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

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

1. Introduction

Natural selection is the main mechanism and most powerful explanation for adaptive evolution, and therefore it is essential for understanding biodiversity [1]. Environmental drivers of selection are expected to shape the evolutionary dynamics of phenotypes of specific populations, as long as a fraction of the variance exhibited by these phenotypes is heritable (i.e. there are additive genetic effects determining phenotypic expression). However, the vast majority of research into species' biogeographic distributions (a key component of biodiversity) does not incorporate the role of the environment in determining species' evolutionary potential. This limits our understanding of the role of the environment in driving phenotypic change, and thus our fundamental comprehension of natural selection, but also the effects of environmental change. The degree to which populations can undergo evolutionary adaptation to new environments is one of the major uncertainties in predicting species' responses to present-day environmental changes and for making conservation

decisions [2,3]. The evolutionary potential of phenotypes in a population is an indicator of the population's capacity to respond to environmental change. However, current estimations of evolutionary potential in wild conditions are limited to a few well-studied species, particularly of birds [4–10] and a few cases in mammals [11,12], of which only single populations are studied. In addition, studies are typically geographically located where their environmental circumstances have not been measured [7], and if so, they do not allow comparisons among populations within species. Thus, our comprehension of the central question of how environmental conditions shape the evolution of phenotypes is rather limited.

A critical step towards deepening our understanding of the evolutionary adaptations of populations would be to consider multiple populations of multiple species covering a wide variety of environmental conditions. Taking this step requires long-term datasets during which environmental conditions have changed and individuals have been monitored [12,13], covering a sufficiently broad geographical region to contain multiple distinct populations from a variety of environments, and in which multiple species can be compared. These considerable data requirements have precluded such an analysis until now.

Linking environmental change and evolutionary dynamics is hampered by challenges in choosing metrics of both evolvability (i.e. evolutionary potential) and environmental favourability that would permit comparisons between species. Estimations of evolvability have been traditionally based on quantifying the narrow-sense heritability (h^2) of specific phenotypes, understood as the proportion of the total phenotypic variance explained by additive genetic variance [5]. However, h^2 is not an appropriate index of evolvability that can be used to compare evolvability among traits, populations or species for two reasons [14]. First, the magnitude of the variance scales with the magnitude of the trait measured. Second, additive genetic variance covaries with other sources of variance that are themselves used to calculate heritability (i.e. phenotypic variance) [14–16]. Instead, the coefficient of additive genetic variation (CV_A) and its square (I_A), are more suitable indexes of evolvability since they represent the additive genetic variation scaled by the mean of the phenotype [15]. Both measures are dimensionless indices that are suitable for comparisons among traits, species and populations [15].

An appropriate metric for environmental variation must integrate the multiple factors that simultaneously affect populations of a given species, but also be comparable among species [5]. The use of just one environmental variable does not summarize the ecological needs of a particular species and therefore the reliability of predicting or understanding environmental change on the adaptive potential of species is extremely biased. For example, temperature is a key factor for breeding of pied flycatchers *Ficedula hypoleuca* in northern Europe, but not in southern European latitudes [17]. In fact, the relative importance of a particular environmental variable might change throughout the distribution of the species when other environmental variables are taken into account. Therefore, considering the environmental circumstances that populations experience throughout a species's geographical distribution requires the integration of multiple environmental predictors. Species distribution models (SDMs) are an excellent tool to integrate multiple

environmental predictors producing a metric of environmental favourability along the species range [18]. Based on presence–absence information on the species, and environmental variables over a geographical area, models can be constructed to predict the probability of the species being present at a given site. However, the probability of occurrence is not comparable between species that differ in their prevalence within the study area [19]. The 'favourability function' resolves this issue [18,20] and indicates how the local probability of presence differs from that expected by chance, regardless of whether a species is rare or common. The favourability function is therefore widely used in analyses where direct comparison among species is necessary, for example, to forecast current or future environmental favourability under climate change [21,22], to analyse interspecific interactions [23] and to prioritize areas for conservation [24]. SDMs based on the favourability function are therefore an ideal tool to explore the association between environmental variation and evolvability (CV_A and I_A) of phenotypes among populations and species.

Here, we explored the evolvability of morphological traits of 23 wild bird populations of 12 species found across Europe in relation to the environmental favourability experienced by each population. To do so, we carried out a comprehensive review of estimations of evolvability (CV_A and I_A) of morphological phenotypes available in the scientific literature. We focused our review on the estimations of CV_A obtained from multiple bird populations in the wild, since evolvability has been heavily studied in wild bird populations. We focused on Europe, where long-term monitoring data have led to much research on phenotypic change through time. For each population for which we obtained estimations of evolvability, we ran SDMs to obtain environmental favourability for each species and population. We tested the association between evolvability and environmental favourability at population level. As stressful conditions result in lower additive genetic variance of morphological traits in different taxa [25], including birds [26], a straightforward prediction would be a decreasing evolvability of phenotypes as environmental conditions worsen. However, our results point to a more complex relationship between evolvability and favourability.

2. Methods

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

(a) Bibliographical search for estimates of evolutionary parameters

We performed a bibliographical search from different sources. First, we compiled all information from published reviews that provided evolvability indices I_A or CV_A [15,27,28]. Note that a previous review [28] also incorporated compilations of different evolutionary parameters provided by different authors [27]. Second, we widened this dataset by a search in the Web of Science with the terms 'heritab*' or 'additive genetic variation'.

When one of the two indices was not provided, we calculated I_A or CV_A as follows [16]:

$$CV_A = \sqrt{I_A} \quad \text{and} \quad I_A = CV_A^2.$$

Original values of CV_A or I_A obtained from transformed variables were all excluded from the analyses as transformation renders these statistics meaningless for comparative purposes [16]. Some of the studies we inspected did not calculate CV_A or I_A but, when possible, we calculated them as follows [15]:

$$CV_A = \frac{\sqrt{V_A}}{\bar{x}} \quad \text{and} \quad I_A = \frac{V_A}{\bar{x}^2}.$$

In these cases, V_A represents additive genetic variation and \bar{x} represents the mean of the trait. If V_A was not provided in the study, we calculated it by multiplying h^2 by total phenotypic variance (V_P), since $h^2 = V_A/V_P$. Previous studies have described a series of miscalculations when obtaining evolvability (CV_A or I_A) in the literature [16]. Any miscalculations were corrected and if so the correct statistics were included in the analyses. Unfortunately, standard errors for CV_A or I_A were provided only in one case in our final dataset, making not possible to consider uncertainty around CV_A or I_A values in our models.

The evolutionary parameters collected were calculated using a variety of methods, including a large combination of parent-offspring regressions and, recently, more complex quantitative genetic models. This heterogeneity might cause problems when comparing evolutionary parameters between studies [28]. We accounted for this effect by considering the method used to derive the calculation of the genetic parameters as a random factor in our analyses (see below—Linking favourability and evolutionary potential).

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

(b) Species distribution models

We used the European region covered by the Atlas of European Breeding Birds, which gives the $50 \times 50 \text{ km}^2$ UTM cells in which breeding populations of each species are found. We modelled environmental favourability for the 12 species for which we obtained CV_A or I_A of morphological traits (see electronic supplementary material, §D for further details).

We used three sets of explanatory variables to construct SDMs that model the presence/absence of breeding bird populations. (i) Geographical data, which include the longitude and latitude of the centroids of the cells in which populations were

found. Geographical data were included as explanatory variables because in addition to environmental conditions, species distributions are affected by historical events such as glaciations or source-sink population dynamics [29]. Geographical variables indicate the spatial structuring of populations and allow the role of historical events to be inferred. (ii) We considered altitude as a topographical predictor. (iii) Temperature- and rainfall-based variables that are considered to be 'bioclimatic predictors' and that are likely to have an effect on the distribution of breeding birds (electronic supplementary material, §E). Raw climatic and topographical variables were obtained from WorldClim (<http://www.worldclim.org/current>) at a spatial resolution of $1 \times 1 \text{ km}^2$. Climatic variables were averaged values for the period 1960–1990. As breeding bird distribution was given at a spatial resolution of $50 \times 50 \text{ km}^2$, we obtained the mean value of each environmental variable in each $50 \times 50 \text{ km}^2$ UTM cell. We excluded those climatic variables that had a variance inflation factor (VIF) value higher than 10 [30] sequentially using a stepwise procedure (electronic supplementary material, §E). We used the function 'multicol' from the R package 'fuzzySim' [31] to calculate VIF values. We considered linear and nonlinear responses to topographical and climatic explanatory variables, including their quadratic terms. Regarding geographical variables, we included latitude and longitude, their quadratic and cubic terms, and the interactions among them [29].

SDMs for each species were constructed using explanatory variables and species distribution data at a spatial resolution of $50 \times 50 \text{ km}^2$ with the function 'multGLM' from 'fuzzySim' R package [31]. We performed a forward-backward stepwise logistic regression based on AIC. If models included the quadratic term of a topographical or climatic variable but not the linear term of the same variable, we removed the quadratic term.

The discrimination performance of SDMs were evaluated through the area under the curve (AUC) of the receiver operating characteristic; and their classification capacity using the correct classification rate (CCR), the specificity, sensitivity and the true skill statistics (TSS) using the 'modeEva' package [32] in R (see electronic supplementary material, §F). For evaluation, we repeated SDMs 15 times (5 times each partition), partitioning each species's presence/absence data into training and testing datasets in three different proportions [33] (see electronic supplementary material, §G). The final models that we used for each species were those calibrated using 100% of the species distribution data as it has been shown that random removal of presence records adds a non-trivial amount of uncertainty in projections [34].

The output of the logistic regression was converted to favourability using the favourability function [18] (see electronic supplementary material, §H). A crucial aspect of the favourability function is that it does not give a probability output but a measure of the degree to which local conditions lead to a local probability higher or lower than that expected at random [18]. Therefore, whereas probability values for different species are not comparable because of the different prevalence of each species, favourability values (F) are directly equivalent. The model outputs are then levelled to the same threshold of favourability and can be compared directly, even if the model is constructed with different predictor variables. The output value of $F = 0.5$ will always correspond to the same neutral environmental threshold for all species, whatever the proportion of presences in the sample. The outcome of the favourability function provides an index of environmental favourability for a species in a given site within the geographical area considered. In addition, the favourability outcome depends solely on the response to the predictors considered [20] and not on the ratio of presence and absences of the species.

The favourabilities at a spatial resolution of $50 \times 50 \text{ km}^2$ were downscaled to $1 \times 1 \text{ km}^2$ resolution (the resolution at which all

predictor variables were originally obtained) as previously described [21]. Once this was computed, we obtained the favourability value at $1 \times 1 \text{ km}^2$ for each population and species from which we obtained a CV_A or I_A .

(c) Linking favourability and evolutionary potential

We assessed whether evolvability of phenotypes in different populations can be explained by the favourability values of the environments encountered by those populations. We ran linear mixed models (LMMs) using ‘*lme4*’ [35] and ‘*lmer.test*’ [36] packages in R. We ran our models using CV_A and I_A as dependent variables. In the electronic supplementary material (SI), we show the outcome of our analyses using the log-transformed CV_A and I_A ; results are qualitatively equivalent to the results shown below. We tested linear and quadratic effects of favourability values. We included two more fixed factors in these models. First, we included the method used (animal model, parent-offspring regression or full-sib analyses) to obtain the evolutionary parameter. Second, we included the type of morphological trait considered, categorized as body mass or body size (see electronic supplementary material, SSB and D). Species and location were included as random factors to avoid pseudoreplication (see electronic supplementary material, SSB and D). We repeated the models at a spatial resolution of $50 \times 50 \text{ km}^2$ and $1 \times 1 \text{ km}^2$ to explore potential scale-dependent patterns.

We further explored the change of the slope between environmental favourability and both CV_A and I_A at three different levels of environmental favourability. We categorized the favourability values at three levels (‘catfav’—low, intermediate and high favourability, corresponding to 0–0.2, 0.2–0.8, 0.8–1, respectively). These categories are split unequally due to the logistic nature of favourability [37]. Then, we used CV_A and I_A as dependent variables, and tested the interaction between environmental favourability and the three favourability categories (favourability \times catfav). We considered the same random variables and factors described above. Factors were sequentially excluded from the analyses if associated p values were higher than 0.05. Note that these analyses exploring the association between CV_A (or I_A) and environmental favourability in three different categories were only performed at $1 \times 1 \text{ km}^2$ scale, since low sample sizes at the $50 \times 50 \text{ km}^2$ scale preclude such analyses.

In our models, we did not control for potential phylogenetic biases for three reasons. First, our study deals with the evolutionary potential of morphological traits measured at *population level*. Thus, in order to properly account for any potential phylogenetic influence, a phylogenetic tree at population level for all species considered in this study at European scale would be needed. This information is rather limited and when available in birds, a very low genetic differentiation among populations has been found [38]. Second, we looked at whether the phylogeny of the species considered in this study could influence our results. To do so, we explored whether the residuals of our model had a phylogenetic signal. We quantified the influence of phylogeny on the residuals of our models for both CV_A and I_A by means of K statistics [39]. We found non-existent phylogenetic signal for neither CV_A nor I_A residuals (all $K < 0.688$; all $p > 0.409$), suggesting that phylogeny at species levels is highly unlikely to explain variance in our models (see electronic supplementary material, SJ). Finally, morphological traits typically have a strong phylogenetic signal but our estimates of CV_A and I_A are corrected by the mean of the trait, partially correcting for this source of error.

3. Results

Results of favourability models for each species at a European scale and their evaluation parameters are detailed in the

electronic supplementary material (SSF and G). According to the thresholds of AUC proposed by Hosmer & Lemeshow [19], our favourability models had an outstanding (72.9% of the models had $AUC \geq 0.9$) or excellent discrimination capacity ($0.9 > AUC > 0.8$; see Methods section for full description of the models).

We obtained 135 indices of evolutionary potential for 12 species and 20 populations. We found a negative quadratic relationship between favourability and CV_A (table 1 and figure 1a), regardless of whether favourability was calculated at a spatial resolution of $50 \times 50 \text{ km}^2$ or $1 \times 1 \text{ km}^2$. Similarly, we found a negative quadratic relationship between favourability and I_A at both scales (table 1 and figure 1b). When analysing only the linear relationship between evolvability (either CV_A or I_A) and favourability at any of the two spatial resolutions considered, we did not find any statistical association (all $p > 0.606$).

Considering CV_A as dependent variable, we found a significant interaction between environmental favourability and the categorical split of environmental favourability (interaction favourability \times catfav; $p = 0.005$ —figure 2a). We ran specific models for each category of favourability (low, intermediate and high). In intermediate-favourability areas, there was a positive relationship between favourability and CV_A (estimate: 0.030 ± 0.011 , $p = 0.0126$). In high-favourability areas, there was a negative relationship between favourability and CV_A (estimate = -0.529 ± 0.238 , $p = 0.050$). The association between favourability and CV_A for the low-favourability category could not be computed because of small sample size.

Regarding I_A , we also found a significant interaction between environmental favourability and the categorical split (interaction favourability \times catfav; $p = 0.016$ —figure 2b). In intermediate favourability areas, there was a statistically significant and positive relationship between favourability and I_A (estimate = 0.0016 ± 0.0005 , $p = 0.004$). In high-favourability areas, there was a statistically marginally significant and negative relationship between favourability and I_A (estimate = -0.529 ± 0.238 , $p = 0.077$). The association between favourability and I_A for the low-favourability category cannot be computed because of small sample size.

4. Discussion

Current scientific knowledge of the evolutionary dynamics of phenotypes in wild conditions is highly biased towards studies performed in single species and populations framed within specific environmental circumstances. This study is the first to integrate the analysis of evolutionary potential with biogeographical knowledge, and does so across many species and between populations experiencing a broad range of environmental conditions. We find that environmental favourability is associated with the evolvability of morphological traits within European populations of wild birds. Specifically, we found a negative quadratic association between environmental favourability and evolvability. The quadratic association indicated by the model may not necessarily suggest that evolvability peaks at an exact intermediate favourability value of 0.5, rather a significant negative quadratic term indicates a decreasing slope with increasing predictor values. Furthermore, the quadratic relationship

Table 1. Linear mixed models exploring the association between environmental favourability and evolvability at resolutions of 1 km^2 and $50 \times 50 \text{ km}^2$ across Europe. Note that we included the method ('method') by which CV_A and I_A were obtained and the type of phenotypic trait considered ('trait') as fixed factors (see Methods for further details). Details on the sample sizes for each measurement by population and species are given in electronic supplementary material, *SSB* and *D*. Italic values highlight variables with $p < 0.05$. Models considering log-transformed CV_A and I_A are given in electronic supplementary material, *SI*.

resolution	$50 \times 50 \text{ km}^2$			$1 \times 1 \text{ km}^2$		
	estimate (\pm s.e.)	<i>t</i> value	<i>p</i>	estimate (\pm s.e.)	<i>t</i> value	<i>p</i>
CV_A						
intercept	0.0082 (\pm 0.0147)	0.558	0.583	0.0077 (\pm 0.0150)	0.513	0.613
favourability	0.1107 (\pm 0.0539)	2.054	<i>0.050</i>	0.1109 (\pm 0.0531)	2.089	<i>0.048</i>
favourability ²	-0.0840 (\pm 0.0406)	-2.071	<i>0.046</i>	-0.0842 (\pm 0.0395)	-2.133	<i>0.042</i>
trait: size	-0.0061 (\pm 0.0035)	-1.746	0.083	-0.0060 (\pm 0.0035)	-1.703	0.090
method: full-sib	-0.0016 (\pm 0.0035)	0.235	0.815	0.0017 (\pm 0.0069)	0.255	0.799
method: parent-offspring	0.0018 (\pm 0.0031)	0.599	0.549	0.0021 (\pm 0.0031)	0.674	0.501
I_A						
intercept	0.0004 (\pm 0.0007)	-0.586	0.563	0.0003 (\pm 0.0007)	-0.526	0.604
favourability	0.0067 (\pm 0.0025)	2.661	<i>0.012</i>	0.0064 (\pm 0.0025)	2.551	<i>0.016</i>
favourability ²	-0.0052 (\pm 0.0018)	-2.761	<i>0.008</i>	-0.0049 (\pm 0.0018)	-2.658	<i>0.012</i>
trait: size	-0.0003 (\pm 0.0001)	-2.427	<i>0.016</i>	-0.0003 (\pm 0.0001)	-2.408	<i>0.017</i>
method: full-sib	-0.000008 (\pm 0.00013)	-0.001	0.999	0.000006 (\pm 0.003197)	0.022	0.982
method: parent-offspring	0.0001 (\pm 0.0001)	0.771	0.442	0.0001 (\pm 0.0001)	0.801	0.424

suggests that the slope of the relationship between environmental favourability and evolvability changes along the gradient of environmental favourability. Contrary to our expectations, our results highlight that evolvability does not increase in areas of high environmental favourability. Importantly, using a two-regression approach on the data, we confirmed that evolutionary potential decreases when environmental favourability approaches the extremes (i.e. low or high favourability), regardless of the precise value of favourability where evolvability peaks.

We hypothesized that stronger selection in areas of low favourability should erode additive genetic variance, and consequently would negatively impact on the evolvability of the traits/populations. It is, however, intriguing that evolutionary potential decreases under the best environmental conditions. Previous studies performed in single species have described a similar quadratic pattern of evolvability (I_A) of multiple traits along a latitudinal gradient in the plants *Arabidopsis lyrata* [40] and *Triticum dicoccoides* [41], where I_A was lowest in the opposite edges of the species distribution. However, our study goes beyond latitudinal variation and quantifies environmental favourability for each population and species considered. Several non-mutually exclusive mechanisms may explain this pattern. First, we cannot rule out the possibility that the mean of the trait of populations in good environmental conditions is higher than in poor conditions, an idea previously supported in wild birds [42]. Assuming that mean of the trait can be high in better environmental conditions, higher trait means would reduce CV_A and I_A , as these statistics are standardized by the trait mean.

Alternatively, several factors related to density-dependent effects might influence the evolutionary dynamics of morphological traits. Most of the estimations of evolutionary traits carried out in highly favourable environmental

conditions came from populations breeding in nest-boxes. It is common that such populations reach the carrying capacity of the habitat [43] and higher bird population density occurs in areas of greater environmental favourability [44,45]. Population sizes near to carrying capacity might lead to negative density-dependent effects and selection [46]. This hypothesis has been widely discussed since Haldane [47], who suggested that local adaptation can be associated with density-dependent patterns. Interestingly, such reduced evolvability in populations at high density can be as small as in low density populations [48]. Morphological traits in populations located in highly favourable areas may be under stronger selection due to negative density-dependent effects [47,49], or may be under stabilizing selection, which would reduce additive genetic variance [50]. Also at high densities, high predation rates [49] and parasitism [51] could explain the reduction in additive genetic variance [52]. In addition, gene flow may also be a mechanism for negative density-dependent effects. In birds, high population densities reduce the rate of emigration [53], along with rates of immigration [54] and recruitment [55]. Thus, reduction of immigration and emigration within high-density populations, likely associated with higher environmental favourability, is expected to increase inbreeding in the population due to reduced gene flow [56]. Regardless of the potential underlying mechanism, our results suggest a link between species geographical distributions and evolutionary dynamics.

Estimations of evolvability of traits could be affected by the inclusion of non-additive sources of variance like between-year variation, or permanent or shared environmental factors. If so, estimations of additive genetic variance, and thus the evolutionary potential of the phenotype, will be lowered compared to situations where such

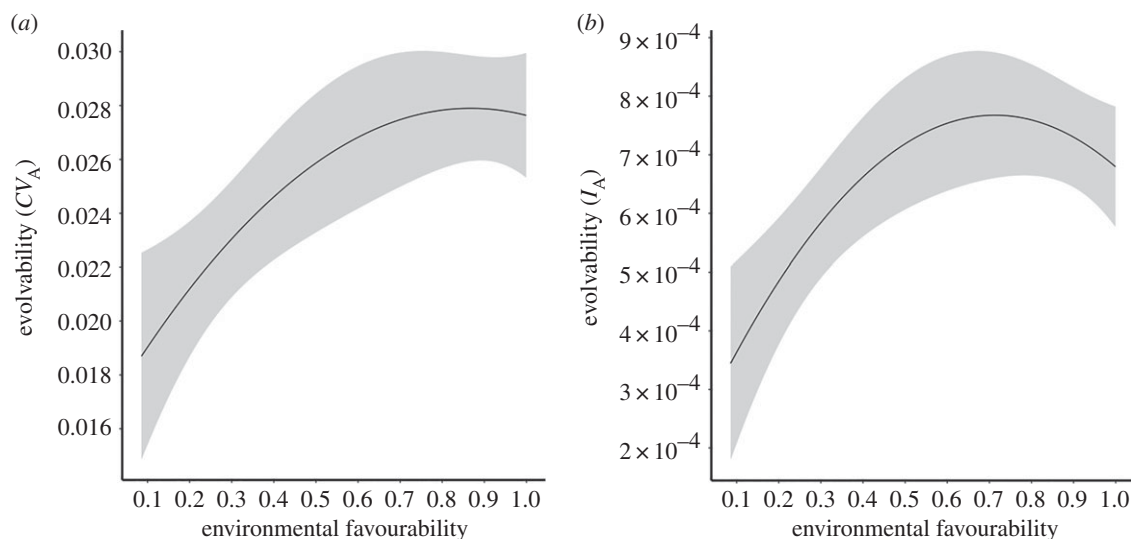


Figure 1. Estimated change in evolvability of morphological traits in wild birds at $1 \times 1 \text{ km}^2$ scale with 95% confidence intervals (shaded in grey) against a gradient of environmental favourability from linear mixed models (see Methods for further details). y -axis represents the predicted values obtained for untransformed (a) CV_A and (b) I_A from the models described in the main text. The function that defines the curve represented for the association between predicted values of CV_A and environmental favourability ('Fav') is $CV_A = -0.01506 \times \text{Fav}^2 + 0.02612 \times \text{Fav} + 0.01657$. Similarly, the function that defines the curve represented for the association between predicted values of I_A and environmental favourability is $I_A = -0.00107 \times \text{Fav}^2 + 0.001532 \times \text{Fav} + 0.00022$. These populations belong to the following species: great reed warbler (*Acrocephalus arundinaceus*), common house martin (*Delichon urbica*), common kestrel (*Falco tinnunculus*), collared flycatcher (*Ficedula albicollis*), pied flycatcher (*Ficedula hypoleuca*), barn swallow (*Hirundo rustica*), common gull (*Larus canus*), blue tit (*Parus caeruleus*), great tit (*Parus major*), house sparrow (*Passer domesticus*), Siberian jay (*Perisoreus infaustus*) and magpie (*Pica pica*). All references containing the raw values of CV_A , I_A or the data used to calculate them are listed in electronic supplementary material, *S4*.

sources of variation are not taken into account [57]. For example, maternal effects have been suggested to be more prevalent under unfavourable environmental conditions [5], which decreases the estimation of additive genetic variance [58], but does not alter its statistical significance. However, given the heterogeneous ways that evolutionary parameters compiled here have been calculated, we consider that it is highly unlikely that there is a systematic bias on the calculations of V_A or any other non-additive source of variation. Taking uncertainty of CV_A or I_A estimates into account would help assessing the robustness of the patterns we have uncovered here. Unfortunately, as has been previously highlighted [16], estimations of additive genetic variance, including mean-standardized measures of additive genetic variation, are typically provided without any approximation of their sampling variance.

The association between ecological and evolutionary parameters found here may have implications for population demography [49], not just within the context of density dependence of populations [59]. For example, small environmental perturbations may have consequences on the evolutionary dynamics of life-history, morphological and fitness-related traits [59,60], influencing population growth [59–61]. Evolutionary parameters are clearly crucial for predicting the effect of environmental change on population demography [62,63], since population growth ultimately determines species geographical distributions. SDMs are constructed based on presence/absence or presence data in given areas, but what drives the distribution of the species is the persistence of their populations, (i.e. their population growth rate). Thus, integrating population dynamics and quantitative genetics [63,64] into biogeographical research [2] will improve our understanding of the influence of environmental change on population persistence.

Our results can have profound implications for predicting or understanding the effect of environmental change on population persistence at biogeographical scales. Among all potential sources of environmental variance, climate change is a crucial one, and is a global threat to biodiversity. Climatic variables tested were accepted for in all SDMs built for our study species (see electronic supplementary material, *SF*), suggesting that climate (both temperature- and rainfall-based variables) has a strong effect on environmental favourability in our models. Based on our results, if climate becomes less suitable for populations in currently highly favourable areas, local adaptation is less likely than in some other areas (electronic supplementary material, *SK*). On the other hand, populations located in areas at the end of current intermediate favourability might be particularly able to evolve in response to climate change if conditions become less favourable, because these populations have a particularly high evolutionary potential (figures 1 and 2; electronic supplementary material, *SK*). Evolution could prolong the period in which these populations are able to survive *in situ* as conditions worsen, or allow these populations to evade local extinction altogether. Our results also suggest that evolutionary 'rescue' from climate change is less likely at species' geographical range margins, where conditions are typically less favourable than at the centre of distributions [65]. This could result in a general trend of population extinction close to species' warm range margins. Instead, while populations located in areas of intermediate favourability might not be threatened by climate change if favourability improves, these populations' high evolvability might mean that they undergo evolutionary adaptation to the new climate conditions regardless. This could have implications for the community the species occupy. Species' ecological traits, particularly the morphological traits measured here, play a strong role in determining the outcome of biotic interactions,

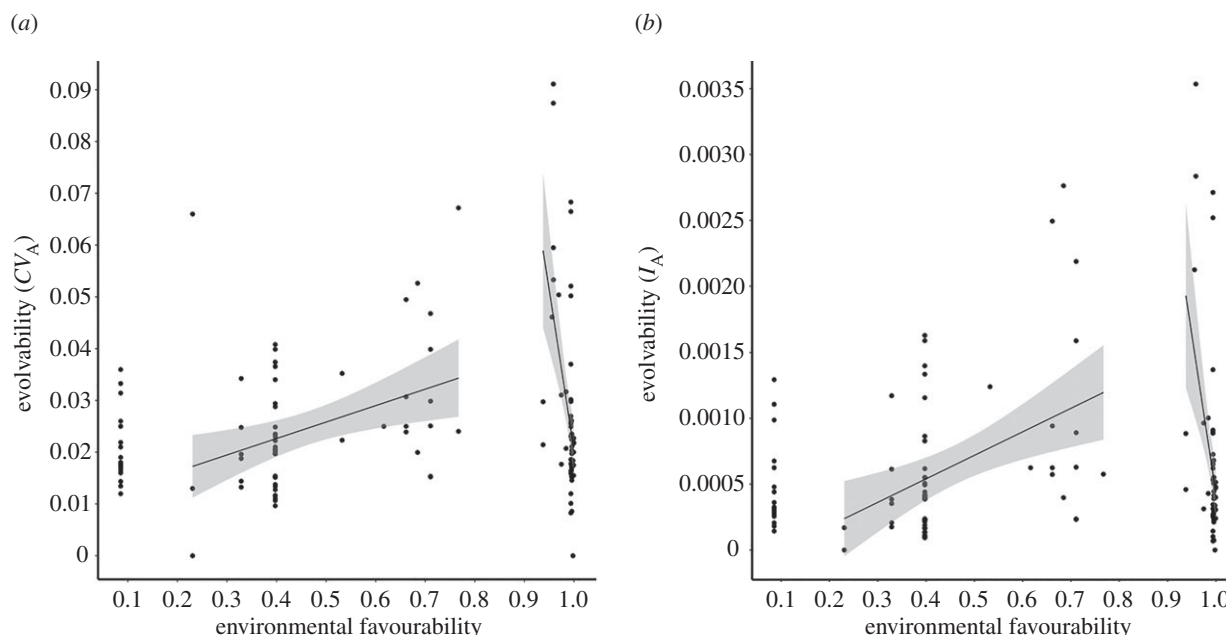


Figure 2. Association between environmental favourability and untransformed values of (a) CV_A or (b) I_A , split for categories of low, intermediate and high environmental favourability.

so evolution of these traits could impact the composition and ecosystem function of an ecological community [66,67]. Thus, understanding the likelihood that evolution will occur could improve our understanding of community-level responses to climate change [66,68].

The potential link between population persistence and evolution represents a challenge for biogeographical and macroecological studies that aim to predict the effect of environmental change [69]. By using biogeographical tools together with evolutionary parameters, we were able to describe how environmental conditions may shape the evolutionary potential of morphological traits of wild birds in Europe. Despite observations of evolutionary adaptation in response to environmental change in a diverse range of species and locations [3], difficulties in drawing general conclusions has made evolutionary potential an understudied and largely unquantified problem within biogeography [68]. Our study highlights the need to integrate evolutionary dynamics into biogeographical research, to understand how environmental variation influences evolutionary dynamics, and to produce more reliable predictions about the effect of environmental change on population persistence and therefore on biodiversity. An important general message arising from our results is that biogeographical forecasts, and particularly those based on species distribution models, would be improved by incorporating information on

population-level demographic and evolutionary responses to the environment, to predict the effect of environmental change on population persistence. We require more information on the evolutionary potential of life-history and fitness-related traits of populations throughout the range of environmental conditions a species occupies, to get further insights into the mechanisms that drive evolutionary dynamics within a geographical perspective.

Data accessibility. Data are available from Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.dh98c> [70].

Authors' contributions. J.M.-P., A.E. and F.G.-G. conceived the idea and decided methodology; R.E. provided information of species distribution; J.M.-P. and A.E. analysed and modelled the data; J.M.-P. wrote the manuscript in collaboration with all co-authors.

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