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Are species' responses to global change predicted by past niche evolution?

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Predicting how and when adaptive evolution might rescue species from global change, and integrating this process into tools of biodiversity forecasting, has now become an urgent task. Here, we explored whether recent population trends of species can be explained by their past rate of niche evolution, which can be inferred from increasingly available phylogenetic and niche data. We examined the assemblage of 409 European bird species for which estimates of demographic trends between 1970 and 2000 are available, along with a species-level phylogeny and data on climatic, habitat and trophic niches. We found that species' proneness to demographic decline is associated with slow evolution of the habitat niche in the past, in addition to certain current-day life-history and ecological traits. A similar result was found at a higher taxonomic level, where families prone to decline have had a history of slower evolution of climatic and habitat niches. Our results support the view that niche conservatism can prevent some species from coping with environmental change. Thus, linking patterns of past niche evolution and contemporary species dynamics for large species samples may provide insights into how niche evolution may rescue certain lineages in the face of global change.

1. Introduction

The increasing evidence for rapid evolution in response to environmental change argues for the potential role of evolutionary processes in altering species' responses to global changes [1,2]. It is now crucial to evaluate when and how evolution must be included in biodiversity modelling and conservation planning [3]. A prerequisite for a species to be rescued from global change via adaptive evolution (i.e. evolutionary rescue) is the retention of enough genetic variation to allow niche shift. Evolutionary rescue of endangered populations might, however, be hampered by slow population growth rates or genetic constraints (covariation among traits), which may cause species niches to be conserved over time [3,4]. A number of theoretical and empirical studies have attempted to better predict the conditions under which populations will be able to adapt to new environmental conditions [5,6], but detailed data on potential adaptive responses are not available for most species. This imposes a serious constraint on the development of biodiversity modelling tools that incorporate evolutionary change. One way to address this problem is to use the increasingly available data on species niches and phylogenetic relationships to infer past rates of niche evolution and identify the subset of species that will benefit most from incorporating evolution into ecological forecasts [7].

Phylogenetic studies of niche evolution have revealed a great deal of heterogeneity in the rate of niche evolution among clades and among different dimensions of species' niches, such as climate, habitat and food requirements [8–10]. Further, phylogenetic inference of past rates of niche evolution can help to identify life-history traits that have triggered or impeded niche

evolution [11,12], and to distinguish between species and lineages that have been prone to niche conservatism versus niche lability [13–15]. Paralleling the prediction that past evolution should affect current-day dynamics of living organisms [16], past niche evolution might be expected to influence species' responses to global change. Species and lineages characterized by a history of fast niche evolution could be more resilient to current-day global changes than the species that have experienced slower niche evolution, and thus might be the best candidates for incorporating evolution into ecological forecasts. Past rates of niche evolution could predict current-day species' abilities to cope with global changes by two non-exclusive scenarios. First, higher rates of past niche evolution would reflect high evolutionary potential within populations, and lineages having experienced relatively rapid niche evolution would thus be able to better adapt to changing environments than others. Second, species emerging from lineages with elevated rates of niche evolution would retain a greater genetic variation at the species level, owing to different populations being adapted to a variety of local conditions. Such species should thus exhibit wider ecological breadth and geographical ranges, hence coping better with environmental changes [17,18]. None of these scenarios, nor the general idea that past niche conservatism could predict species' demographic decline when the environment is changing abruptly, have yet been tested in a phylogenetic context.

Phylogenetic data have increasingly been used in conservation biology over the past decade. Detailed analyses of phylogenetic patterns of species threat have become an important ingredient in efforts to quantify the drivers and consequences of the current-day biodiversity crisis [19,20], though the utility of phylogenetic comparative analyses for conservation planning has been debated [21]. For instance, phylogenies have been used in comparative analyses to determine the biological attributes that predispose species to greater extinction risk [22] or to determine the amount of phylogenetic diversity that is being threatened by global change [23,24]. A recurrent pattern emerging from these studies is that declining or threatened species tend to be phylogenetically clustered, i.e. more closely related than species randomly drawn from the same phylogeny. This pattern is usually interpreted to be a consequence of shared ancestral characters or niche features leading related species to respond similarly to the same threats [25]. This suggests that one fundamental driver of phylogenetic patterns of species' extinction threats is their history of niche lability. But the link between current threat and past rates of niche evolution has remained virtually unexplored so far (for a study linking species threats and speciation rates, see Davies *et al.* [26]).

Here, we explicitly tested whether recent population trends of European birds can be predicted by their past niche lability. We inferred rates of niche evolution based on phylogenies and multivariate niche data [27,28], thus accounting for the multidimensional nature of species' niches as well as correlations between different niche dimensions. Specifically, we analysed demographic trends of 409 European bird species over the 1970–2000 period and related these trends to rates of niche evolution inferred at both the species and the family level. To do so, we used a set of molecular phylogenetic trees recently published for this species assemblage [23], and parametrized species' niches in terms of climatic requirements, habitat use and

trophic characteristics, using data on species' traits and geographical distributions. By examining both species-level and family-level patterns, we attempt to capture the possibility that relationships between evolutionary rates of different niche types and species responses to global changes vary at different phylogenetic scales. Given that life-history and ecological features may also influence population trends in birds, our analysis considered the following covariates: species' thermal tolerance [29–31], migration strategy [32,33], generation length or body mass [30,33–35], absolute breeding population size in Europe [29,36] and specialization for grassland and farmland habitats [29,37].

2. Methods

(a) Species and demographic data

We obtained data on breeding population size and demographic trend for bird species that breed in Europe from BirdLife International [38,39]. Breeding population size was the median estimate of the total number of breeding pairs over Europe. Trend data comprise six and nine categories for the 1970–1990 and 1990–2000 time periods, respectively. After eliminating those species falling into the categories 'unknown' and 'fluctuating', we converted the 1970–1990 and 1990–2000 trend data into binary variables, each consisting of declining versus not declining species. To do so, we grouped together degrees of decline (i.e. moderate and large decline) into a single category contrasted against all other categories, for each time period.

On the basis of the trend data in these two time periods, we constructed a third binary variable intended to capture the possibility of species having been 'rescued' over the course of the two time periods. Rescued species were those that experienced the following sequence of trends in 1970–1990 and 1990–2000: decline–increase, decline–stable or stable–increase. Note that we do not assume at this point that these rescue events were only due to adaptation to changing environment, as the factors causing a species' decline could also be alleviated. For instance, some birds may have been rescued as a result of their protection status, in addition to their niche or life-history characteristics. Thus, we coded a binary variable depicting whether species are listed on Annex I of the European Union's Birds Directive (79/409/EC) and hence subject to special protection measures.

(b) Niche and life-history data

(i) Climatic niches

We defined species' breeding ranges at a resolution of 50 × 50 km on the basis of the EBCC atlas [40], and extracted the data for 19 bioclimatic variables from the WorldClim database [41] at this resolution. Species' climatic niches were estimated using a method of discriminant analysis known as the outlying mean index (OMI, hereafter) analysis [42], which has the advantage of giving equal weight to all sites, and making no assumption about the shape of species' response curves (implemented in the R-package *ade4* [43]). The first two axes captured 82 per cent and 15 per cent of climatic niche variation between species, and represented temperature and precipitation axes, respectively. We extracted the minimum, median and maximum scores on these two climatic axes for each species, to describe their climatic niches.

(ii) Habitat and trophic niches

We compiled habitat and trophic niches as a set of binary variables (as described in electronic supplementary material, table S1), on the basis of the information available in standard bird

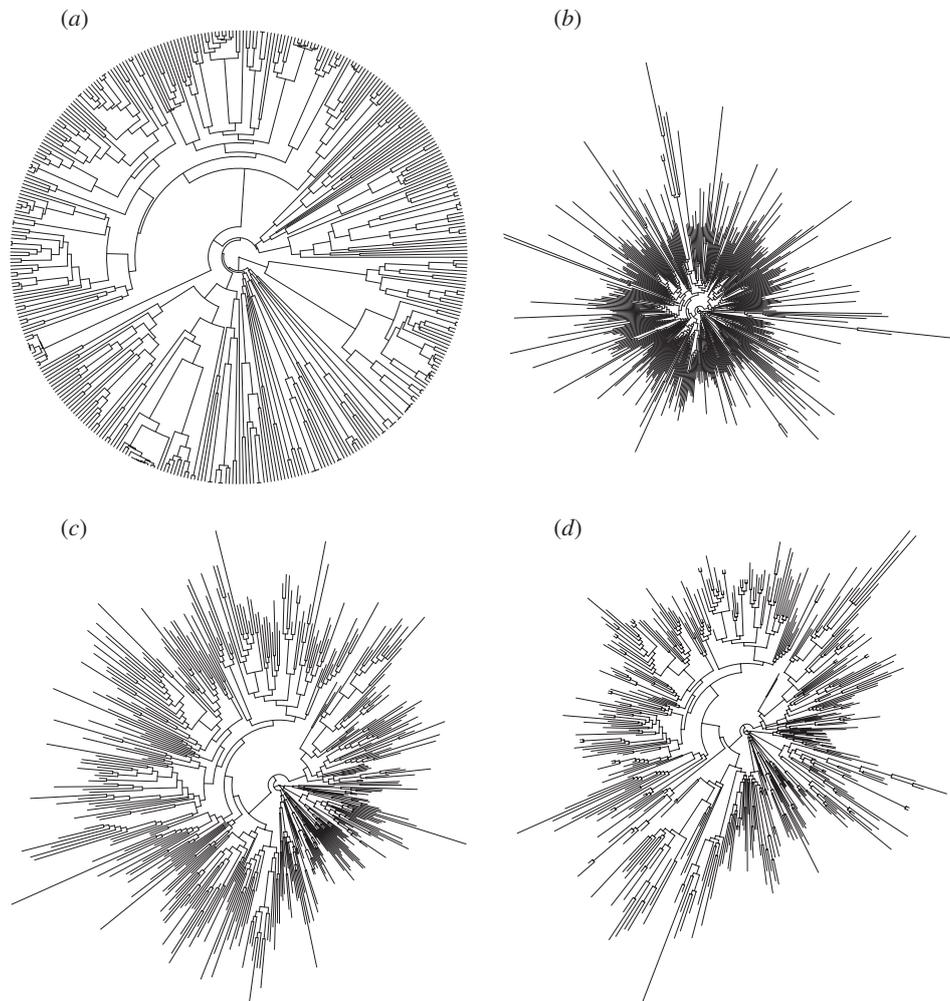


Figure 1. Phylogenetic trees of the 409 European bird species included in this study. (a) These trees are the original fossil-calibrated molecular tree and the trees with branch lengths rescaled to reflect niche evolution (longer branches indicating more rapid evolution). (b) Niches included climatic requirements, (c) habitat use and (d) food habits.

handbooks [44]. For habitat niche, species were scored as breeding in one or several habitats, out of nine possible breeding habitats, and as foraging in one or several habitats, out of 14 possible foraging habitats. For trophic niche, each species was scored as feeding on one or several food sources (nine possible types), as using one or several foraging strategies (out of seven possible) and as foraging during one or several periods of the day (three possible periods). For each species, we also computed two indices of niche breadth, namely habitat breadth (total number of breeding possible habitats) and diet breadth (total number of possible food types).

(iii) Life-history traits

On the basis of BirdLife International's atlas [39] and bird handbooks [40], we compiled data on body mass, generation length and migration strategy (short distance migratory or sedentary species versus long-distance migratory species) for each species. Body mass was estimated as the average body mass for adults of both sexes [44], whereas generation length was estimated as the average age of the parents of current cohorts in natural populations (for more details, see BirdLife International [39]).

(c) Phylogenetic trees

All the earlier-mentioned data were available for an assemblage of 409 birds that breed in Europe. We used a recently published, well resolved, fossil-calibrated molecular phylogeny for this species assemblage (figure 1a; [23]). This phylogeny was inferred

via a mixture of supertree and supermatrix approaches [45], using GenBank sequences for 19 mitochondrial and nuclear gene regions. For each region, we selected the best alignment among those produced by four different algorithms, followed by the removal of ambiguous and poorly aligned regions from the selected alignment. Phylogenetic analyses were conducted using maximum-likelihood (ML) estimation by constraining heuristic searches with a family-level supertree built from previous literature. All details on phylogenetic inference are found in the supplementary material of Thuiller *et al.* [23], including links to access the ML tree in TreeBase. Although this tree is fairly well resolved, there remains uncertainty in some parts of the tree (see nodes' support in the electronic supplementary material, figure S1), so we ran final comparative analyses in parallel on 100 best ML candidate trees. For family-level analyses, we pruned the phylogenetic tree to the family level, yielding a tree that was robust enough to run analyses on a single tree.

(d) Data analyses: niche evolutionary rates

(i) Inference of rates of niche evolution

All data manipulation and statistical analyses were carried out in R v. 2.12.0 [46]. We inferred species-level and family-level rates of niche evolution in multivariate niche space, including climatic niche characteristics (minimum, median and maximum positions on the first two OMI axes), habitat niche characteristics (feeding and breeding habitats) and trophic niche characteristics (food sources, foraging strategies, foraging periods).

To compute species-level rates of niche evolution, we first computed matrices of pairwise niche differences between all study species for each of three types of niches (i.e. climatic, habitat and trophic). For species' climatic requirements, niche differences were measured with a Euclidean distance. For habitat and trophic characteristics, niche differences were quantified using the Gower distance [47], which provides a unified metric of distances between entities from all types of variables—quantitative, nominal or binary. On the basis of these matrices of pairwise niche differences, we estimated species' rates of niche evolution following an approach that recently gained renewed interest [27]. This approach consists of using matrices of pairwise niche differentiation to rescale the branch lengths of the ultrametric molecular phylogenetic tree, while keeping its topology unchanged, so that branch lengths reflect niche evolution (for previous examples in the literature, see [48,49]). This yields a non-ultrametric tree where the root-to-tip distance of each species reflects its accumulated niche differentiation relative to other species (figure 1*b–d*). As all species had the same time to evolve from their common ancestor, any difference of root-to-tip distance between extant species represents a difference in the relative rate of niche evolution. We computed the 'niche-rescaled' phylogenetic tree using non-negative least-square optimization, implemented in the R-package phangorn [50], and computed root-to-tip distance of each species using the R-package adephylo [51]. This yielded species-level rates of evolution for multivariate climatic, habitat and trophic niches (figure 1*b–d*). Our approach for computing species-level rates of niche evolution could potentially be biased by a node density artefact. That is, species with more nodes separating them from the root of the phylogeny could tend to get higher estimates of niche evolutionary rates. To assess this bias, we computed node density below each species and tested whether species rates of niche evolution were significantly related to node density. When this was the case, node density was included as an additional covariate in models of species demographic trends versus rates of niche evolution (see §2e(ii)).

To estimate family-level rates of niche evolution, we estimated multi-trait variance–covariance matrices (vcv, hereafter) in a phylogenetic framework, i.e. so-called macroevolutionary vcv matrices [28]. To do so, we used a recently developed ML method for fitting multiple evolutionary vcv matrices to different branches of a phylogenetic tree, following a multivariate Brownian motion model of trait evolution [28]. Using the implementation available in the R-package phytools [52], we fit a model with 23 different evolutionary vcv matrices: 22 matrices corresponding to bird families with five or more species in the study region, and one corresponding to a 'background' vcv matrix for all other branches in the phylogenetic tree. Computing the trace (sum of the diagonal elements) of each vcv matrix provided an estimate of the family-level rate of niche evolution (see [14]), for each niche type (climatic, habitat, trophic), taking into account the multidimensional nature of niches.

(ii) Patterns of rates of niche evolution

We first explored the extent of variation in rates of niche evolution at the species and family level. In particular, we tested whether rates of niche evolution were related to species' life-history characteristics (body mass, generation length, migration strategy), ecological amplitude (habitat breadth, diet breadth) and European breeding population size. We also tested whether rates of evolution estimated at the family level were related to family-level features, such as species richness in Europe and relative evolutionary age. Here, the purpose was to explore whether rates of niche evolution were related to particular evolutionary contexts in terms of lineage age or diversity, or to life-history traits that influence population dynamics or dispersal capacity, and thus possibly evolutionary

rates. The results of these analyses also allowed us to diagnose potential collinearity effects between predictors of species' trends, especially life-history and ecological covariates versus evolutionary rates. It also allowed us to explain potential demographic effects of past evolutionary rates through indirect relationships with species or family characteristics.

These relationships were tested using phylogenetic generalized least-square models (PGLS hereafter; [53]), as implemented in the R-package caper (available at <http://cran.r-project.org/web/packages/caper/index.html>), because rates of evolution inherently exhibit phylogenetic structure. PGLS models allow one to model a dependent variable while controlling for the estimated degree of phylogenetic signal, as measured by Pagel's λ [54]. As multiple tests were thus performed in parallel, we controlled our results for type I error by implementing a false discovery rate control [55]. We also examined correlations between rates of evolution of the three different niche types (climatic, trophic, habitat), using Spearman rank correlations [56] to check potential collinearity effects between the three types of rates.

(e) Data analyses: demographic trends

In a second step, we analysed the phylogenetic patterns of demographic trends at the species and family level, and tested whether trend patterns were related to past rates of niche evolution.

(i) Phylogenetic patterns of demographic trends

We explored the phylogenetic pattern of declining species during both 1970–1990 and 1990–2000, and rescued species over the course of the two time periods. At the species level, the phylogenetic clustering of species with equivalent demographic trends was tested using two different metrics, each tailored for discrete data. The first test is based on the retention index, which was originally developed by Farris [57]. This index has been shown to accurately quantify the degree of non-convergence of discrete traits [58], and is now commonly used in comparative analyses of species' niche characteristics [59]. The second test was based on the recently developed D statistic [60], which aims at measuring phylogenetic clustering of binary data (typically extinction threat), and varies from zero (phylogenetic signal expected under neutral evolution) to unity (no phylogenetic signal, as expected for a trait distributed randomly with respect to the phylogeny). We applied both tests because they may be differently affected by data structure (number and dispersion of alternative trait states) and phylogenetic tree structure (tree imbalance, polytomies). The retention index and the D statistic were computed using the R-packages phangorn [50] and caper, respectively, and their significance was tested by drawing 9999 randomizations from the data.

We also computed the proportion of declining species (1970–1990, 1990–2000) and rescued species for each family. We used Pagel's λ parameter [54] to measure phylogenetic signal of family-level proportions of declining and rescued species, after normalizing the data with an arcsine square root transformation. Pagel's λ has recently been shown to provide a robust estimate of phylogenetic signal, even in situations of imperfect phylogenetic resolution [61]. The significance of each λ statistic was evaluated with a likelihood ratio test, as implemented in the R-package geiger [62]. For each family, we also performed exact Fisher tests on 2×2 contingency tables [56] to assess which families have more or fewer declining species compared with random expectation.

(ii) Demographic trends versus rates of niche evolution

We tested how species' current population trends are related to past rates of niche evolution. At the species level, we sought to include in our analyses several intrinsic characteristics and extrinsic factors that have been shown to be associated with

demographic decline or rescue in birds. On the basis of previous literature (see §1), we first considered the following covariates: lower thermal tolerance (as captured by the minimum position of each species on the first OMI axis), grassland–farmland specialization, body mass, generation length, migration strategy, European breeding population size and European Union protection status. At this first stage, species' demographic trends were modelled as a binomial process in a generalized linear model [63] with all of these covariates. Because of their collinearity with other covariates or their lack of explanatory power, two covariates were discarded from further analyses: body mass and breeding population size.

We then ran generalized linear-mixed effect models to test whether rates of niche evolution explained variation in species' demographic trends after controlling for the set of covariates selected above. Because rates of climatic, habitat and trophic niche evolution were correlated with one another, we added each of the rates of niche evolution separately to a model containing the minimum set of covariates. These models were implemented in the R-package MCMCglmm [64], treating species' trends as a binomial response, with a correlation structure accounting for phylogenetic relationships (under the 'animal' model). The Markov chain Monte Carlo (MCMC) simulations of model parameters were run for 2×10^4 iterations, eliminating the first 5×10^3 samples as burn-in, and thinning to every 500th sample. We integrated phylogenetic uncertainty into the analysis of each dependent variable by running parallel MCMC simulations on the 100 best ML phylogenetic trees, and combining samples from these 100 chains into one large sample of the joint posterior distribution of model parameters. Posterior distributions of fixed effects were examined for overlap with zero, using the 95 per cent highest posterior density as the confidence interval.

At the family level, proportions of declining and rescued species were modelled as binomial responses, with family-level rates of niche evolution as explanatory variables. The analyses were conducted using generalized linear models fitted by maximum likelihood (GLM; [63]) without phylogenetic structure because family-level trends showed no significant phylogenetic signal (see §3). Residuals were inspected to check for phylogenetic autocorrelation.

3. Results

(a) Rates of evolution of niches

We found significant but weak correlations between the rate of evolution of climatic and habitat niches ($\rho = -0.16$, $p < 0.001$), climatic and trophic niches ($\rho = -0.14$, $p < 0.01$) and habitat and trophic niches ($\rho = 0.30$, $p < 0.001$). Inter-specific variation in niche evolutionary rates was partly explained by certain life-history and ecological characteristics, although not all correlations remain significant after accounting for false discovery rate (table 1). The rate of trophic niche evolution was related to body mass, with large-bodied species tending to have experienced a higher rate of trophic niche evolution (table 1). Rates of habitat and trophic niche evolution were each positively related to both diet and habitat breadth (table 1). Finally, breeding population size was negatively correlated with the rate of climatic niche evolution, and positively related to the rate of habitat niche evolution (table 1).

Node density did not bias estimates of the rates of evolution of the climatic niche (PGLS, $F_{1,409} = 0.27$, $p = 0.601$) or habitat niche (PGLS, $F_{1,409} = 2.94$, $p = 0.087$). Estimates of the rate of evolution of food niches, however, were higher for those species with more nodes separating them

Table 1. Results of phylogenetic regressions testing the relationship between species-level rates of niche evolution (climatic, habitat, trophic) and life-history and ecological features, namely body mass, generation length, migration strategy, habitat specialization, diet specialization and median breeding population size in Europe. All models were fitted by maximum likelihood, and correcting for the appropriate degree of phylogenetic signal as estimated by Pagel's lambda (λ). For each predictor, the effect estimate (E), its standard error (s.e.), the Fisher test statistic (F) and its associated p -value for one degree of freedom (p) are given. All predictors were quantitative variables except migration strategy, which was categorical, with the states 'short migratory' in contrast to 'long migratory'. p -values under the 0.05 threshold are indicated in bold, and the ones remaining significant after accounting for false discovery rate are marked with $\$$.

Predictors	rates of climatic niche evolution			rates of habitat niche evolution			rates of trophic niche evolution		
	λ	$E_{(s.e.)}$	F	F	p	F	p	F	p
body mass		0.01 _(0.03)	0.14	0.709	0.709	5.08	0.025	9.86	0.002 $\$$
generation length		-0.01 _(0.09)	0.01	0.933	0.681	0.17	0.681	2.09	0.149
migration strategy		0.07 _(0.07)	1.13	0.286	0.106	2.63	0.106	4.66	0.031
habitat breadth		-0.12 _(0.05)	4.71	0.031	<0.001 $\$$	57.6	<0.001 $\$$	7.47	0.007 $\$$
diet breadth		-0.02 _(0.06)	0.07	0.785	0.004 $\$$	8.05	0.004 $\$$	62.1	<0.001 $\$$
breeding population		-0.18 _(0.02)	80.2	<0.001 $\$$	<0.001 $\$$	22.1	<0.001 $\$$	1.31	0.192

Table 2. Tests of phylogenetic signal in species-level demographic trends. Results are presented for both the retention index and the *D*-statistic. For both tests, the *p*-value (*p*) indicates the estimated probability that demographic trends show no phylogenetic clustering on the species-level phylogeny, based on 9999 randomizations. For the retention index, both the observed value (RI_{obs}) and the mean randomized value (RI_{rand}) are given, with a greater RI value indicating a stronger phylogenetic signal. The *D*-statistic integrates the comparison with randomized values, with values below unity indicating stronger phylogenetic signal than expected for a trait distributed randomly with respect to the phylogeny.

variables	retention index			<i>D</i> -statistic	
	RI_{obs}	RI_{rand}	<i>p</i>	<i>D</i>	<i>p</i>
declining species 1970–1990	0.105	0.048	<0.001	0.64	<0.001
declining species 1990–2000	0.130	0.100	0.043	0.88	0.022
rescued species	0.176	0.145	0.063	0.91	0.060

from the root of the phylogeny (PGLS, $F_{1,409} = 5.83$, $p = 0.016$). For this reason, we included node density as a covariate in models of species demographic trends as a function of trophic niche evolutionary rates (see §3b).

We found substantial variation among families in rates of niche evolution (see the electronic supplementary material, table S2). Some families, namely the Charadriidae, Laridae, Falconidae and Ardeidae, had high rates of evolution for the three types of niches. The Picidae and Alaudidae, by contrast, had low rates of niche evolution for all three types of niches. In general, family-level rates of niche evolution were quite strongly correlated between different types of niches (Spearman rank correlations: climatic versus habitat, $\rho = 0.83$ $p < 0.001$; climatic versus trophic, $\rho = 0.75$ $p < 0.001$; habitat versus trophic, $\rho = 0.81$ $p < 0.001$). Family-level rates of niche evolution did not show any significant relationship with relative family age or species richness across Europe (PGLS models, *p*-values ranging from 0.587 to 0.893). We observed a tendency for older families to have more species in Europe, but this relationship was not significant at the 0.05 level (PGLS, $F_{1,19} = 3.811$, $p = 0.066$).

(b) Patterns of declining and rescued species

We found significant phylogenetic clustering of declining species during both 1970–1990 and 1990–2000 (table 2), although estimated phylogenetic signal was lower for the second time period. Species showing rescued dynamics across the two time periods also tended to be phylogenetically clustered, although this trend was only marginally significant (table 2). At the family level, however, the proportion of declining species during the 1970–1990 and 1990–2000 periods and the proportion of rescued species did not show significant phylogenetic signal (Pagel's λ tests, *p*-values equal to 0.874, 0.791 and 0.650, respectively).

As expected, life-history and ecological covariates were significant predictors of some of the variance in species' demographic trends (posterior distributions of fixed effects not overlapping zero; figure 2 and electronic supplementary material, table S3). Concerning declining species, the sign of the effects of covariates was consistent between the two time periods, suggesting that each covariate had a similar effect on the probability of decline during the two monitoring periods (figure 2). However, these effects were not always significant in both time periods (see the electronic supplementary material, table S3). Only short-migration/sedentary strategy had a consistently negative effect on the probability of decline, indicating that long-distance migratory

species had an elevated risk of decline (figure 2). Lower thermal tolerance and generation length also had a negative effect on the probability of decline, but this effect was significant only during 1990–2000 for thermal tolerance and during 1970–1990 for generation length (figure 2 and electronic supplementary material, table S3). Grassland specialists were prone to decline in the period 1990–2000 (figure 2 and electronic supplementary material, table S3). Finally, species falling under EU protection status had a greater chance of decline during the 1970–1990 period, but were also more likely to be rescued between the two time periods (figure 2 and electronic supplementary material, table S3). After accounting for these effects, there were few significant effects of rates of niche evolution on species' trends. The past rate of habitat niche evolution had a consistent negative effect on the probability of species decline during 1970–1990 and 1990–2000 (see figure 2 and electronic supplementary material, table S3).

Declining species were not randomly distributed among bird families. Some families had a significantly higher proportion of declining species during 1970–1990 and/or 1990–2000 (table 3). A few families had a significantly lower proportion of declining species in either one or both of the time periods, namely the Fringillidae, Strigidae, Sylviidae and Turdidae (table 3), which also tended to have high rates of niche evolution (see the electronic supplementary material, table S1). Some families showed a very high proportion of declining species during at least one of the two time periods (table 3); these were the Alaudidae, Lariidae, Phasianidae and the Sturnidae. Family-level rates of niche evolution were negatively related to the proportion of declining species during 1970–1990 and 1990–2000; this relationship was significant for climatic and habitat niches in the first time period (table 4 and figure 3). We found no relationship between the proportion of rescued species per family (1970–2000) and estimates of niche evolutionary rate (table 4). Neither the proportion of declining species per family during the 1970–1990 and the 1990–2000 periods, nor the proportion of rescued species across the two time periods was related to estimated ages and species richness of study families (Spearman rank correlations: $\rho = [-0.13-0.16]$, $p = [0.48-0.83]$).

4. Discussion

How past evolution predicts the current-day dynamics of species facing global change has been virtually unexplored. Here, we examined whether past rates of niche evolution in terms of climatic, habitat and food requirements can explain

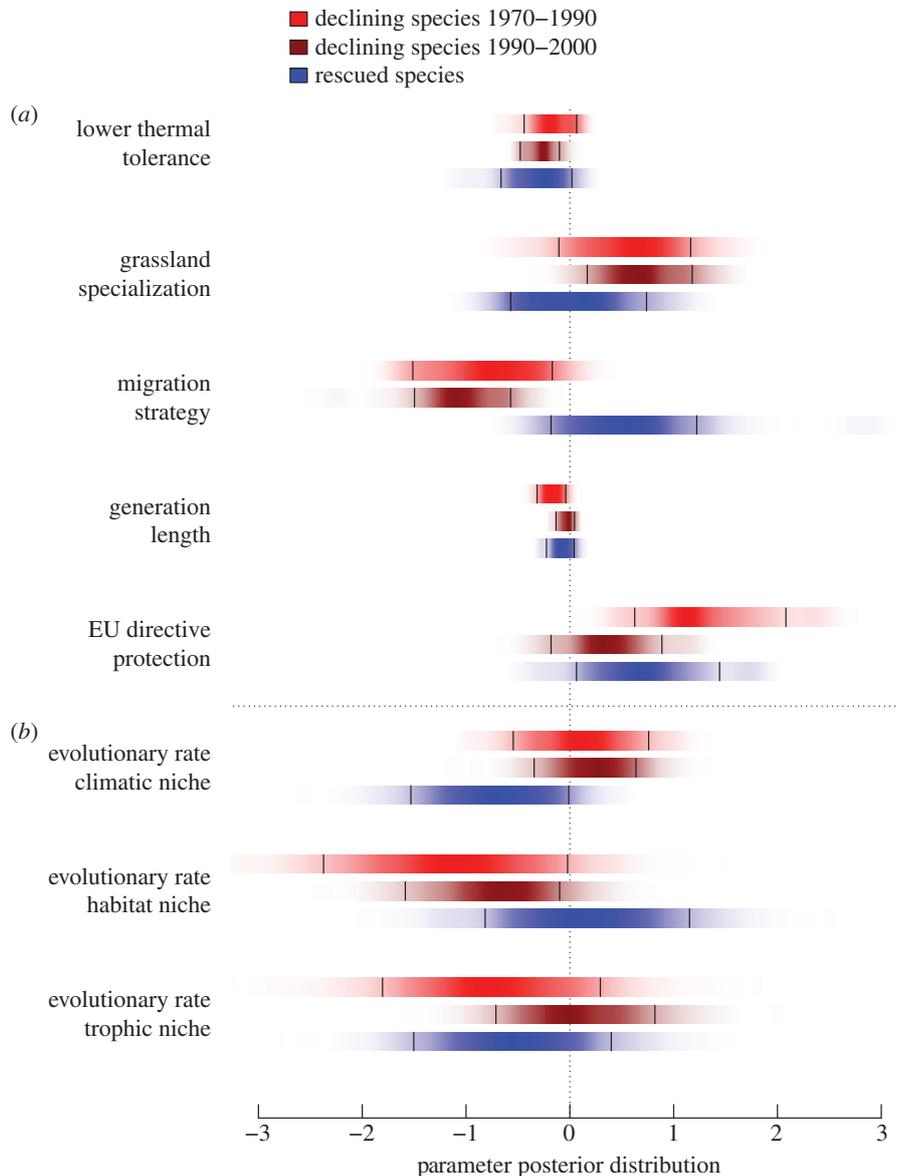


Figure 2. (a) Influence of species-level life-history traits and ecological characteristics, and (b) species' niche evolutionary rates on the probability of decline during 1970–1990 (red strips) and 1990–2000 (dark red strips), and the probability of species being rescued between the two time periods (blue strips). Each strip depicts the posterior density of each estimated effect on the probability of species declining or being rescued. Black ticks indicate the limits of the 95% highest posterior density of each effect.

species' current-day demographic trends within the European bird assemblage. The primary and original finding of our study was that species and families that have experienced slower niche evolution are more prone to demographic decline than those that have experienced higher rates of niche evolution. At the species level, only rates of habitat niche evolution, i.e. foraging and breeding habitats, had a consistent negative effect on the probability of decline during 1970–1990 and 1990–2000. Interestingly, this effect persists after accounting for life-history and ecological covariates known to directly affect contemporary species trends. This pattern is repeated at a higher taxonomic level as well: bird families that are less prone to decline have experienced faster niche diversification, not only in terms of habitat use but also in terms of climate requirements. Overall, these results suggest that lower rates of past niche evolution, in terms of breeding and foraging habitats, predispose bird species to demographic decline in Europe. Thus, our results suggest that niche conservatism may lead species or clades to be less resilient to current environmental changes.

That past rates of niche evolution constrain evolutionary potential of current-day populations remains, however, to be demonstrated and certainly cannot be extrapolated from our study. Although there are many theoretical arguments positing that increased historical niche lability may ameliorate a species' potential for evolutionary rescue in the face of global change [16], further work is needed to estimate species' evolvability for adaptive traits in natural populations and relate it to past rates of phenotypic evolution inferred from phylogenetic comparative analyses for the same traits. Without positing a possible link between long-term and short-term evolutionary potential, a suite of correlated factors may explain this influence of evolutionary past on current species demographic trends. We found that species that had higher rates of habitat and trophic niche evolution tend to have wider current-day ecological amplitude, and hence larger breeding population or geographical ranges. That is, increased past rates of niche evolution, and greater exploration of niche space, have contributed to contemporary species' ecological and geographical success. Recently, a

Table 3. Distribution of declining species during 1970–1990 and 1990–2000 among different bird families, and results of contingency analyses of those data. Only families that were under- or over-represented amongst trends classes are presented, with a significance threshold of $p < 0.1$. Tests are Fisher exact tests for 2×2 contingency tables, with each family tested against all other families. The results for rescued species are not shown because they yielded exactly inverse results compared with declining species. Total species number per family is given (N), along with the number of declining species (n) during 1970–1990 and 1990–2000 time periods, and the p -value from Fisher exact test.

	total species number	declining species 1970–1990		declining species 1990–2000	
	N	n	p	n	p
under-represented families					
Fringillidae	18	0	0.005	1	0.005
Strigidae	12		n.s.	1	0.063
Sylviidae	40	4	0.008	9	0.082
Turdidae	26		n.s.	5	0.090
over-represented families					
Alaudidae	9	8	<0.001		n.s.
Anatidae	34		n.s.	17	0.091
Charadriidae	9		n.s.	6	0.075
Gaviidae	2	2	0.077		n.s.
Laniidae	5	5	0.002	5	0.006
Otididae	2	2	0.077		n.s.
Phasianidae	10	7	0.006		n.s.
Podicipedidae	5		n.s.	4	0.057
Pteroclididae	2	2	0.077		n.s.
Sternidae	9	6	0.016		n.s.
Threskiornithidae	2	2	0.077		n.s.

Table 4. Relationship between family-level rates of climatic, habitat and trophic niche evolution and family-level proportions of declining or rescued species. These relationships were tested using GLMs with a binomial response, with the effects of predictors tested using a likelihood ratio test with one degree of freedom. For each effect, the table gives the effect estimate (E), along with its standard error (s.e.), likelihood-ratio statistic (LR) and associated p -value (p). p -values under the 0.05 threshold are indicated in bold.

	proportion of declining species 1970–1990			proportion of declining species 1990–2000			proportion of rescued species		
	$E_{(s.e.)}$	LR	p	$E_{(s.e.)}$	LR	p	$E_{(s.e.)}$	LR	p
predictors: evolutionary rates									
climatic niches	– 0.26 _(0.09)	9.41	0.002	– 0.01 _(0.08)	0.02	0.878	– 0.02 _(0.07)	0.10	0.749
habitat niches	– 0.23 _(0.10)	6.15	0.013	– 0.10 _(0.09)	1.43	0.232	0.03 _(0.08)	0.12	0.731
trophic niches	– 0.11 _(0.09)	1.61	0.203	– 0.02 _(0.08)	0.04	0.838	– 0.07 _(0.07)	0.88	0.349

meta-analysis of genetic variation at micro-satellite loci from 194 bird species (not only European) showed that species with larger geographical ranges and reduced extinction risk retained greater genetic diversity than narrowly distributed and threatened species [65]. This suggests that species with higher rates of evolution in the past have larger current geographical ranges with genetically variable populations spread along larger environmental gradients. This might allow such species to better cope with environmental change because they may have a greater chance of having populations that are pre-adapted to shifting environmental conditions.

We estimated rates of niche evolution at two different evolutionary scales, i.e. both at the species and at the family levels.

This highlighted interesting patterns of evolutionary rates in the three fundamental niche realms of European birds, namely climatic requirements, habitat use and trophic position. When estimated at the family level, rates of niche evolution show that increased niche evolution has occurred in concert for the three types of niches, suggesting that bird lineages have tended to diversify ecologically along all niche dimensions at the same time. Estimates of rates of niche evolution obtained at the species level, however, paint a different picture. Rates of evolution in habitat and trophic niches were positively correlated, suggesting that ecological differentiation of bird species has generally occurred in terms of habitat use and trophic position. Conversely, rates of climatic niche

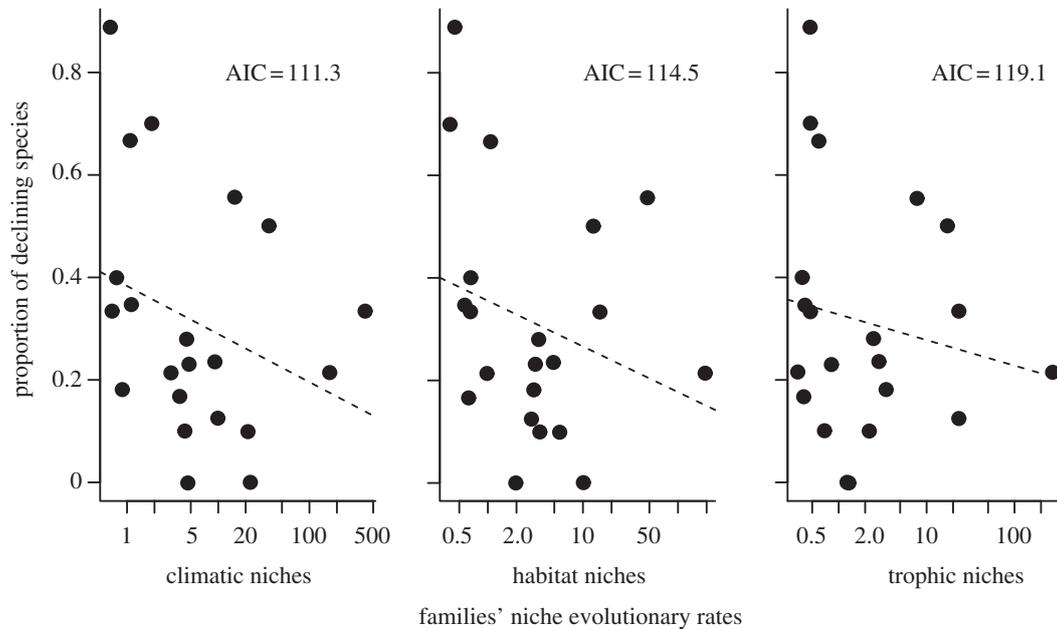


Figure 3. Relationships between the family-level proportion of declining species during 1970–1990 and estimated rates of niche evolution for climatic, habitat and trophic requirements. Akaike's information criterion is given for each relationship, each of which was estimated using a separate logistic regression.

evolution were usually negatively correlated with rates of habitat and trophic niche evolution, suggesting that differentiation in ecological space (e.g. habitat use, trophic habits) and climatic space (e.g. temperature and precipitation preferences) have been decoupled. That is, accelerated divergence for climatic requirements, for instance due to a geographical barrier causing allopatric speciation, tends to be associated with niche conservatism between daughter species in terms of habitat use or food habits.

Our results also identify life-history correlates of slow versus rapid niche evolution. This had thus far only been tested in plants and mammals, in two studies that found larger body mass (or individual biomass) to be associated with a decrease in the rate of climatic niche evolution [11,12]. Here, we did not find any life-history trait related to rates of climatic niche evolution, but we did find body mass to be correlated with the rate of trophic niche evolution. Interestingly, larger body mass correlates with higher rates of niche evolution in terms of the trophic niche. This suggests that larger body mass is associated with increased niche lability and ecological differentiation for food type, foraging strategy and foraging period. Although not all the results remained significant after accounting for false discovery rate, these patterns suggest that the evolution of the so-called Grinnellian and Eltonian realms of species' niches [66] may have followed different evolutionary dynamics, and been differently influenced by life-history traits. An interesting follow-up would be to contrast rates of Grinnellian and Eltonian niche evolution, using more densely sampled phylogenies and in other groups of animals.

Although it was not the primary aim of our study, we reported interesting results with respect to threats in the European bird assemblage. Some bird families were disproportionately prone to decline in 1970–1990 and/or 1990–2000, which contributed to significant clustering of threatened species on the phylogeny. The families that contributed the most to this clustering included seabirds and grassland–farmland species. In addition, certain life-history and ecological features significantly explained patterns of

decline or rescue at the species level. A primary finding was that long-distance migratory species suffer from sustained severe demographic decline over the entire study period (1970–2000), which is consistent with previous findings [32]. During 1970–1990, species with longer generation length were less prone to decline, probably because populations of long-lived species are better buffered against environmental changes or stochasticity (because of higher survival rates). During 1990–2000, species prone to demographic decline were grassland–farmland specialists and species with a lower minimum temperature limit (i.e. species less tolerant to warm climates). This latter result is consistent with the observed trend of accelerated climate warming following the 1980s, which has likely caused a sharper decline of species adapted to colder climates during the second time period, as previously documented [67]. Finally, an interesting result was that species falling under the EU directive protection status were more likely to be rescued during 1970–2000, that is, their demographic trend improved between the two time periods. This confirms, via a different modelling approach, a previous report of this pattern [68]. More broadly, this result suggests that the main driver of demographic rescue in European birds has been the lifting of current threats by protection status, and not ecological or evolutionary characteristics of these species.

Although we believe the analyses presented here are quite robust, our study is limited to a single continent, owing to the limited availability of demographic data. To the best of our knowledge, comprehensive estimates of demographic trends for such a large sample of bird species are available only for regions or continents such as Europe or North America. Nonetheless, our results are unlikely to be biased owing to this geographical scope. The matrices of pairwise niche differences that were used to estimate rates of niche evolution at the species level remain unchanged by any addition or removal of species. Thus, absolute estimates of niche evolutionary rates, as well as relative species rankings based on these estimates, are unaffected by species sampling. At the family level, poorly sampled families were

present both among the ones having the highest and the lowest estimates of niche evolutionary rates; so our region-based species sampling should have little influence on the family-level patterns highlighted here. However, our species assemblage may not reflect other regions such as the Tropics where the mechanisms of species diversification may have been radically different. Hence, it is possible that in other regions of the world or among other organisms, current-day species dynamics may be predicted by past niche evolution in a different way compared with what we report here. We hope that our study will pave the way for others to infer past rates of niche evolution, on the basis of phylogenies of tropical species assemblages or entire species clades at the global scale, and we compare niche rates to recent species' demographic trends.

Our results thus support the view that niche conservatism may serve as one among other predictors of species' vulnerability to global change. We suggest that more studies and tests are necessary to firmly assess whether knowledge on past evolution of niches will be useful for conservation actions. Linking past patterns of niche evolution to contemporary species dynamics for large species samples may thus constitute an interesting approach to understand whether and how niche evolution may rescue certain lineages in the face of global change. Comparing the potential of species to shift spatially in order to track the conserved niche versus evolve within the global niche space in order to remain in their historical distribution should provide further insights on the

potential for evolutionary rescue of populations facing global change. Future research should now try to relate past rates of niche or trait evolution with contemporary response to selection in order to establish potential links between micro- and macroevolutionary rates of phenotypic change.

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The data discussed in this article can be accessed from the Dryad repository at [doi:10.5061/dryad.rk775](https://doi.org/10.5061/dryad.rk775) [69].

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