

Consequences of climate change on the tree of life in Europe

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Many species are projected to become vulnerable to twenty-first-century climate changes^{1,2}, with consequent effects on the tree of life. If losses were not randomly distributed across the tree of life, climate change could lead to a disproportionate loss of evolutionary history^{3–5}. Here we estimate the consequences of climate change on the phylogenetic diversities of plant, bird and mammal assemblages across Europe. Using a consensus across ensembles of forecasts for 2020, 2050 and 2080 and high-resolution phylogenetic trees, we show that species vulnerability to climate change clusters weakly across phylogenies. Such phylogenetic signal in species vulnerabilities does not lead to higher loss of evolutionary history than expected with a model of random extinctions. This is because vulnerable species have neither fewer nor closer relatives than the remaining clades. Reductions in phylogenetic diversity will be greater in southern Europe, and gains are expected in regions of high latitude or altitude. However, losses will not be offset by gains and the tree of life faces a trend towards homogenization across the continent.

Evidence is accumulating that ongoing climate changes already affect living organisms⁶. Although species have been continuously exposed to climate changes throughout their evolutionary histories⁷, there is concern that the pace of current changes poses unprecedented challenges for many species⁸. Evidence exists that certain clades are more vulnerable to anthropogenic pressures than others⁹, causing portions of Earth's evolutionary history to be disproportionately altered. Here we investigate whether climate change could have a similar effect.

Climatic tolerances vary across species, causing some species to be more vulnerable to climate change than others¹⁰. Because climate tolerances are not randomly distributed across phylogenies¹¹, species sensitivities to climate change are expected to be clustered along the phylogeny. It follows that if vulnerable species are closely related, shared internal branches of the tree of life have higher risks of collapsing¹² (Supplementary Fig. 1). In contrast, overdispersed extinctions in the phylogeny would mitigate the loss of internal edges⁹. However, phylogenetically clumped extinctions should cause disproportionate loss of phylogenetic diversity only when extinctions are in clades with long edges overall⁵ (Supplementary Fig. 1, scenario A). In contrast,

extinctions clumped in recent—often widespread and fast-evolving—clades, with short branches (Supplementary Fig. 1, scenario B), should have impacts no different, or even smaller, than under a model of random extinctions⁹ (Supplementary Fig. 1, scenario C).

We report a comprehensive analysis of the impacts of climate change on the European tree of life (see Supplementary Fig. 2 for a workflow of the analysis). First, we test whether changes in suitable climate (consensus projections extracted from several species distribution models and high-resolution climate model projections) among 1,280 plant, 340 bird and 140 mammal European species show a significant phylogenetic signal. Second, using contractions of suitable climate as proxies for extinction risk, we test whether losses would cause greater decline in phylogenetic diversity than expected under a null model of extinction. Third, we ask whether expected changes in phylogenetic diversity are spatially structured. To this end, we map the current and future phylogenetic diversity of each study group and investigate changes in regional phylogenetic diversity and its spatial turnover¹³ across Europe.

Changes in suitable climate among European species were generally more similar between closely related species, but the strength of the phylogenetic signal was weak (Fig. 1, Supplementary Table 1 and Supplementary Figs 3 and 4). This pattern of clustering appeared consistently across the high-resolution phylogenies, emission scenarios and periods studied (Supplementary Table 1 and Supplementary Figs 3 and 4). For example, among plants, most suitable climate for *Draba* (whitlow grasses) and *Arabis* (rockcress) species contracted (72% of *Draba* species contracted by >30% and 50% of *Arabis* species contracted by >50%). Among birds, most *Tringa* (shanks and tattlers) and *Numenius* (curlew) species had suitable climate contractions of >30%, whereas most *Ardeidae* (herons and egrets) expanded their ranges. Mammals were generally less vulnerable to climate change, although more than half of the *Sorex* (long-tailed shrews) species could lose more than 30% of their suitable climate (Fig. 1 and Supplementary Fig. 5).

Reductions in phylogenetic diversity arising from climate change were not greater than expected under a model of random extinctions

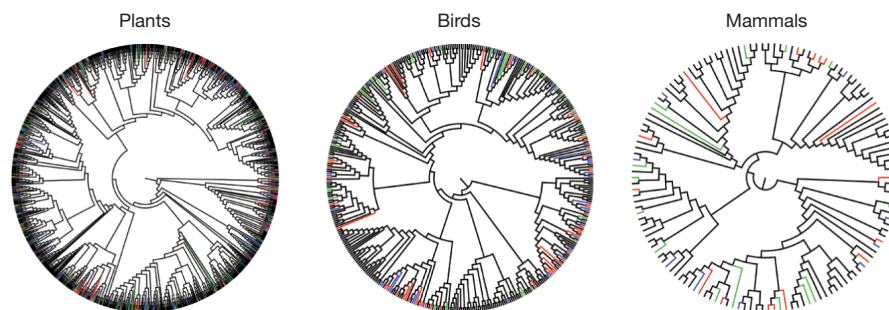


Figure 1 | Changes in suitable climate (A1FI scenario for 2080) mapped onto the phylogeny of European plants, birds and mammals. Black edges indicate positive changes in suitable climate (CSC), that is, range expansion.

Other colours indicate negative changes in suitable climate (range contraction): green for CSC > -15%, blue for CSC > -30% and red for CSC > -50%.

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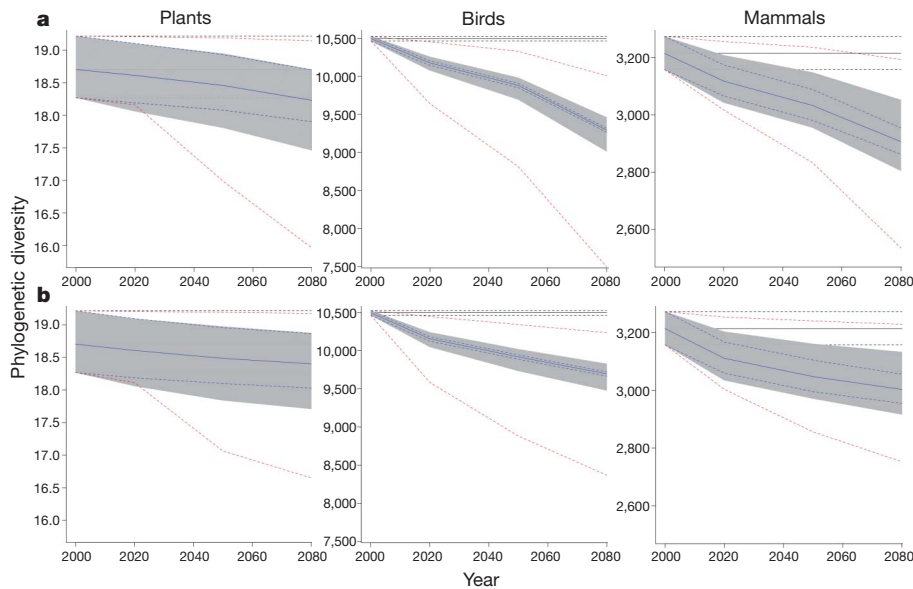


Figure 2 | Changes in phylogenetic diversity versus scenarios of random extinction for plants, birds and mammals. **a**, Emission scenario A1F1; **b**, emission scenario B1. Black solid and dashed lines depict the median, maximum and minimum current phylogenetic diversities across the sample of trees. Blue solid and dashed lines represent the median, maximum and minimum projected phylogenetic diversities due to range change across the

sample of trees. The grey area is the quantile range of projected phylogenetic diversity due to range contraction (from 2020 onward), randomly scattered across the sample of trees. The red lines are the remaining phylogenetic diversity when the risk of extinction is positively (lower line) or negatively (upper line) related to the evolutionary distinctiveness of the taxa.

across the phylogeny (Fig. 2 and Supplementary Fig. 6). That is, species whose suitable climates contract are not clustered in species-poor clades with long branches (where projected future phylogenetic diversity should be lower than under random species losses), nor are they clustered on the shortest branches (where projected future phylogenetic diversity should be higher than under random species losses). Instead they are clustered across both long and short edges of the tree. Again, these results were consistent across the three clades studied, the sampled trees, the four emission scenarios and the time slices 2050 and 2080. Sensitivity analysis across climate model projections and species distribution models revealed that results were also not affected by variability across models (Supplementary Fig. 7). For plants at risk, reductions in phylogenetic diversity were relatively low: approximately 2.7% in the worst-case scenario (A1F1) and for the time slice with greater impacts, that is, 2080 (current phylogenetic diversity, 18.7; future phylogenetic diversity, 18.2). Reductions of the same order of magnitude were recorded for phylogenetic diversity in birds (11.5% reduction) and mammals (9.6% reduction).

Spatial analyses of projected phylogenetic diversity revealed a marked homogenization of phylogenetic diversity across Europe, with strong reductions of spatial turnover (approximately -34% , -32% and -30% for plants, birds and mammals, respectively) following climate change. However, regions are not all equally affected by climate changes (Fig. 3). At present, the spatial distribution of plant phylogenetic diversity separates the northern Iberian Peninsula, Italy and France, with high total phylogenetic diversity, from northern European countries and the Alps, with low total phylogenetic diversity (Fig. 3). Similar patterns are found for birds, with higher phylogenetic diversity in the Mediterranean basin than in the rest of Europe, and mammals, with higher phylogenetic diversity in the southeast of Europe than in the northeast. Increases in phylogenetic diversity in northern Europe and in the Alps are accompanied by consistent decreases in phylogenetic diversity in southern Europe, causing a general reduction in the spatial variation of phylogenetic diversity (Fig. 3). These predicted spatial changes in phylogenetic diversity are not entirely due to changes in species richness (Supplementary Fig. 8). Indeed, regions such as Scandinavia (for plants), Germany (for birds) and Sweden (for mammals) are projected

to have more phylogenetic diversity in the future than is expected on the basis of their future projected species richness (Supplementary Fig. 8). This can be explained by northern biotas being more likely to sample species that are less phylogenetically redundant in the future. The projected reduction of phylogenetic diversity in southern Europe could, however, be alleviated by species immigration from Northern Africa, especially if immigrant species belong to phylogenetic clades that are not present in the northern Mediterranean basin.

Linking phylogenetic and biogeographic information can help identify regions of past production and present maintenance of biodiversity (so-called cradles and graves)¹⁴, but projecting them into the future is challenging. Our study addresses this challenge and presents a unique large-scale assessment of the potential impacts of climate change on the evolutionary history of plants, birds and mammals. Although our assessment integrates uncertainty in phylogenetic reconstructions, it should be noted that projected changes in evolutionary history are also inevitably sensitive to the species distribution and climate models used. To address this problem, we have used cutting-edge bioclimatic ensemble forecasting methodologies. Because high-resolution climate projections have large uncertainties (owing to the difficulty of simulating local climates and the inaccuracy of interpolation techniques¹⁵), we have included three well-known global change models encompassing a large variation in future climate and shown that our results were robust to this variation. Accordingly, we show that although different metrics of species vulnerability to climate change tend not to be randomly distributed with regards to the tree of life, the loss of European phylogenetic diversity is not greater than expected under a model of random extinctions⁴. The International Union for Conservation of Nature Red List of Threatened Species provides clear evidence that extinction risk is selective among particular groups such as the amphibians, birds and mammals¹⁶. The prevalence of threatened species differs significantly among these groups and among the families and orders within each group^{9,16}. The fossil record also provides evidence of phylogenetically clustered extinctions, although the previous five mass extinctions provide examples of less extreme selectivity^{17,18}. Our projections do not predict a large drop in total phylogenetic diversity, but they do suggest a future restructuring of the spatial distribution of

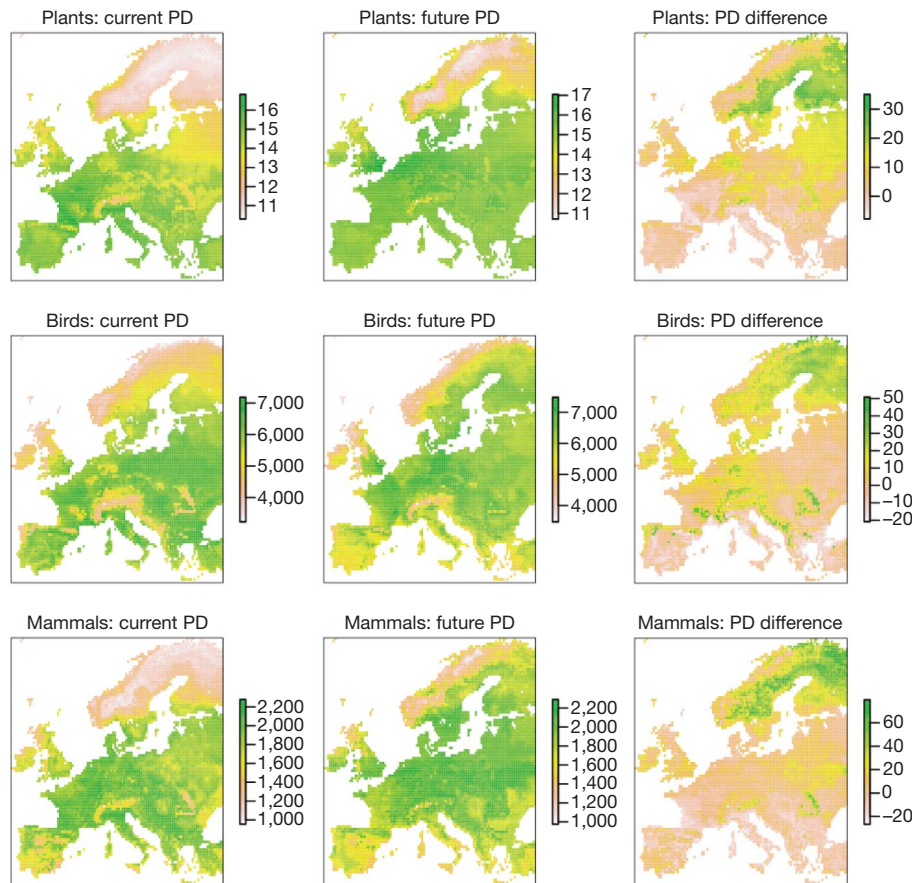


Figure 3 | Map of current and future phylogenetic diversities (A1FI scenario for 2080) and their relative differences for the three species groups. Maps represent average phylogenetic diversity (PD; colour scale) across the sample of 100 phylogenetic trees used for each study group.

the tree of life. Phylogenetic diversity over Europe will be homogenized owing to the reshuffling of species assemblages and the migration of the tree of life into higher latitudes and elevations.

METHODS SUMMARY

We modelled changes in suitable climate for 1,280 European plants, 140 mammals and 340 birds, using six species distribution models¹⁹, three 10' high-resolution global climate models (HadCM3, CSIRO2, CGCM2¹⁵ from CRU-TYN-SC-1.0) and four emission scenarios (A1FI, A2, B1 and B2²⁰), over the periods 1961–1990, 1991–2020, 2021–2050 and 2051–2080. Given the low variability across species distribution models and global climate models (Supplementary Information and Supplementary Fig. 7), we kept the median consensus projection for each scenario and time slice²¹.

Species vulnerability was estimated as the change in the total area of suitable climate assuming unlimited dispersal (CSC, ranging from -100 to >100). Another measure ('loss' of suitable climate (LSC), ranging from -100 to 0) gave similar results (Supplementary Figs 4 and 5).

We developed mega-phylogenies by mixing supertree and supermatrix approaches²² with sequences from GenBank. Optimal alignment for each region was obtained with four algorithms, and by choosing and deparating the best alignment with TRIMAL. Phylogenetic analyses were conducted using maximum-likelihood estimation by constraining heuristic searches with a family-level supertree. We retained 100 maximum-likelihood trees for plants and birds. For mammals, we used 100 phylogenetic trees based on ref. 23 with polytomies randomly resolved.

Estimation and test of phylogenetic signal in species vulnerability was performed using Abouheif's test²⁴, Blomberg's K (ref. 25) and Pagel's λ (ref. 26).

To estimate the potential impacts of climate change on the tree of life, we used CSC as a surrogate for probability of extinction, $p(\text{ext})$, and calculated future phylogenetic diversity by weighting the probability of an edge persisting as $1 - p(\text{ext})$ of all its descendent species²⁷. The null model expectation was extracted by randomizing $p(\text{ext})$ across the tips and recalculating phylogenetic diversity.

Spatial distribution of phylogenetic diversity was estimated on the pixel basis with species projected to be present. Spatial turnover was measured as the total projected phylogenetic diversity minus the mean local phylogenetic diversity over Europe¹³.

Received 7 June; accepted 29 November 2010.

Published online 16 February 2011.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements This research was funded by the EU ECOCHANGE (GOCE-CT-2007-036866) and DIVERSITALP (ANR-2007-BDIV-014) projects. C.R. was supported by a grant from Fundación Ramón Areces. We thank P. Pearman and A. Mooers for comments on earlier drafts. Computations were performed using the CIMENT infrastructure (<https://ciment.ujf-grenoble.fr>), supported by the Rhône-Alpes region (GRANT CPER07-13 CIRA).

Author Contributions W.T. and S.L. designed the study, C.R. built the plant and bird phylogenies, I.B. and B.L. helped with R code writing, and W.T. performed all the analyses. W.T., S.L. and M.B.A. wrote the manuscript with substantial contributions from all authors.

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