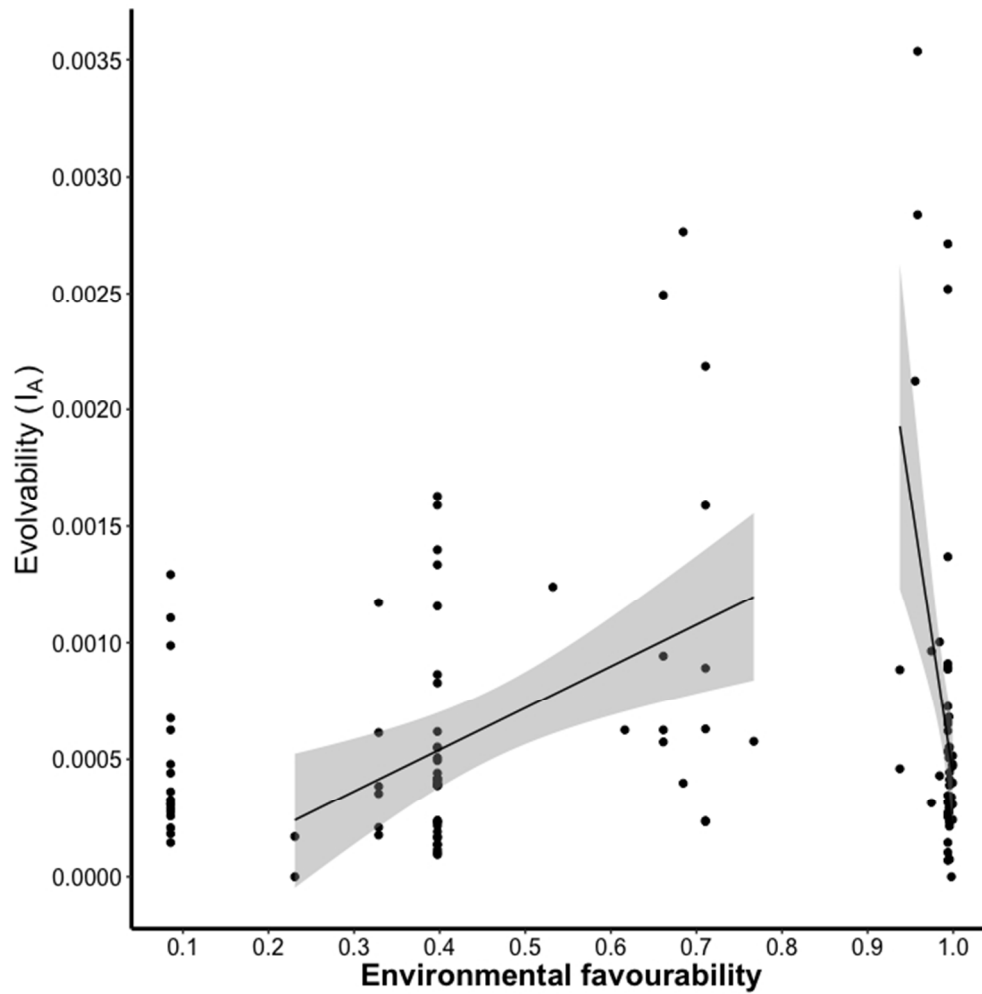


Figure 2a - CV<sub>a</sub> and favorability, categoric  
246x246mm (72 x 72 DPI)



Figure 2b -  $I_A$  and favorability, categoric

246x246mm (72 x 72 DPI)