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Does habitat specialization shape the evolutionary potential of wild bird populations?

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Abstract

Because specialist species evolved in more temporally and spatially homogeneous environments than generalist species, they are supposed to experience less fluctuating selection. For this reason, we expect specialists to show lower overall genetic variation as compared to generalists. We also expect populations from specialist species to be smaller and more fragmented, with lower neutral genetic diversity. We tested these hypotheses by investigating patterns of genetic diversity along a habitat specialization gradient in wild birds, based on estimates of heritability, coefficients of variation of additive genetic variance, and heterozygosity available in the literature. We found no significant effect of habitat specialization on any of the quantitative genetic estimators but generalists had higher heterozygosity. This effect was mainly a consequence of the larger population size of generalists. Our results suggest that evolutionary potential does not differ at the population level between generalist and specialist species, but the trend observed in heterozygosity levels and population sizes may explain their difference in susceptibility to extinction.

Keywords: heritability; additive genetic variance; neutral diversity; individual specialization; niche width

Introduction

Native specialist species are becoming less abundant in disturbed landscape to the benefit of generalist species (Shultz et al. 2005, Le Viol et al. 2012). There is some evidence that climate (Davey et al. 2013) and land use (Devictor et al. 2008a, b) changes are driving this decline of specialization in wild communities, leading to a functional biotic homogenization (Clavel et al. 2011). The higher sensitivity of specialists to global changes is expected to result from their narrower ecological niche, which is associated with smaller and more fragmented populations, more vulnerable to the destruction of their habitat. The persistence of species will ultimately depend upon two mechanisms: range shift or adaptation to environmental changes, through phenotypic plasticity or microevolution (Lynch and Lande 1993). Anthropogenic changes are now considered as the greatest evolutionary force (Palumbi 2001, Steffen et al. 2011) and it therefore becomes crucial to determine how specialist and generalist species differ in their ability to respond to these changes. Assessing whether generalist and specialist species differ in terms of evolutionary potential should give valuable information on their respective ability to defer extinction through evolution.

The two alternative strategies (specialist vs generalist) are generally thought to arise depending on fitness trade-offs between alternate phenotypes across environments (Richmond et al. 2005, Poisot et al. 2011): spatially and temporally variable environments should favour generalist strategies, because generalists can achieve higher average performance than specialists across multiple environments. In turn, stable environments should favour specialists which are able to exploit more efficiently a single resource (see Moran 1992 for theoretical evidence, and Kassen 2002 for experimental evidence). Expressed in terms of selection pressures, heterogeneous environments generate fluctuating selection, while in a homogeneous or stable environment, selection is more likely to be stabilising, or persistently directional (Keightley and Hill 1988). Additionally, generalist strategies may become less profitable under high levels of local stabilizing selection, because trade-offs for the performance in different niches become accordingly strong (Svardal et al. 2014). Specialists can therefore be expected to evolve under stronger and more consistent selection pressures that could deplete overall genetic variability. In contrast, the exposure of generalists to a variety of environments, and to spatially and temporally fluctuating selection, could help maintain a higher genetic diversity. For these reasons, we expect to find higher evolutionary potential in generalist species than in specialist ones, which could partly explain the highest sensitivity of specialists to environmental changes.

Only a scarce number of empirical studies support this prediction so far. Hägele and Rowell-Rahier (2000) showed in a herbivorous insect genera that host specialist species have a lower heritability (and thus a lower evolutionary potential) of growth rate than host generalists. A review of selection experiments in bacteria by Kassen (2002) also suggests that environmental heterogeneity may be driving both the quantity of genetic variation in a population and the niche width of individuals, resulting in the evolution of generalists and the maintenance of genetic variation in heterogeneous environments. However, the link between specialization and evolutionary potential is largely unknown in wild populations.

Here, we review available estimates of evolutionary potential in relation to habitat specialisation and population size in wild bird populations. As emphasised in the univariate breeder's equation, $R = h^2 S$ (Lande 1979), the predicted evolutionary response (R) depends on the selection gradient (S) and on the evolutionary potential of a trait, measured as its heritability (h^2, the ratio between the amount of genetic additive variance and total phenotypic variance). We thus mainly focused on estimates of heritability and additive genetic variance as they also represent the most widely reported estimates of evolutionary potential for quantitative traits (Postma 2014). We predict higher genetic variance for generalist species (heritability, hereafter h^2, and the additive genetic coefficient of variation, hereafter CV_A, are the two standardized estimates of genetic variance we used).

We also reviewed estimates of heterozygosity (hereafter Hz), a widely available measure of genetic diversity known to depend on demographic processes such as inbreeding level, drift and population size (Soulé 1976, Frankham et al. 2002). Hz is not a direct estimator of evolutionary potential, as it does not relate to additive genetic variance, but rather a proxy for overall genetic diversity, which is often considered in conservation study as an indicator of population health. More specifically, Hz has been correlated with extinction risks (Evans and Sheldon 2008) and population fitness (Reed and Frankham 2003). On this topic again, little empirical work can be found, but a study carried out on the bark beetle (Kelley et al. 2000) indicated that specialist sister-species indeed had reduced levels of Hz when compared to generalist ones. Simply because of a narrower ecological niche, specialist species have access to a more limited range of habitats than generalist ones. For this reason, populations of specialists may be smaller and more fragmented which is likely to negatively impact genetic diversity by limiting effective population size and gene flow (Whitlock and Barton 1997). We therefore predict that specialists should have lower Hz than generalists, mainly as a result of smaller population size.

Material & Methods

Data collection

Habitat specialization indexes

Assessing specialization by categorizing habitat types has been criticized as too subjective and unrealistic (Bazzaz 1991, Thompson et al. 1998, Fridley et al. 2007). Therefore, we used two different indices based on independent methods: The Species Specialization Index (SSI), as defined by Julliard et al. (2006) and the relative niche width measurement (θ) as introduced in plants by Fridley et al (2007) and in birds by Ducatez et al. (2014). Both indices use different approaches and are therefore not strongly correlated, but rather represent the diversity of methods available to measure habitat specialisation.

The SSI is defined as the coefficient of variation of a species abundance across a set of predefined habitats (Julliard et al. 2004). A high SSI thus implies that a species abundance varies strongly across habitats. Specialist species have higher values of SSI, generalists have lower values. SSI was calculated for 234 species at the European scale, the territory being partitioned into 98 habitat categories defined in the EUNIS database (see Le Viol et al., 2012 for details). Affinity of each species for nesting and foraging in a given habitat is coded by experts on three levels (3: primary habitats; 2: secondary; 1: others). Note that because the coefficient of variation is the standard deviation scaled to the mean, SSI does not depend on population size.

The niche width (Θ) is based on the expectation that a generalist species occurs in a range of habitat categories that vary considerably in species composition, whereas a specialist species is found in habitats that contain a consistent suite of other species. The idea of using the compositional diversity of species that co-occur with a target species to measure the degree of specialization was introduced by Colwell and Futuyma (1971). Specialist species have lower values of θ, generalists have higher values. To avoid a bias due to differences in species range, this index is based on habitat co-occurrence (rather than realized species co-occurrence), meaning that two species that occupy the same habitat type in different places are considered as co-occurring, even if their range does not overlap, e.g. this avoids island species to be automatically considered as specialists. The niche width was estimated using species co-occurrence data within each of the 82 IUCN habitat subcategories, and considering all extant 9870 species listed by the IUCN (see Ducatez et al., 2014 for details). For a given species, habitat width was measured as $\theta = \gamma / \mu(\alpha)$, where γ is the cumulative number of species in the habitats used by a given species and $\mu(\alpha)$ is the mean habitat species richness calculated over the different habitats inhabited by that species. This specialization index is positively correlated with population size (Pearson's product-moment correlation $\rho = 0.25$, 95 % Confidence Interval [0.044, 0.43], p-value = 0.02, see supplementary material S1 for the correlation of both specialization indexes with population size).

Habitat specialization was chosen over other available specialization indices as it gathers the greatest number of niche axes in one parameter and is consequently the most integrative. Indeed, temperature and food availability depend on habitat, which makes habitat specialization linked with thermic and food specialization (Barnagaud et al. 2012). Our dataset of quantitative estimates of evolutionary potential (i.e. quantitative genetic parameters) includes species that cover a range of 3.1 in SSI (from 2.3 to 5.4) and of 6.4 in niche width (from 1.58 to 8), and the neutral diversity data (i.e. Hz) covers a range of 4.6 in SSI (from 2.3 to 6.9) and of 10.6 in niche width (from 1 to 10.6), when the total range available for SSI is 8, ranging from 1.8 to 9.9 and the total range for niche width is 13.54, ranging from 1 to 14.54. The distributions of both specialization index for each of our datasets can be found in supplementary figure S2.

Population size

Information on local population size was not available so the population size data we used was extracted from the BirdLife International website in May 2014 (*http://www.birdlife.org/*). Population sizes correspond to the total number of individuals in the world according to the censuses published by BirdLife (2005, 2008).

Quantitative data: heritability and coefficient of additive genetic variance

We chose the bird taxon because it gathers the greatest number of quantitative estimators across all taxa (Postma, 2014). In order to gather estimates of evolutionary potential (h^2 and CV_A) in bird populations, we performed a search in the *Web Of Knowledge* research engine. We used the key-words: Topic= (« bird* ») AND (« heritabil* » OR « genetic* estimate* ») and the search was performed in February 2013. When studies aimed at quantifying the response of quantitative parameters to different environmental conditions (e.g. food quality), only parameters estimated under natural conditions were used. These references were further checked against the list gathered by Postma (2014), in order to maximize the number of references providing estimates of heritability and coefficients of additive genetic variance. h^2 and CV_As can be estimated with two different methods: the parent offspring regression and the animal model. The former is the earliest method and has been used since the end of the 19th century. It estimates heritability by the phenotypic correlation between parents and offspring (Lynch and Walsh 1998). The latter, the *animal model*, has been applied in ecology for merely more than a decade. The animal model is a mixed model using information about relatedness among individuals to infer the part of phenotypic variance due to additive genetic variance (Henderson 1973, Kruuk 2004). Because parent offspring regression may overestimate heritability (shared environments increase the resemblance between parents and offspring), the method used to estimate quantitative parameters was specified in our dataset and subsequent analyses.

Only life-history and morphological traits (See supplementary material, table S3 for trait classification) were kept, as for behavioural traits the type of traits were extremely heterogeneous and for physiological traits, data were available for only four traits from two studies. We considered here that pooling heritabilities or CV_As from different traits measured in a population is relevant, as we were not looking for an accurate estimate of evolutionary potential, but for an estimate of the general level of additive genetic variance in the population. Both h^2 and CV_A represent standardised measures of additive genetic variance, respectively to the total phenotypic variance and to the mean.

Genetic diversity

We used the heterozygosity (Hz) data published by Evans and Sheldon (2008). They collected Hz values measured at microsatellite loci for wild bird species in the literature and used expected Hz because it is less sensitive to sample size (Nei 1978) and the occurrence of null alleles (Callen et al. 1993). When multiple studies were available for one species, Evans & Sheldon (2008) kept the study with the largest sample size and the highest number of microsatellites loci used to estimate Hz. Thus, while the quantitative genetics estimates are available for several populations in some species, the estimates for Hz are only available for one population per species. We used the Hz values for the 54 species that matched our SSI specialization index and for the 183 species in their dataset that matched our estimation of the niche width (θ).

Phylogeny

To account for the non-independence of species, we used species relatedness extracted from phylogenetic trees. Phylogenetic trees were obtained from the website *www.birdtree.org* that provides subsets of the first complete bird phylogeny (Jetz et al. 2012). Each model was run with 100 alternative trees.

Statistical analyses

To assess the effect of habitat specialization on evolutionary potential (h^2, CV_A) or neutral genetic diversity (Hz) we used linear mixed models. Ideally, models should include as fixed effects population size (log-transformed) and an estimator of habitat specialization (SSI or niche width Θ). However, for h^2 and CV_A, population size was only available for few species, resulting in a too small sample size to run our models. We thus included population size in models considering Hz but not in models considering h^2 and CV_A. In terms of random variables, a phylogeny effect was included in all models to account for species non-independence.

Because of a more complex data structure, analyses of h^2 and CV_A included several additional fixed and random effects compared to models run for heterozygosity. First, we expected systematic differences between certain types of traits (morphological or life history traits, Postma, 2014). Consequently, we added “Type of trait” as a fixed effect in models with two levels, “morphological” and “life-history”. Similarly, as the method used to estimate heritabilities (animal model or parent-offspring regression) entails a systematic difference, we added an “Estimation method” fixed effect in models investigating heritability.

Second, h^2 and CV_A estimates are trait and population specific because they are based on observations of some characteristics of individuals sampled from a given population. Therefore it was necessary to include in the models two additional random effects: “population identity” and “trait”, with a nested structure. “Trait” was nested within “population identity” and “population identity” within “phylogeny”. The MCMCglmm R package (Hadfield 2013) does not model nested effects, but the variables were designed in order to account for this nested structure: each species/population/trait combination was given a unique ID allowing to take into account each level in a meaningful way (phylogeny (species), population within species, trait within population within species). Some species (e.g. *Fulica atra*) were represented by one estimator for only one population when others (e.g. *Passer domesticus*) were represented by multiple populations, and multiple traits for each population. The random effects “population identity” and “trait” allow taking this lack of balance into account.

Finally, the standard error associated with heritability estimates was included as a random effect to account for measurement error. Unfortunately, this was not possible with CV_A, due to the paucity of errors reported, nor with heterozygosity for which standard errors were not available. The random effects were assumed to follow normal distributions with a mean of 0 and a variance equal to σ_a^2A for the phylogeny **(**where σ_a^2 is the phylogenetic variance and **A** is the phylogenetic relatedness matrix), a variance equal to σ_m^2M for the error effect (where σ_m^2 is the measurement error variance and **M** is a diagonal matrix containing the square standard error of the published estimates; we fixed the variance σ_m^2 to 1 as the sampling variances are known, see Hadfield & Nakagawa 2009 for details) and variances equal to σ^2I for the remaining effects (where σ^2 represents the population variance within species, the trait variance within population within species or the residual variance; **I** is the identity matrix).

These models were run using Bayesian methods as implemented in the MCMCglmm R package. 1 000 000 iterations of each model were run. The first 50 000 iterations were used to initiate the chain, not to estimate parameters, and the thinning interval was set to 10. The amount of iterations was considered sufficient as autocorrelations were low (<0.06) for fixed and random effects.

An inverse-gamma prior for random effects was used (V = 1 and nu = 0.002), in order to minimise the effect of prior information on posterior distribution. To assess prior sensitivity, the same models were run using a parameter expanded prior (V = 1, nu = 1, alpha.mu = 0, alpha.V = 10000) and a weakly informative prior (V = $\sigma/4$, n = 1 where σ is the total variance of the dependent variable). Using different priors did not affect the results (Supplementary Table S5 and S6).

To account for phylogeny uncertainty, each model was run with each of the 100 alternative trees provided by Jetz et al. (2012), and the estimates presented in the result section represent the average over the 100 models.

Results

Available data for quantitative genetics estimates

For the analysis using the SSI index, 520 estimates of h^2 and 150 estimates of CV_A from respectively 64 and 13 studies were gathered, with an average of 3.52 traits per study for h^2 and 6.62 per studies for CV_A. Variance among studies in number of estimates is large, ranging from 1 to 48 for h^2 and from 1 to 14 for CV_A. The number of estimates calculated from parent offspring regression is 363 for h^2 against 157 from “animal model” and 39 for CV_A against 111 from “animal model”. Only life-history and morphological traits were kept, with respectively 132 and 388 estimates for h^2, and 43 and 107 for CV_A.

For the analysis using the niche width measurement (θ), a total of 923 h^2 and 190 CV_A estimates from respectively 64 and 20 studies were gathered, with an average of 2.6 traits per study for h^2 and 5.7 per study for CV_A. Variance among studies in the number of estimates was large, ranging from 1 to 48 for h^2 and from 1 to 14 for CV_A. 707 h^2 estimates came from parent-offspring regressions and 216 from “animal models”. For CV_A, 52 were estimated from parent offspring regression and 139 from “animal models”. Only life-history and morphological traits were kept in the analyses (due to the low number of physiological and behavioural traits), with respectively 176 and 747 estimates for h^2, and 61 and 129 for CV_A.

Effect of specialization on additive genetic variance (h^2, CVA)

Heritability was not predicted by specialization, whether considering the SSI (Table 1, posterior mean = 0.054, 95% CI [-0.022, 0.14], pMCMC = 0.13, Fig 2a) or the niche width (θ, Table 2, posterior mean = -0.018 95% CI [-0.057, 0.023], pMCMC = 0.36, Fig 3a) as indices of habitat specialization. Morphological traits had higher heritability than life-history traits in both data sets (Table1 & Table 2), and estimates from the animal model were lower than estimates from parent-offspring regressions for the SSI data (Table1).

Similarly, CV_A was not predicted by either the SSI (posterior mean = 0.66, 95% CI [-1.3, 2.7], pMCMC = 0.48, Fig 2b) or the niche width (θ) (Table2, posterior mean = -0.26, 95% CI [-1.9, 1.5], pMCMC = 0.71, Fig 3b).

Effect of specialization and population size on genetic diversity (Hz)

Heterozygosity was not predicted by either the SSI (Table 3, posterior mean=0.014, 95% CI [-0.025, 0.053], pMCMC = 0.48) or the niche width (Table 3, posterior mean=0.051, 95% CI [-0.021, 0.12], pMCMC = 0.16), but population size did have a significant effect on heterozygosity (Table 3, posterior mean=0.044, 95% CI [0.023, 0.064], P <0.001, and posterior mean=0.036, 95% CI [0.020, 0.054], P <0.001). Species with larger global population sizes had higher levels of heterozygosity. Because niche width and population size are positively correlated (Pearson's product-moment correlation=0.25, df=88, P=0.020), an effect of niche width on heterozygosity appears when population size is not part of the model (posterior mean=0.071, 95% CI [0.022, 0.12], pMCMC =0.0045). The SSI however was not correlated to population size (Pearson's product-moment correlation=-0.27, df=35, P=0.10)

Discussion

The ability of wild populations to persist in a changing environment depends largely on their evolutionary potential (Hoffmann and Sgrò 2011, Vander Wal et al. 2013). We expected a higher evolutionary potential in generalists as compared to specialists, based on the different selection pressures their ecology suggests they are exposed to. In contrast with this, across 36 wild bird populations and using two different specialization indexes, we found no significant effect of specialization on evolutionary potential -as estimated by quantitative genetics estimates, h^2 and CV_A. Specialization did not correlate with genetic diversity measured by Hz either, but we found a significant positive relationship between population size and heterozygosity. In turn, population size correlates positively with niche width (but not with the SSI index), indicating that species with larger niches (generalists) also tend to exhibit more genetic diversity, as a consequence of their larger population sizes. The fact that populations of generalist species are larger than populations of specialist species can be explained by several factors, such as larger available habitat patches, better connectivity between patches, or higher dispersal rates (Kattan 1992, Stireman 2005). In turn, higher genetic diversity in larger populations is in line with theoretical and empirical expectations (Soulé 1976, Frankham 1996). Our results thus suggest that the effect of specialization on genetic diversity results from demographic processes rather than evolutionary processes such as long-term differences in selection pressures. Indeed, we found that specialization had an effect on heterozygosity through population size, but not on quantitative genetic estimates: neutral markers are tightly linked to demography, migration, drift and mutation while selection is expected to shape variance of quantitative traits (Sgrò et al. 2011).

The prediction that specialists should have in general lower evolutionary potential than generalists due to stronger and more consistent selection pressures was not confirmed by this study. So far, the empirical support for this hypothesis was limited, to our knowledge, to two local scale study in insects (Hagele & Rowell-Rahier 2000 and Kelley et al. 2000) and to experimental evolution in bacteria, as reviewed by Kassen (2002). Several reasons (outlined below) may explain the absence of pattern, but in any case, the generality of this result will need to be confirmed (or infirmed) by more empirical studies from wild populations.

First, we know little about the origin of generalism. For example, if a species niche is fully covered by specialized populations, each population exploiting a part of the niche only, the species will be described as generalist. In this case, high genetic diversity is expected among populations, but not necessarily within populations, making the pattern undetectable when genetic parameters are sampled at the population level (as it is the case for h^2 and CV_A). This particular genetic structure may have evolved under large spatial scale environmental variation. The ability of populations to respond to new selection pressures may then depend on the amount of gene flow among populations. To provide further insights in this direction, an informative index would be the F_{ST}, which compares within population genetic variation to among-population genetic variation, a core question in our investigation. Unfortunately, estimating F_{ST} requires heterozygosity measures in multiple populations for each studied species, which would be available only after implementing new field studies.

A second major issue is the definition of “evolutionary potential”. Because it was the most readily provided estimate of additive genetic variance in natural populations and because of its central role in the breeder’s equation, we used heritability. However, because it is a ratio and because of its univariate definition, heritability can be a misleading estimate of evolutionary potential. Heritability is a ratio of variances and as such its direction of variation can be interpreted in multiple ways, i.e. higher heritability can be the result of either higher additive genetic variance or lower environmental variance. This is of fundamental importance here since environmental variance could be larger for generalist species dealing with more heterogeneous environments than specialist species, hence masking any potential increase in additive genetic variance. A solution around this issue is the use of coefficients of variation of additive genetic variance rather than heritability (Houle 1992, Hansen et al. 2003, 2011, Hansen and Houle 2008). Unfortunately, CV_A was reported for only 15 species, and often published without associated standard errors. Moreover, 45% of those estimators are likely to be biased (Garcia-Gonzalez et al. 2012). It was thus not possible to reliably assess the effect of specialisation on CV_A but this is an avenue worthwhile pursuing in the future. Another aspect through which heritability may not be a suitable estimate of evolutionary potential is its univariate and trait specific nature as it may not reflect overall evolvability and constraints (e.g. genetic correlations, Sih et al. 2004). Multivariate approaches are therefore be needed to bring further light on these issues (Walsh and Blows 2009, Hansen et al. 2011, Teplitsky et al. 2014).

Third, on a more functional note, the absence of patterns for quantitative genetic estimates in our study may also be explained by a lack of knowledge about the functionality of the traits. Indeed, in the study of Hagele & Rowell-Rahier (2000), growth rate heritability was related to a diet specialization index. As a selection pressure resulting from food availability is expected to directly impact growth rate, the niche parameter used to assess specialization index was thus tightly linked to the trait for which evolutionary potential was measured. In this way, the effect of selection pressure is more likely to be detected when measuring heritability. However, this would not mean overall lower evolutionary potential in specialists, but only for a subset of traits closely associated to the specialization parameter. In our case, with the dataset obtained from the literature, such a clear functional link between traits and habitat specialization is not available: we chose a integrative specialization parameters and investigated the additive genetic variance for all available traits together. However, a population can be submitted to strong selection pressures, for instance on wing size (Hall et al. 2004) or beak shape (Grant, B., Grant 2003), that would reduce genetic variance for these traits, a pattern that would not be detected in our analyses because we pooled genetic variance estimates irrespectively of the traits’ function. In the case of reduced overall evolutionary potential, we would expect a decreased genetic variance in traits closely associated to fitness. We thus tried to restrict the data to heritability estimates related to fitness traits (e.g. clutch size, breeding success) but the sample size was drastically reduced in this case (90 heritabilities for 24 species), which didn’t allow us to estimate effects properly.

In conclusion, our study indicates that there is no detectable effect of habitat specialization on evolutionary potential in birds, at least when considering estimates of additive genetic variance currently available in the literature. However, this does not mean that specialist and generalist species stand the same chances when facing environmental changes: our study suggests that species with narrower habitat niches have smaller populations with reduced levels of neutral genetic diversity, which indicate increased extinction risks (Evans and Sheldon 2008). In the close future, new estimates of additive genetic variance for wild populations may be available, such as multivariate ones, allowing for further exploration of the relationship between specialization and evolutionary potential.

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Supporting information

S1 Correlation between both specialization indexes and population size.

S2 Specialization indexes distributions

S3 Trait Classification

S4 Phylogenetic trees

S5 Results with weakly informative priors

S6 Results with parameter expanded priors

S7 References for heritability

S8 References for CV_As

S9 List of species taken from Evans &Sheldon (2007)

S10 Visualization for heritability data

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Table1. Effect of Species Specialization Index (SSI) on two quantitative estimates of evolutionary potential: heritability and coefficient of variation of additive genetic variance (CV_A).. Estimates of effects are given by posterior means (Post. Mean) and their associated 95% confidence intervals (CI 95%). pMCMC values are also given for fixed effects. For the effect of type of trait, the reference level is ‘life history’ as compared to ‘morphological’. For the effect of the estimation method, the reference level is ‘animal model’ as compared to ‘parent offspring regression’.

Explanatory var.		**Heritability**			**CV_A**		
	Effect	**Post. mean**	**CI 95%**	**Pc**	**Post.mean**	**CI 95%**	**Pc**
Fixed	**Intercept**	0.0299	-0.261/0.281	0.866	9.81	2.79/16.5	0.013**
	SSI	0.0535	-0.0218/0.139	0.128	0.664	-1.31/2.67	0.479
	Type of trait: morphological	0.192	0.130/0.252	<0.001***	-8.25	-11.3/-5.03	<0.001***
	Estimation method: regression	0.0452	0.00283/0.0871	0.036*	-0.848	3.71/1.96	0.549
Random	**Phylogeny**	0.004	0.000/0.017		4.07	0.000/18.7	
	Population	0.002	0.000/0.013		0.677	0.000/3.39	
	Trait	0.021	0.016/0.029		17.3	8.25/30.7	
	Residual	0.004	0.003/0.006		25.8	19.0/36.0	

Table2 Effect of species niche width Index (θ) on two estimates of genetic variance: heritability and coefficient of variation of additive genetic variance (CV_A). Estimates of effects are given by posterior means (Post. Mean) and their associated 95% confidence intervals (CI 95%). pMCMC values are also given for fixed effects. For the effect of type of trait, the reference level is 'life history' as compared to 'morphological'. For the effect of the estimation method, the reference level is 'animal model' as compared to 'parent offspring regression'.

Explanatory var.		**Heritability**			**CVa**		
	Effect	**Post.mean**	**CI 95%**	**Pc**	**Post.mean**	**CI 95%**	**Pc**
Fixed	**Intercept**	0.34	0.086 / 0.59	0.011	12	4 / 20	0.012
	Ө	-0.018	-0.057 / 0.023	0.36	-0.26	-1.9 / 1.5	0.71
	Type of trait : Morphological	0.21	0.17 / 0.25	<0.001	-7.0	-10 / -4.0	<0.001
	Estimation method : regression	-0.00097	-0.045 / 0.044	0.97	-1.5	-5.4 / 2.2	0.44
Random	**Phylogeny**	0.040	0.012 / 0.074		3.8	0.00013 / 19	
	Population	0.0060	0.0026 / 0.0096		1.7	0.00012 / 8.1	
	Trait	0.0061	0.0020 / 0.011		4.8	0.00014 / 21	
	Residual	0.017	0.014 / 0.021		74	54 / 93	

Table3. Effect of species niche width (θ) and Species Specialization Index (SSI) on heterozygosity (Hz). Estimates of effects are given by posterior means (Post. Mean) and their associated 95% confidence intervals (CI 95%). pMCMC values are also given for fixed effects. The second model includes population size as a fixed effect.

Explanatory var.		**Heterozygosity**			**Response var.**	**Heterozygosity**		
	Effect	**Post.mean**	**CI 95%**	**Pc**	**Effect**	**Post.mean**	**CI 95%**	**Pc**
Fixed	**Intercept**	0.047	-0.21 / 0.29	0.71	**Intercept**	0.058	-0.28 / 0.39	0.72
	Ө	0.051	-0.021 / 0.12	0.16	**SSI**	0.014	-0.025 / 0.053	0.48
	Log Population size	0.044	0.023 / 0.064	<0.001	**Log Population size**	0.036	0.020 / 0.054	<0.001
Random	**Phylogeny**	0.0047	0.00023 / 0.012		**Phylogeny**	0.010	0.00020 / 0.030	
	Residual	0.020	0.014 / 0.028		**Residual**	0.014	0.0044 / 0.024	

Fig1 Distribution of coefficients of variation of genetic additive variance (CV_A, a), heritabilities (b) and heterozygosity (c) along gradient of habitat specialization (SSI).

Fig2 Distribution of coefficients of variation of genetic additive variance (CV_A, a), heritabilities (b) and heterozygosity (c) along gradient of habitat niche width (θ).

Fig 1 Distribution of coefficient of additive genetic variance (a), heritability (b), and heterozygosity (c) along a habitat specialization gradient. Each SSi value represents a species which name appears below

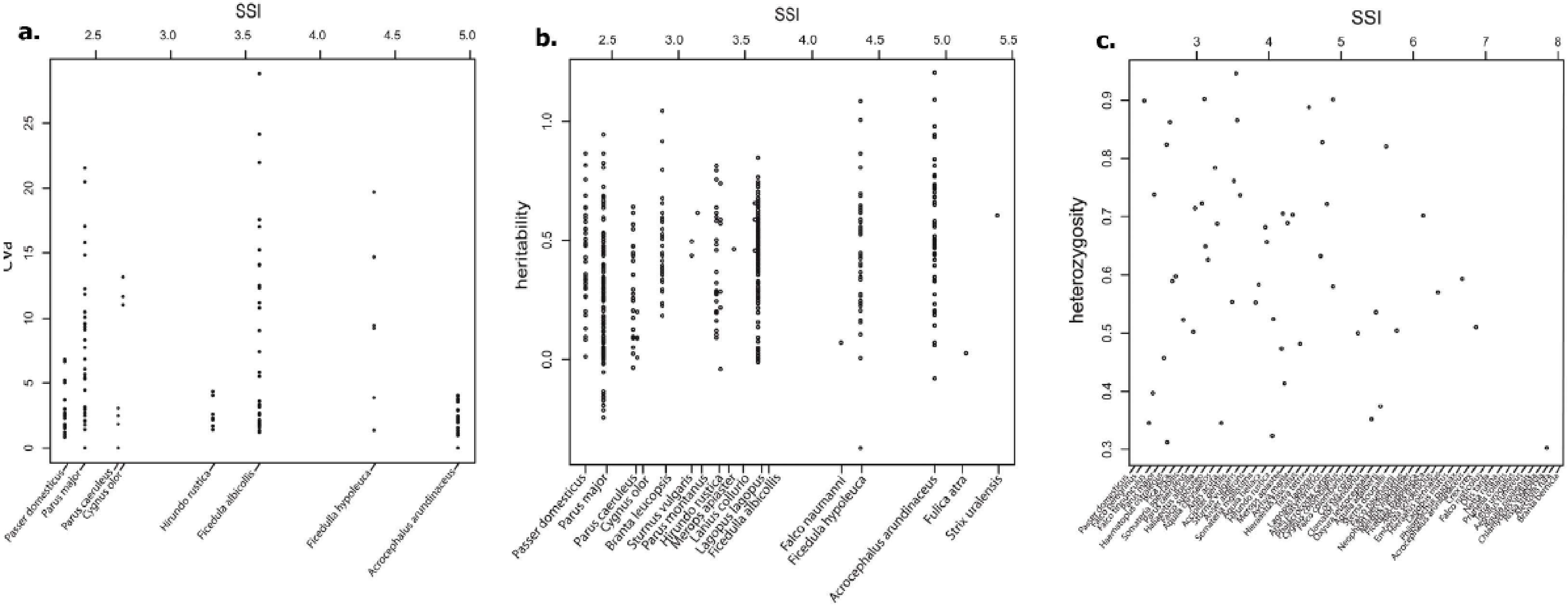
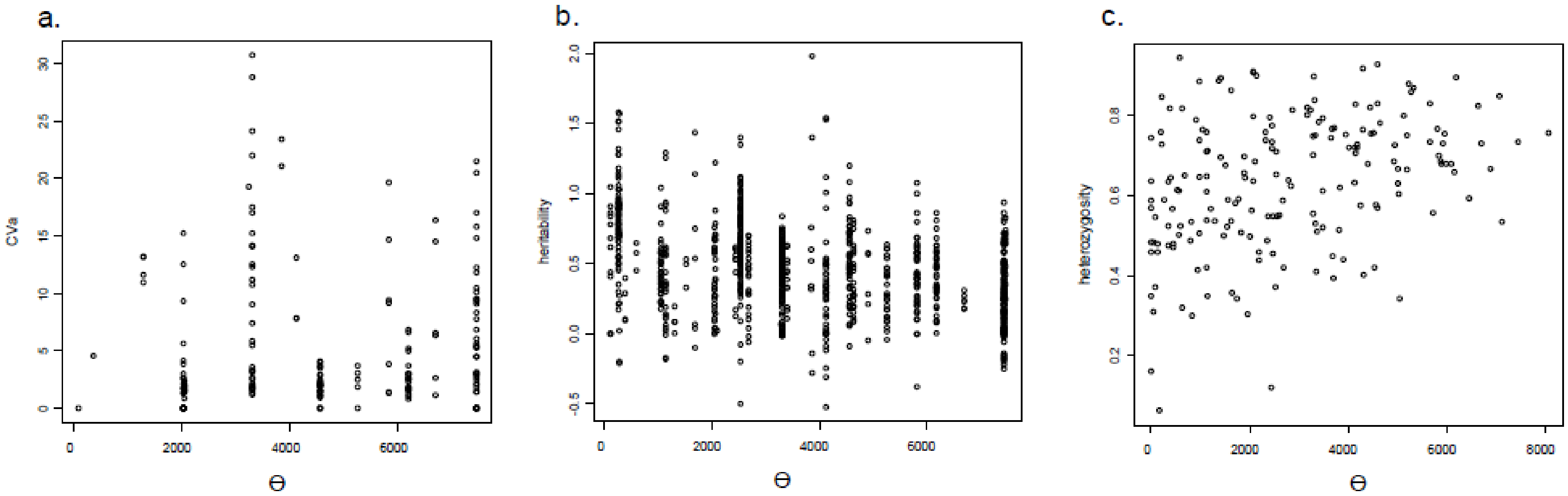
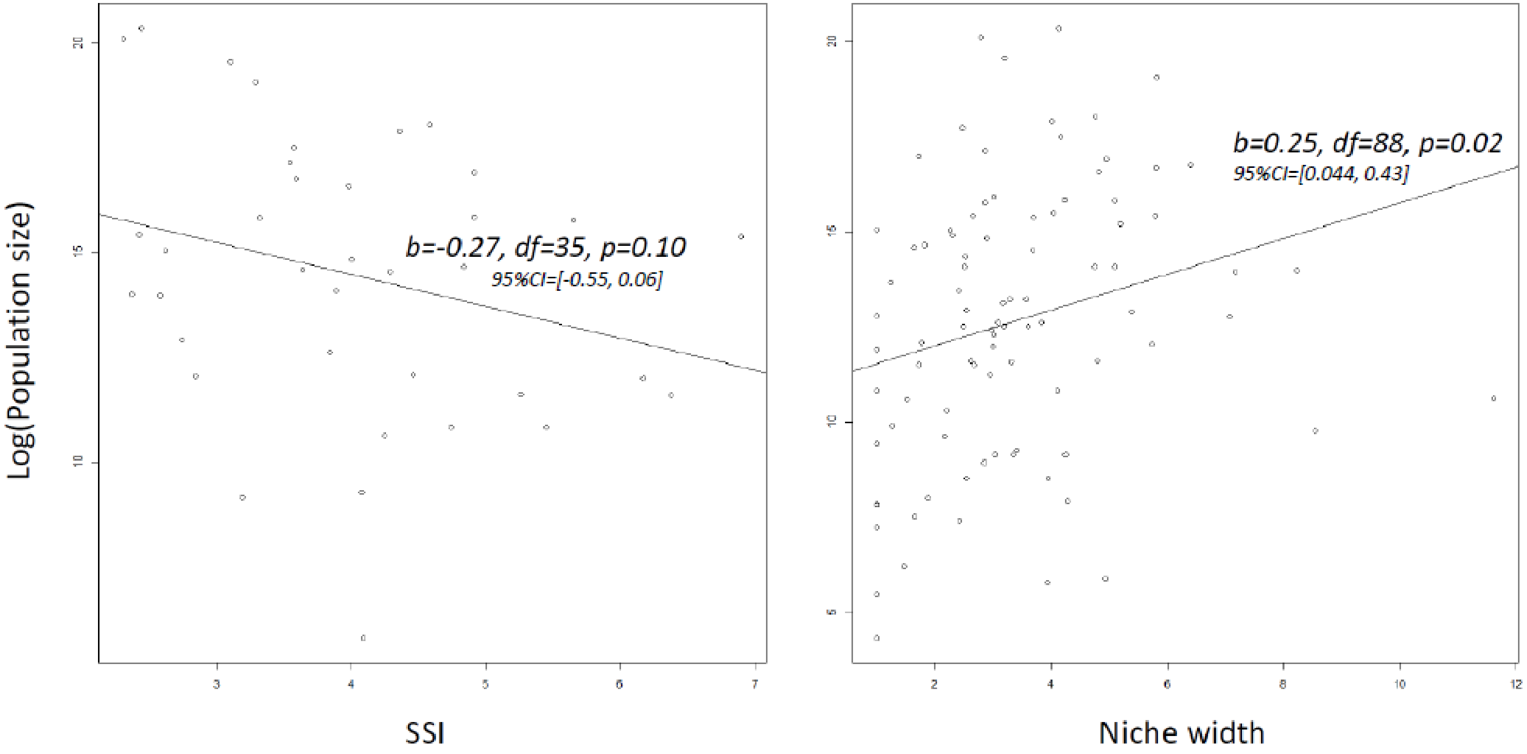


Fig 2 Distribution of coefficient of additive genetic variance (a), heritability (b), and heterozygosity (c) along a habitat niche width gradient. Each ϴ value represents a species.



S1. Pearson's product-moment correlation of both the Species Specialization Index and Niche width with population size



S2. Distribution of specialization indexes, SSI and niche width, for available data.

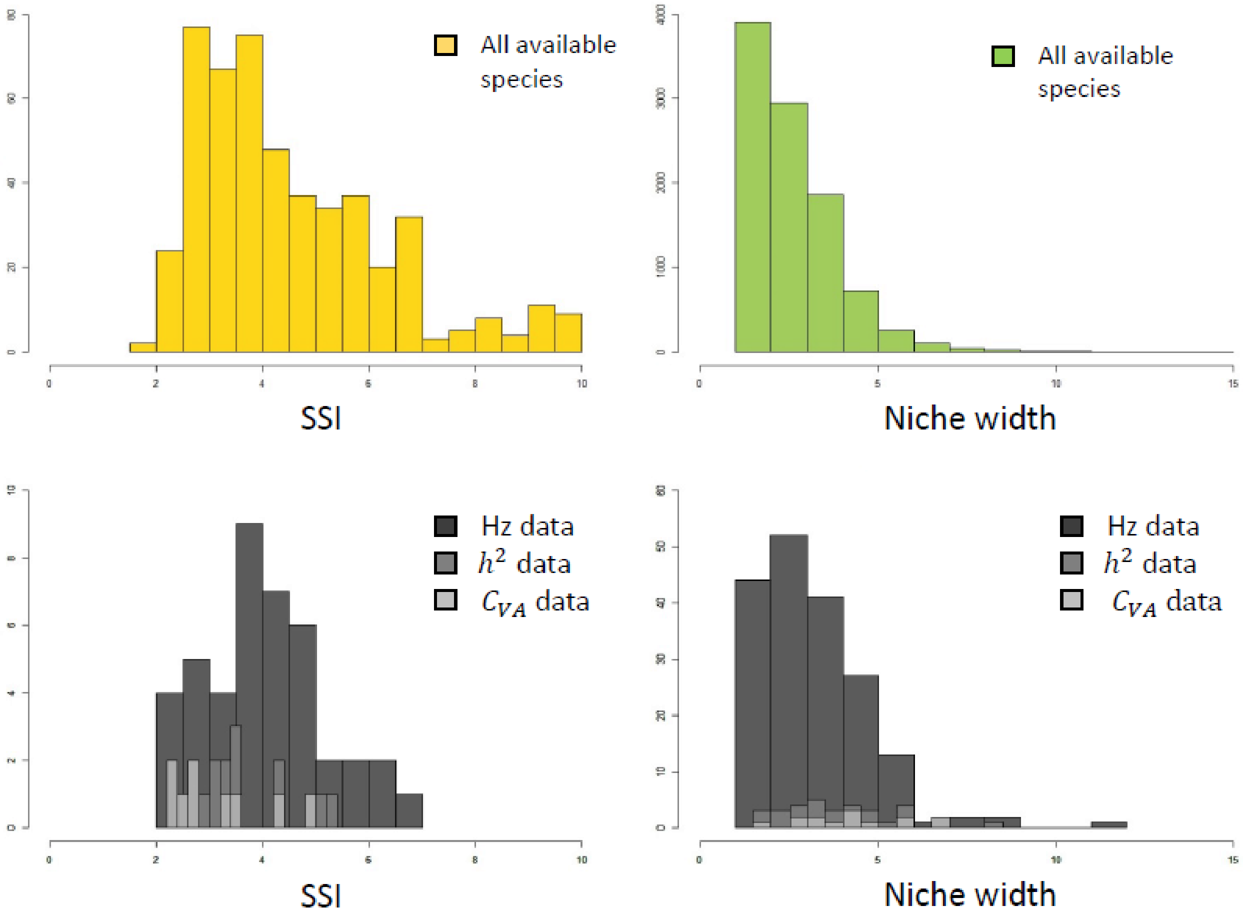


Table S3. List of traits for heritability and coefficient of additive genetic variance data sorted in “life-history” and “morphology” trait categories.

Life-history (h^2)

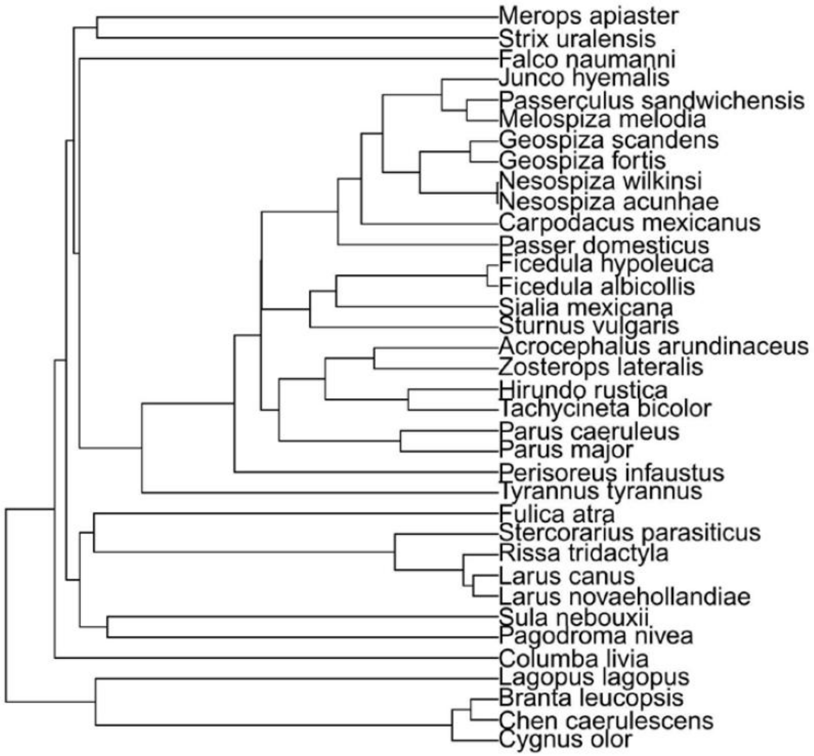
- actual egg weight
- actual egg weight adjusted for annual variation
- adult survival probability
- age at first reproduction
- age at last reproduction
- anual productivity
- arrival date
- breeding time
- calendar hatching date
- clutch size
- clutch size adjusted for annual variation
- delay before breeding
- egg breadth
- egg length
- egg mass
- egg shape
- egg size
- egg volume
- elevation of the laying date-temperature reaction norm
- estimated egg weight
- estimated egg weight adjusted for annual variation
- femal annual fitness
- female annual fitness
- female extra-pair paternity rate
- female first-year fledging success
- female first-year recruits
- female life span
- female lifetime fledging success
- female lifetime reproductive success
- first egg volume
- hatch date
- hatch weight
- laying date
- laying date elevation
- laying date plasticity
- life span
- lifetime fledgling production
- lifetime reproductive success
- lifetime reproductive success
- log10-transformed recruiting age
- longevity
- male annual fitness
- male extra-pair reproductive success
- male first-year fledging success
- male first-year recruits
- male life span
- male lifetime fledging success
- male lifetime reproductive success
- max chroma (egg colour trait)
- max lightness (egg colour trait)
- mean chroma (egg colour trait)
- mean egg size
- mean egg weight
- mean lightness (egg colour trait)
- median egg size
- nr of eggs fledged
- nr of eggs hatched
- number of fledglings
- number of nesting attempts per year
- relative hatching date
- SD chroma (egg colour trait)
- SD lightness (egg colour trait)
- settling date
- sex ratio at 6 days old
- sex ratio at independence
- standardized laying date
- start of wing moult
- time of laying
- total number of eggs laid per year
- total number of young raised to 30 days of age
- total number of young raised to 6 days of age
- .
- .
- .
- .

Morphology (h^2)

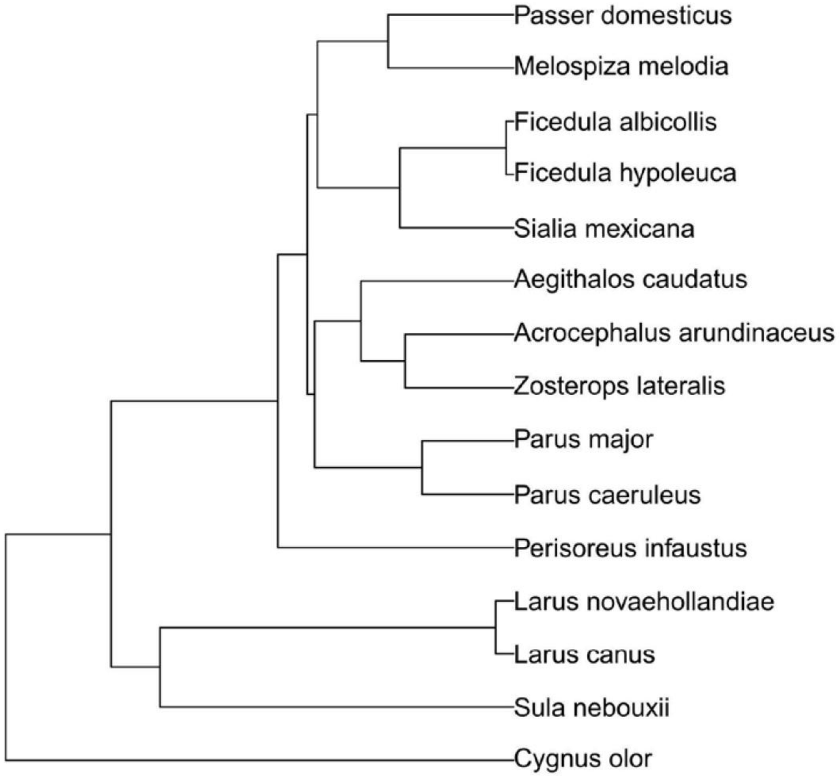
- Backcolour
- badge size
- bill depth
- bill depth (excl. Extra pair youngs)
- bill length
- bill length (excl. Extra pair youngs)
- bill length . fall-spring
- bill length . summer
- bill length at 2 days
- bill width
- bill width (at a depth of 4mm)
- bill width (excl. Extra pair youngs)
- bill width . fall-spring
- bill width . summer
- body condition index
- body mass
- body mass . fall-spring
- body mass . summer
- body mass at day 10
- body mass at day 5
- Brownness scores
- Capcolour
- central tail length
- Chestcolour
- chick condition
- culmen depth
- culmen length
- culmen width
- Drostian colour
- fat breeding season
- fat winter
- feather growth bar width
- female bill depth
- female bill length
- female body condition index
- female body mass
- female nestling mass
- female tarsus length
- female wing length
- first primary length
- flattened wing chord
- forehead patch size
- forehead patch size old
- forehead patch size young
- forhead patch size of a female's mate
- GreenvsRed
- head length
- head size
- head-length good condition
- head-length normal condition
- head-length poor condition
- height of white patch
- male bill depth
- male bill length
- male body condition index
- male body mass
- male nestling mass
- male tarsus length
- male wing length
- mate's forehead patch size
- muscle breeding season
- muscle insertion length left
- muscle insertion length right
- muscle winter
- nestling mass
- nestling tarsus length
- offspring condition
- outer tail length
- patch heigth
- patch width
- PC1-bill
- PC1-bill (excl. Extra pair youngs)
- PC1-body
- PC1-body (excl. Extra pair youngs)
- PC2-bill
- PC2-bill (excl. Extra pair youngs)
- PC2-body
- PC2-body (excl. Extra pair youngs)
- skull length
- tail length
- tail white
- tarsus length
- tarsus length (excl. Extra pair youngs)
- tarsus length . fall-spring
- tarsus length . summer
- tarsus length at day 10
- tarsus length at day 5
- total badge size (black throat badge; sexual ornament)
- UV/bluevsGreen/Red
- UVvsBlue
- visible badge size
- weight
- Weight (excl. Extra pair youngs)
- width of white patch
- Wing
- Wing (excl. Extra pair youngs)
- wing length
- wing patch size old
- wing patch size young
- wing projection

Life-history (C_{Va})		
age at first reproduction	egg laying date standardized spring temperature 1	lifetime reproductive success
age at last reproduction	egg laying date standardized spring temperature -1	lifetime reproductive success
annual fitness	egg mass	log10-transformed recruiting age
annual reproductive success	female fitness	longevity
breeding time	female mate choice	male extra-pair reproductive success
clutch size	first egg volume	male fitness
clutch size standardized spring temperature 0	first-year fledging success	mean egg weight
clutch size standardized spring temperature 1	first-year recruits	nr of eggs fledged
clutch size standardized spring temperature -1	laying date	nr of eggs hatched
clutch size standardized spring temperature NA	life span	nr of seasons bred
egg laying date	lifetime fledging success	.
egg laying date standardized spring temperature 0	lifetime fledgling production	.

Morphology (C_{Va})		
adult body mass	forehead patch size	SD lightness (egg colour trait)
adult tarsus length	head-length good condition	skull length
bill depth	head-length normal condition	tail length
bill length	head-length poor condition	tarsus length
bill width	max chroma (egg colour trait)	total badge size (black throat badge; sexual ornament)
body mass	max lightness (egg colour trait)	visible badge size
culmen depth	mean chroma (egg colour trait)	weight
culmen length	mean lightness (egg colour trait)	wing length
culmen width	nestling mass	wing patch size
feather growth bar width	patch heigth	wing projection
first primary length	patch width	
fledgling mass	SD chroma (egg colour trait)	



S4.a **Phylogenetic tree for heritability data**



S4.b **Phylogenetic tree for coefficient of additive genetic variance data**

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Table S3 Estimators (Post.mean), confidence intervals (CI) and critical probabilities (Pc) for the fixed and random effects of the three mixed models corresponding to each estimator of evolutionary potential: heritability, CVa and Heterozygosity. **For weakly informative priors.**

	Response var.	**Heritability**			**CVa**			**Heterozygosity**		
	Effect	**Post.mean**	**CI 95%**	**pMCMC**	**Post.mean**	**CI 95%**	**Pc**	**Post.mean**	**CI 95%**	**pMCMC**
Fixed	**Intercept**	0.050	-0.210/0.309	0.680	9.21	-1.63/20.1	0.088^{**}	0.657	0.419/0.887	$<10^{-5***}$
	SSI	0.046	-0.023/0.117	0.139	0.740	-2.24/3.82	0.607	-0.003	-0.047/0.041	0.158
	Type of Trait : morphologique	0.198	0.140/0.256	$<10^{-5***}$	-7.77	-11.28/-4.24	2.10^{-5***}			
	Calcul method : regression	0.046	0.005/0.088	0.030^{*}	-1.40	-4.36/1.61	0.355			
Random	**Phylogeny**	0.008	0.001/0.021		13.7	1.01/39.7		0.025	0.000/0.072	
	Population	0.007	0.001/0.014		5.75	1.02/13.53				
	Trait	0.021	0.015/0.027		18.74	8.18/30.12				
	Residual	0.004	0.003/0.006		27.19	19.1/36.2		0.016	0.015/0.031	

Table S4 Estimators (Post.mean), confidence intervals (CI) and critical probabilities (Pc) for the fixed and random effects of the three mixed models corresponding to each estimator of evolutionary potential: heritability, CVa and Heterozygosity. For parameter expanded prior.

	Response var.	**Heritability**			**CVa**			**Heterozygosity**		
	Effect	**Post.mean**	**CI 95%**	**pMCMC**	**Post.mean**	**CI 95%**	**Pc**	**Post.mean**	**CI 95%**	**pMCMC**
Fixed	**Intercept**	0.053	-0.162/0.270	0.579	9.59	-0.194/19.9	0.057.	0.695	0.411/0.980	$<10^{-5}$***
	SSI	0.044	-0.018/0.103	0.136	0.656	--2.05/3.37	0.583	-0.012	-0.078/0.052	0.704
	Type of trait : morphological	0.198	0.142/0.255	$<10^{-5}$***	-7.93	-11.2/-4.49	$<10^{-5}$***			
	Estimation method : regression	0.048	0.007/0.090	0.022*	--1.17	-4.05/1.74	0.426			
Random	**Phylogeny**	0.004	0.000/0.017		14.8	0.000/55.8		0.007	0.000/0.026	
	Population	0.005	0.000/0.013		2.03	0.000/7.81				
	Trait	0.022	0.015/0.028		19.6	9.03/31.6				
	Résidual	0.004	0.002/0.006		26.6	18.8/35.3		0.052	0.030/0.077	

Fig S7. References for heritability data

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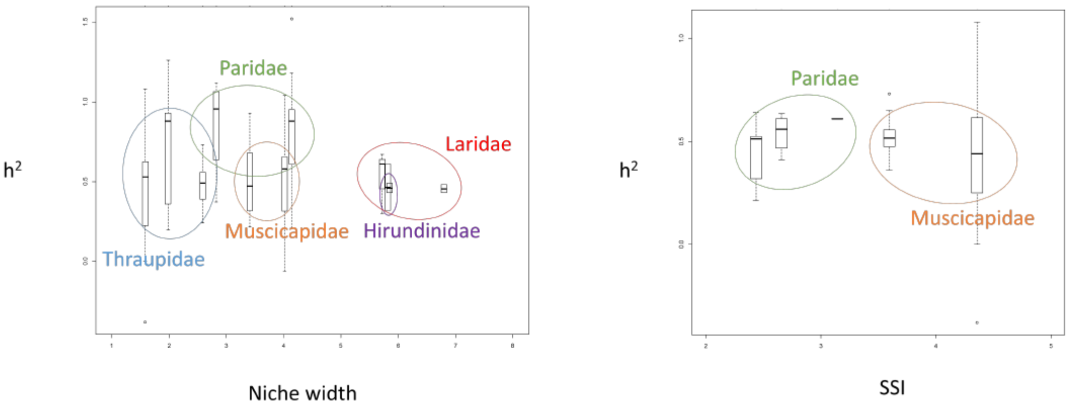
S10. Data visualisation: heritability of body mass and tarsus length as a function of SSI and Niche width

In this figure we present heritability of tarsus length and body mass, the two most represented traits in our dataset, for families that had more than one species represented. Species belonging to the same family are linked by hand-drawn ellipses.

Heritability of Tarsus length



Heritability of Body mass