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

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1 **Evolvability meets biogeography: evolutionary potential**
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19 Keywords: Birds, environmental change, Europe, evolutionary ecology,
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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 50x50km² 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 1x1km². Climatic
226 variables were averaged values for the period 1960-1990. As breeding bird
227 distribution was given at a spatial resolution of 50x50km², we obtained the mean
228 value of each environmental variable in each 50x50km² 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 50x50km² 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 ± 0.011 , $p = 0.0126$). In high favourability areas, there was a
344 negative relationship between favourability and CV_A (estimate = -0.529 ± 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 ± 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 ± 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 1km² and 50x50km² 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

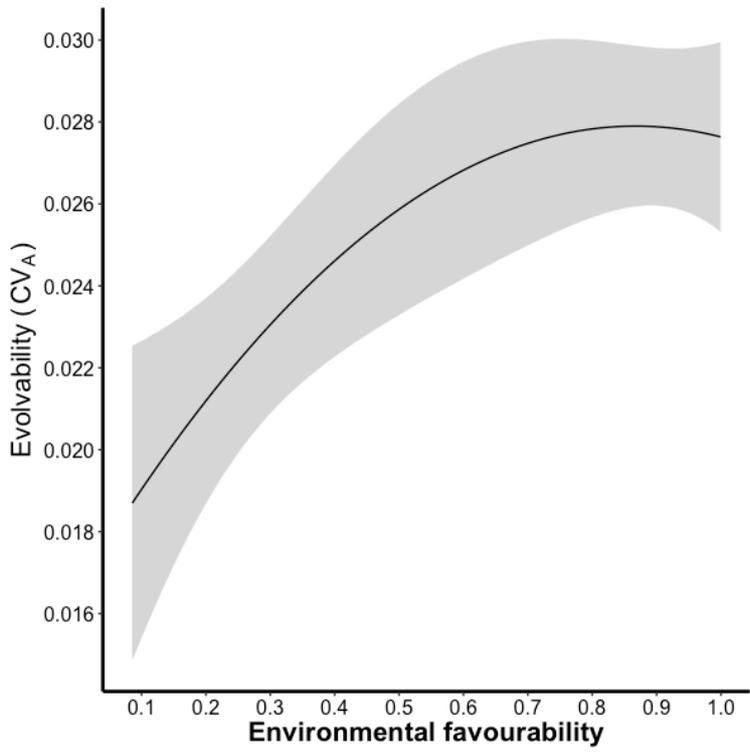
Resolution	50x50Km ²			1x1Km ²		
CV_A	Estimate (±SE)	t value	p	Estimate (±SE)	t value	p
Intercept	0.0082 (±0.0147)	0.558	0.583	0.0077 (±0.0150)	0.513	0.613
Favourability	0.1107 (±0.0539)	2.054	0.050	0.1109 (±0.0531)	2.089	0.048
Favourability ²	-0.0840 (±0.0406)	-2.071	0.046	-0.0842 (±0.0395)	-2.133	0.042
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	0.012	0.0064 (±0.0025)	2.551	0.016
Favourability ²	-0.0052 (±0.0018)	-2.761	0.008	-0.0049 (±0.0018)	-2.658	0.012
Trait: size	-0.0003 (±0.0001)	-2.427	0.016	-0.0003 (±0.0001)	-2.408	0.017
Method: full-sib	-0.000008 (±0.00013)	-0.001	0.999	0.000006 (±0.003197)	0.022	0.982
Method: parent-offspring	0.0001 (±0.0001)	0.771	0.442	0.0001 (±0.0001)	0.801	0.424

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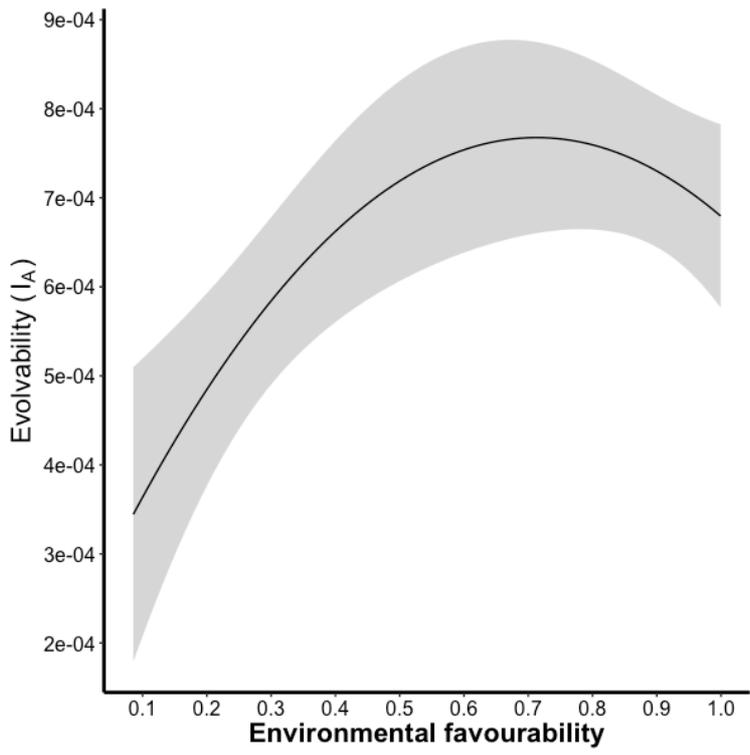
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738

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.



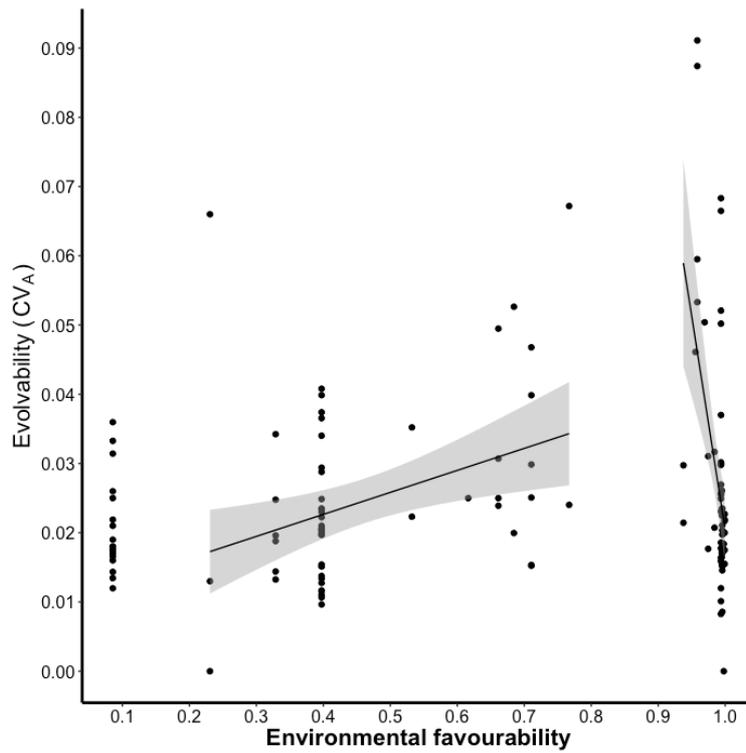
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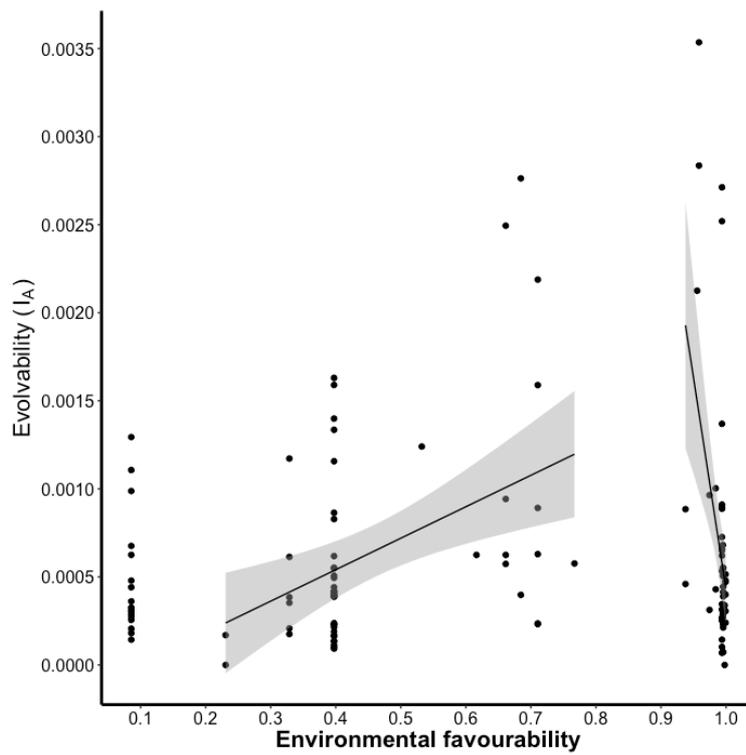
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760 **Figure 2.** Association between environmental favourability and untransformed
761 values of CV_A (a) or I_A (b), split for categories of low, intermediated and high
762 environmental favourability.



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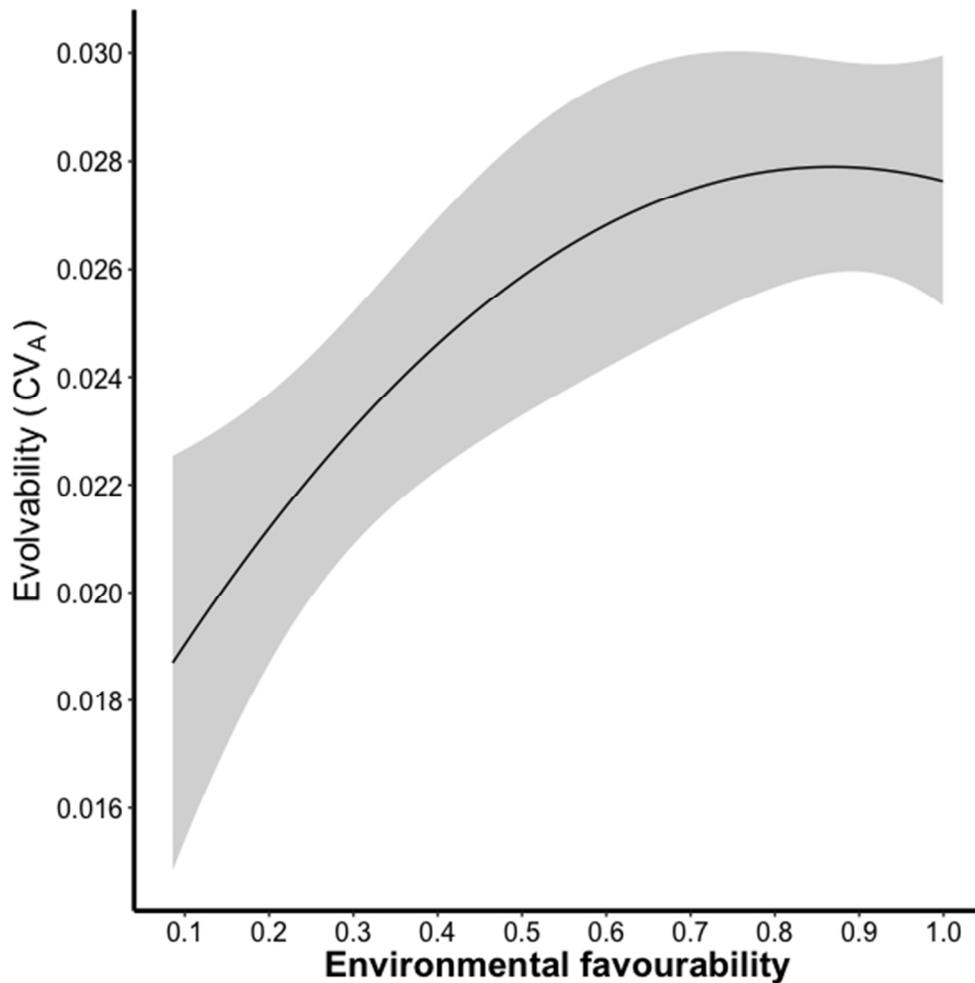
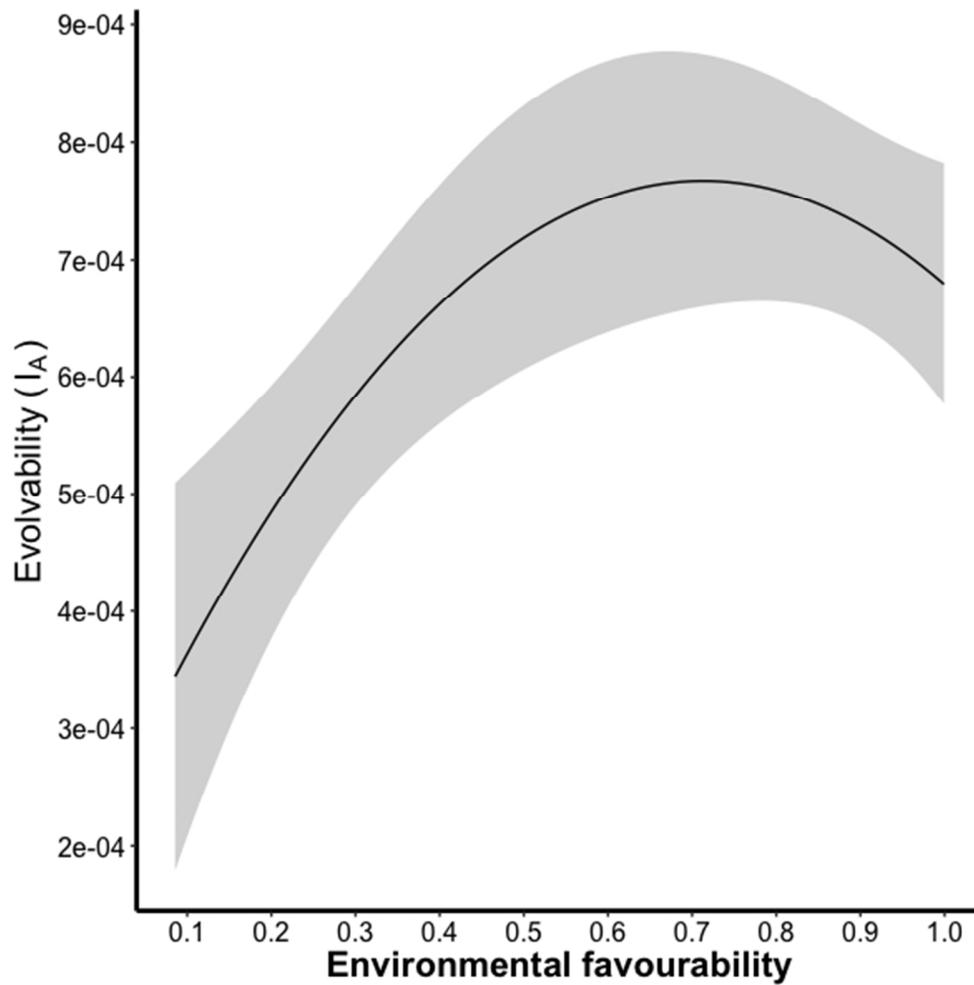


Figure 1a - CV_A and favourability

211x211mm (72 x 72 DPI)

Figure 1b - I_A and favourability

211x211mm (72 x 72 DPI)

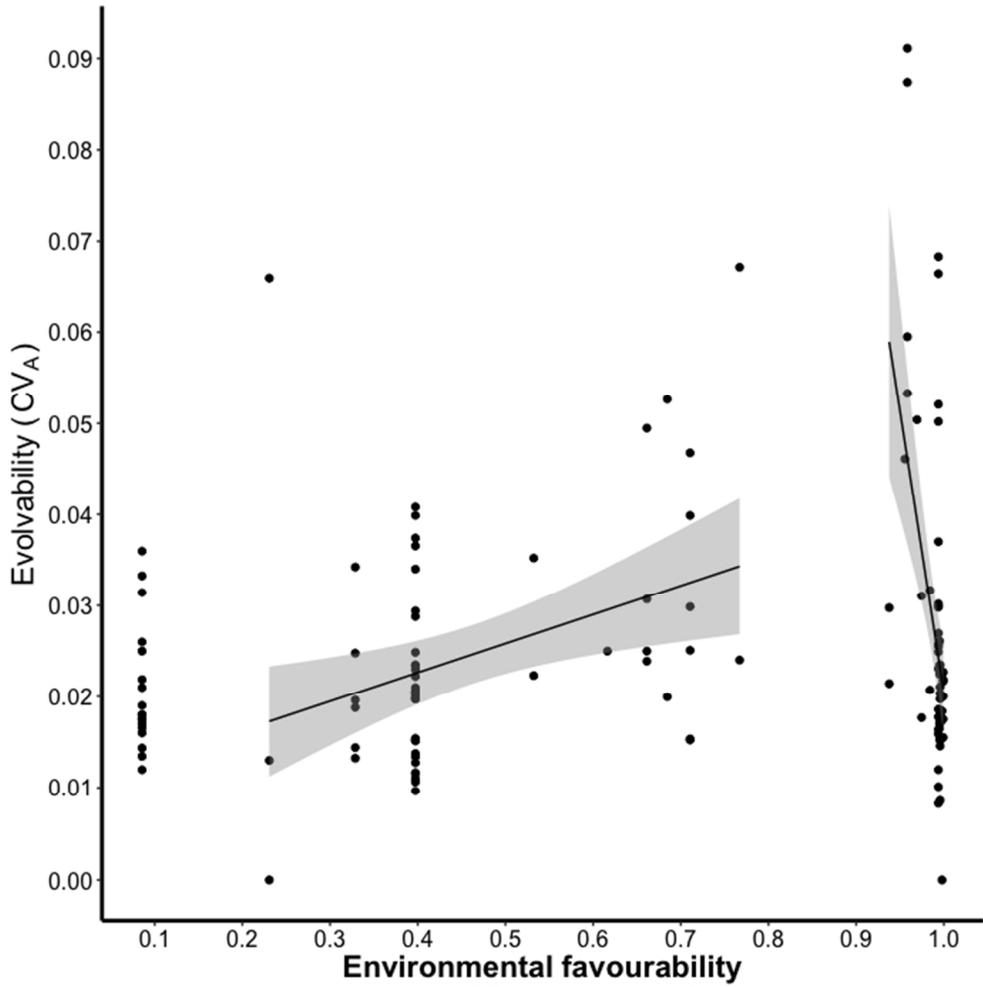
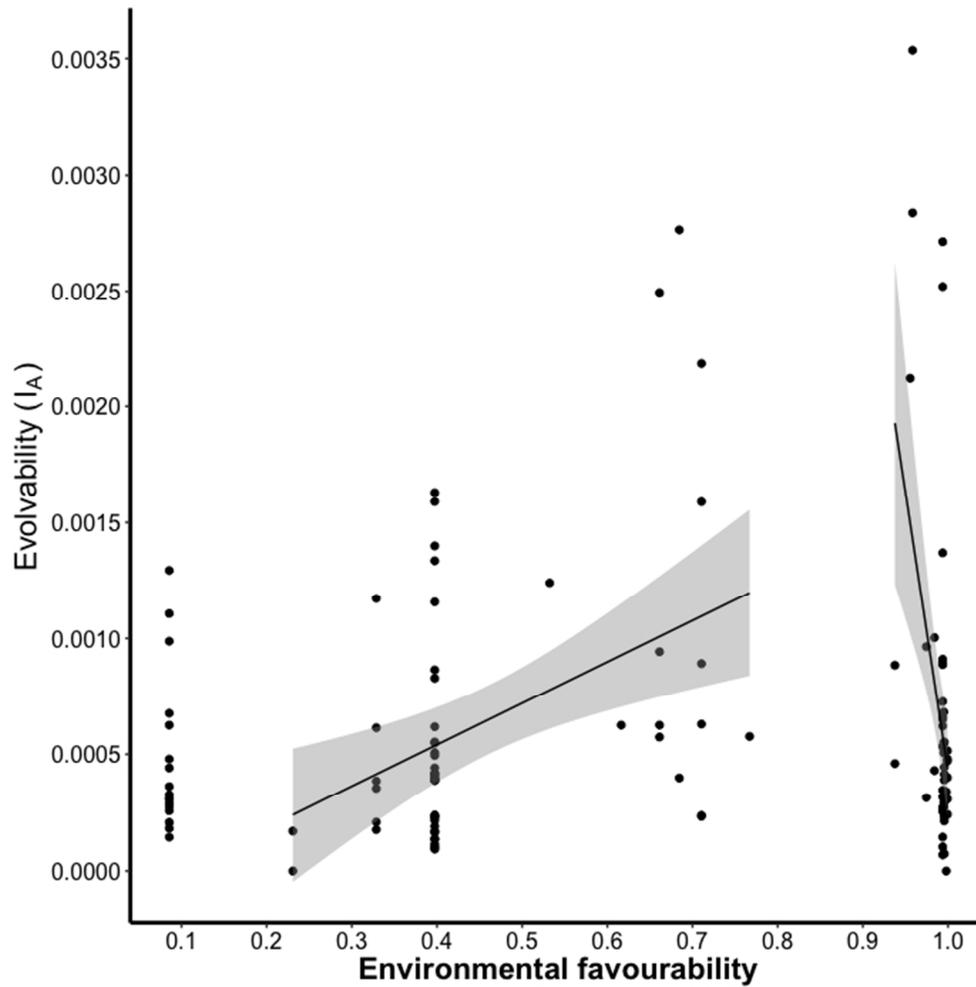


Figure 2a - CV_A and favorability, categoric
246x246mm (72 x 72 DPI)

Figure 2b - I_A and favorability, categoric

246x246mm (72 x 72 DPI)