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# Amplified plant turnover in response to climate change forecast by Late Quaternary records

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**Conservation decisions are informed by twenty-first-century climate impact projections that typically predict high extinction risk<sup>1,2</sup>. Conversely, the palaeorecord shows strong sensitivity of species abundances and distributions to past climate changes<sup>3</sup>, but few clear instances of extinctions attributable to rising temperatures. However, few studies have incorporated palaeoecological data into projections of future distributions. Here we project changes in abundance and conservation status under a climate warming scenario for 187 European and North American plant taxa using niche-based models calibrated against taxa–climate relationships for the past 21,000 years. We find that incorporating long-term data into niche-based models increases the magnitude of projected future changes for plant abundances and community turnover. The larger projected changes in abundances and community turnover translate into different, and often more threatened, projected IUCN conservation status for declining tree taxa, compared with traditional approaches. An average of 18.4% (North America) and 15.5% (Europe) of taxa switch IUCN categories when compared with single-time model results. When taxa categorized as ‘Least Concern’ are excluded, the palaeo-calibrated models increase, on average, the conservation threat status of 33.2% and 56.8% of taxa. Notably, however, few models predict total disappearance of taxa, suggesting resilience for these taxa, if climate were the only extinction driver. Long-term studies linking palaeorecords and forecasting techniques have the potential to improve conservation assessments.**

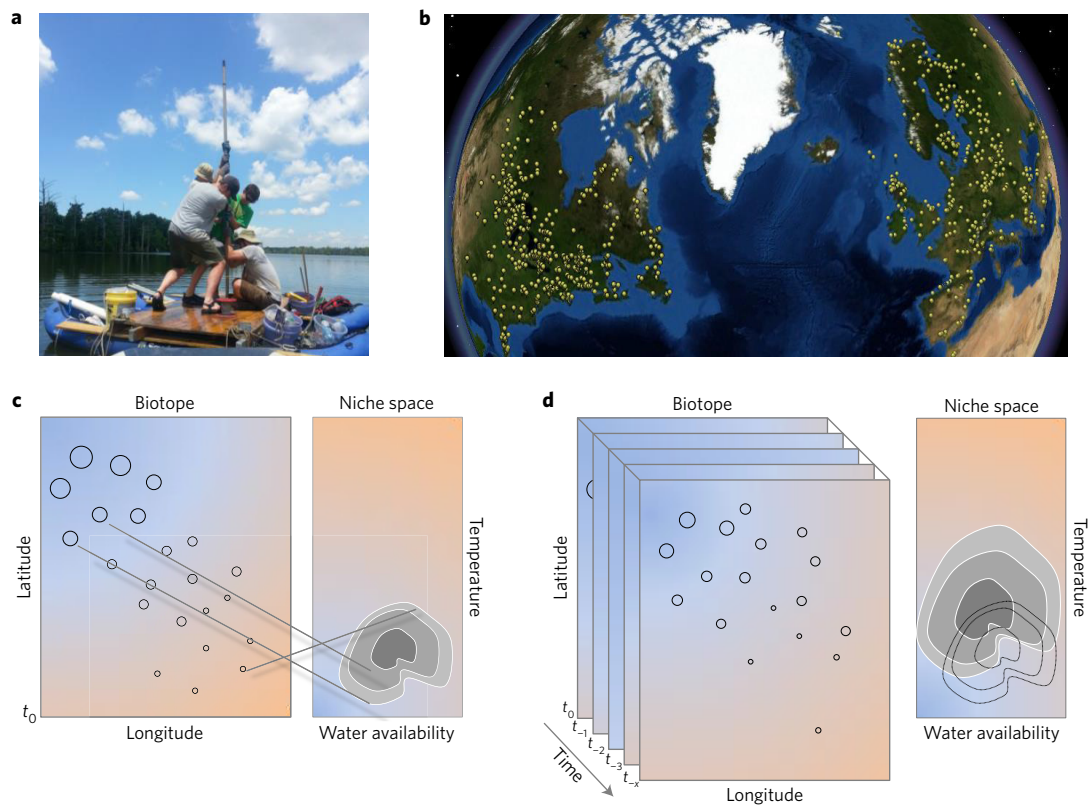
Climate change is often projected to increase extinction risk and accelerate losses of biological diversity in the coming decades<sup>1</sup>. However, almost all extant species have persisted through past glacial–interglacial cycles, although usually with major changes in abundance and distribution. Those dynamics, which are well described by the recent fossil record, remain underutilized when building quantitative scenarios of biological responses to current climate trends<sup>4–7</sup>. Most projections of species responses to twenty-first-century environments are based on correlative niche-based models, calibrated against spatial data sets of species occurrences and climate for the late twentieth century. This approach has been criticized for rarely using more responsive indicators, such as changes in species abundances, thus not fully capturing species sensitivity to climate change<sup>8,9</sup>, and for a lack of long-term perspective<sup>2</sup>. Shifts in species abundances under past climate change

offer an opportunity to assess and predict the resilience of Earth's biodiversity to rapidly changing environments<sup>3,10,11</sup>. Combining contemporary and palaeoecological data on abundance–climate relationships under multiple states of the climate system, for multiple taxa, may provide novel and more robust insights into biotic changes under future climate change<sup>4,5,12–14</sup> and thereby provide enhanced science-based input to conservation policies. Moreover, assessments based on a single recent time period may consider only part of the environmental gradients over which a species could occur<sup>15</sup>, truncating portions of species' fundamental climatic niches<sup>16</sup>. If so, extinction-risk estimates based on these truncated niches may be biased.

To address those challenges we provide a predictive modelling framework that combines climate envelope models (CEMs) with palaeo-data in a temporal extension of Hutchinson gradient analysis<sup>17</sup> (Fig. 1). We combine databases of fossil pollen relative abundances with climatic simulations for the Late Quaternary and the end of the twenty-first century from general circulation models, CEMs (Fig. 1) and ensemble forecasting<sup>18</sup> (Methods and Supplementary Information) to develop thousands of projections predicting future changes in abundance for 100 and 87 plant taxa for Europe and North America, respectively (see Methods and Supplementary Information). We evaluate the influence of incorporating palaeo-data by comparing results from future projections based distributional data for a single time period (1,000 years ago; 1 ka), with a multi-temporal approach in which pooled species niches are built using data spanning 20,000 years, from 21 to 2 ka (Fig. 1c,d).

Most projections show large changes in abundance over this century, with most taxa projected to increase abundance (Fig. 2a,b), consistent with estimates based on area-based assessments instead of abundance (Supplementary Information). Multi-temporal models predict larger changes in future abundance, for both expanding and contracting taxa, than those employing the single-time approach, for 59.0 to 64.8% of the taxa in Europe and 73.5 to 80.5% in North America, for the best model (random forests) and ensemble solution respectively. If we translate abundance changes into conservation status, based on A3b IUCN criteria<sup>19</sup> (see Fig. 2c,d and Supplementary Information), most projections predict no future extinctions (Fig. 2c,d). The A3b threat criterion is based on projected changes in taxa abundance using an index of abundance appropriate to the taxon. An average of 18.4% and 15.5%

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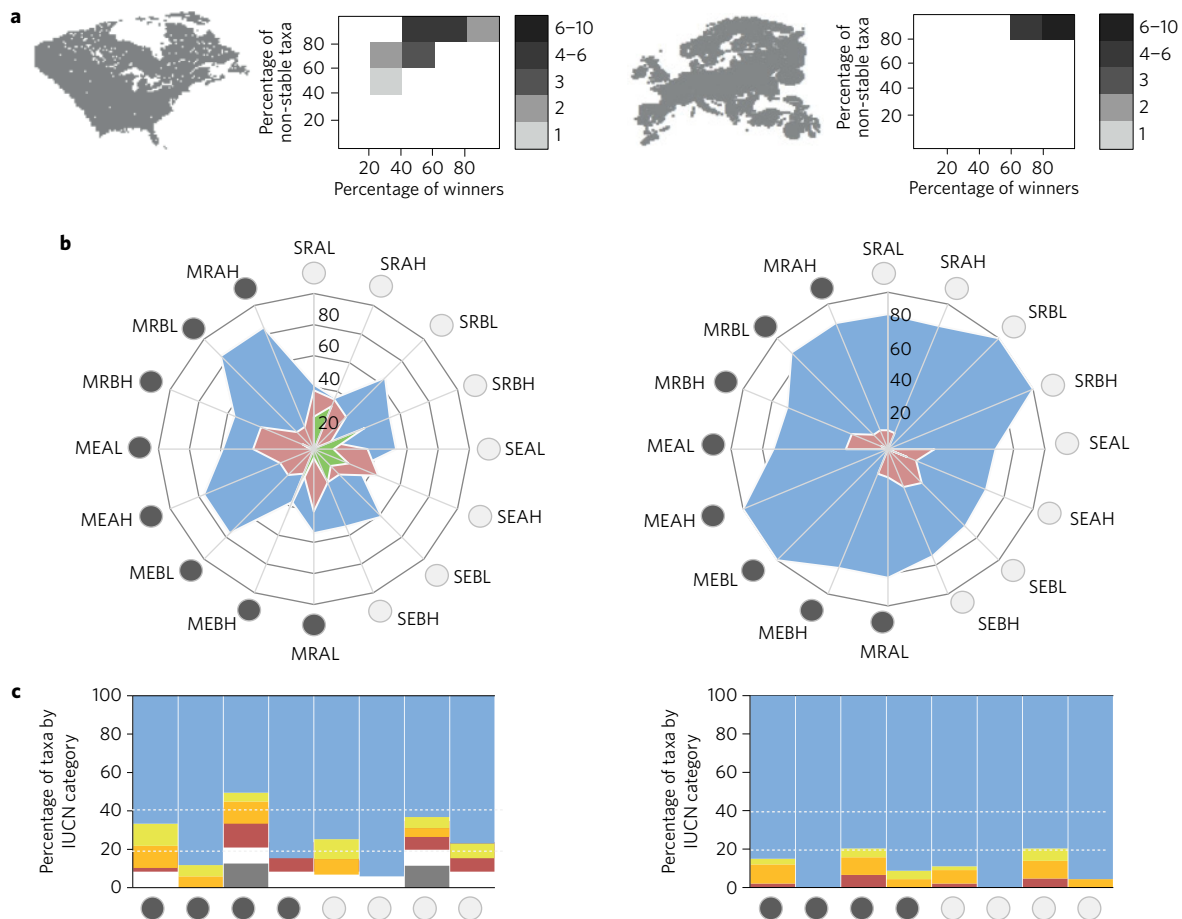
**Figure 1 | A framework for harnessing fossil data to temporally extend Hutchinsonian niches and improve future species predictions.** **a**, During the past decades, scientists have cored many lakes and mires to establish past distributions of plant abundances from fossil pollen and macrofossils. Photo credit: J.W.W. **b**, We compiled a database of pollen records from the Neotoma Paleocology Database and European Pollen Database (yellow dots) to describe spatio-temporal abundance trends for 187 taxa for the Late Pleistocene and Holocene in North America and Western Europe. **c**, Classic Hutchinsonian<sup>18</sup> niche–biotope duality. The biotope at a specific time period,  $t_0$ , consists of the geographical range of a taxon with populations of varying abundance (denoted by circle size), across a climatic gradient (colour gradient). This biotope can be projected into a niche space defined by climatic dimensions, to quantify a niche featured by taxa abundances (grey contours) varying across climatic space. **d**, Temporal extension<sup>4</sup> of Hutchinsonian niches by matching palaeoabundances and palaeoclimatic conditions for multiple biotopes through time:  $t_0, t_{-1}, t_{-2}, t_{-3} \dots t_{-x}$ . Climatic niches estimated by modern-only data (in black outlines), or palaeo-data (filled contours) can differ.

of taxa in North America and Europe respectively switch IUCN categories in the multi-temporal approach versus the single-time approach (Fig. 2). When taxa of the IUCN category ‘Least Concern’ are excluded and averaging across projections, the multi-temporal approach increases the IUCN conservation threatened status of 33.2% and 56.8% taxa in North America and Europe respectively (Fig. 2) when compared with the single-time approach.

Conceptually, the multi-temporal approach is preferable because it accounts for niche truncation and encompasses a broader portion of plants’ fundamental climatic niches, as climates change over time<sup>20</sup> (Supplementary Figs 2 and 3 and Supplementary Information). Our multi-temporal model provides more accurate predictions than the single-time approach when tested against every time period from 21 ka to 2 ka (Fig. 3). This finding still holds even after randomly resampling the multi-temporal data to match the number of occurrences in the single-time data set (Supplementary Fig. 1 and Supplementary Section 7). The improved accuracy is especially strong for Europe where climatic dissimilarities between time periods were higher than in North America (Supplementary Fig. 4). However, the single-time approach performs better for tests in which predictions are tested against adjacent and climatically similar time periods, with random resampling of the multi-temporal data to match the number of occurrences of the single-time approach (Fig. 3 and Supplementary Information; see Supplementary Information for a full description of cross-validation results and Supplementary Fig. 1). This result

suggests that when climatic change between time intervals is small, the multi-temporal approach adds power mainly by increasing sample size, but that when climatic change is large, the multi-temporal approach adds predictive power by increasing the range of climates experienced by taxa. Overall, the accuracy of CEMs is affected by the dissimilarity of climatic conditions between calibration and projection intervals<sup>21</sup>, with the multi-temporal approach performing better between climatically dissimilar time periods. Since the extent of twenty-first-century change is widely expected to be large, with many future climates expected to have no close contemporary analogues<sup>3</sup>, multi-temporal approaches may provide better projections of ecological responses to future climatic conditions.

Our finding of large projected changes in taxon abundances for the future and heightened threat—but few projected extinctions for taxa—is consistent with the profound changes in species abundances and distributions observed during the glacial–interglacial cycles of the Quaternary. These past changes occurred across multiple marine and terrestrial taxonomic groups and across continents and latitudes<sup>3,22</sup>. These findings suggest profound and widespread climate-driven turnover in the composition of ecological communities during this century, including large distribution shifts and the emergence of novel species associations, as occurred during the Late Quaternary, but it does not necessarily support that these changes will lead to climate-driven waves of extinction.



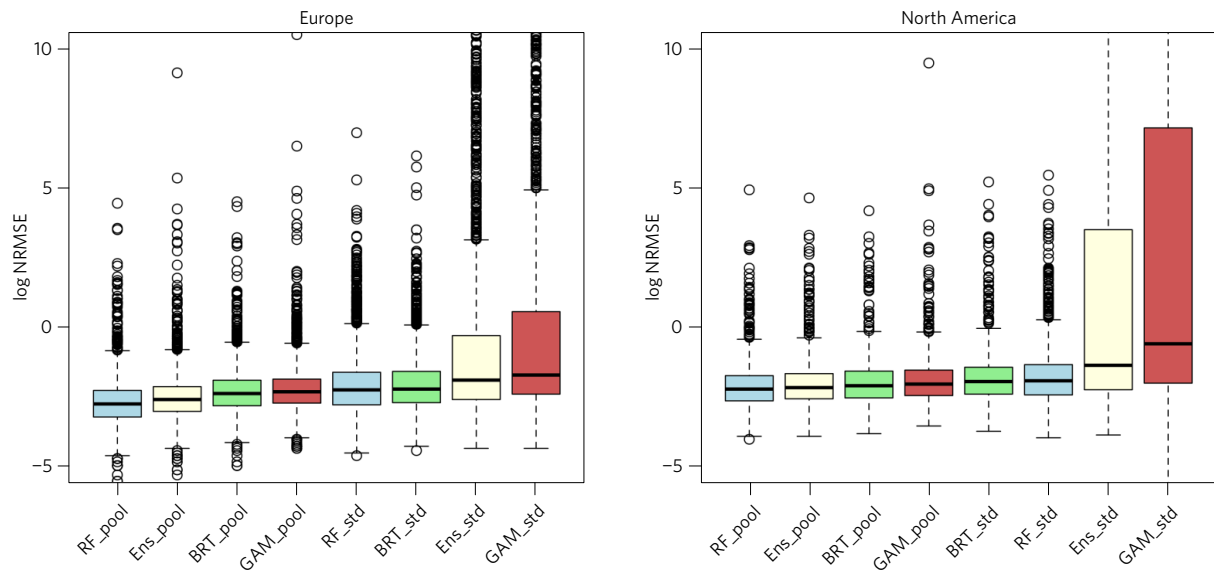
**Figure 2 | Projected abundance changes and IUCN conservation status for 2050. a,** Inter-model agreement for taxa with changing abundances (percentage of non-stable taxa) and with increasing abundances (percentage of winners) for North American and European plant taxa, based on the 16 sets of projections defined in the Methods and Supplementary Section 5. **b,** Percentage of taxa projected to increase abundance (blue), decrease abundance (red) or remain stable (green) across 16 sets of projections. Sets of projections based on long-term and single-time approaches are represented by dark and light grey spheres respectively. Four-letter codes indicate projection set: S/M, single-time/multi-temporal; R/E, random forest/ensemble; A/B, all taxa/taxa with the most accurate models; L/H, Low/High threshold of pollen change defining stability ( $\pm 5\%$  and  $\pm 15\%$ ). **c,** Proportion of taxa by conservation status projected for 2050 under criterion A3b of IUCN Red List of Threatened Species, for North America and Europe. Colour indicates IUCN categories of conservation status: blue for taxa of Least Concern, yellow for Vulnerable, orange for Endangered, red for Critically Endangered, and dark grey for Potential Extinctions. See Methods and Supplementary Section 5 for description of projections for **b** and **c**.

Of the 16 modelling scenarios considered here, for 14 scenarios our models project no threat of climate-driven extinctions (Fig. 2). The results for most taxa would place them in the IUCN category of 'Least Concern'. This result is consistent with the rarity of plant extinctions during the warming phase of recent glacial–interglacial cycles<sup>23</sup>. The consensus across sets of projections suggests also higher conservation concern for plant taxa in North America than in Europe. The European Red List reports that 25% of listed plants are threatened. However, in these analyses, only between 5% and 20% of the European taxa would be threatened due to climate change (Fig. 2). Conservation interpretations based on these analyses come with several caveats. First, the relationship between pollen and plant abundances<sup>24</sup> is positive but usually not 1:1 or linear (Supplementary Information). Second, estimates of threat to plant survival are conservative because these models assume a full dispersal scenario, whereas in reality many taxa may be dispersal-limited<sup>25,26</sup>. A further development of this approach should be to add migration rates into modelled projections. Lastly, these analyses consider only climate change as a driver of abundance and exposure to extinction, but land-use changes or invasive species are also major drivers of extinctions<sup>27</sup>. South and Central Europe and the central and west regions of North America, plus areas of the Arctic,

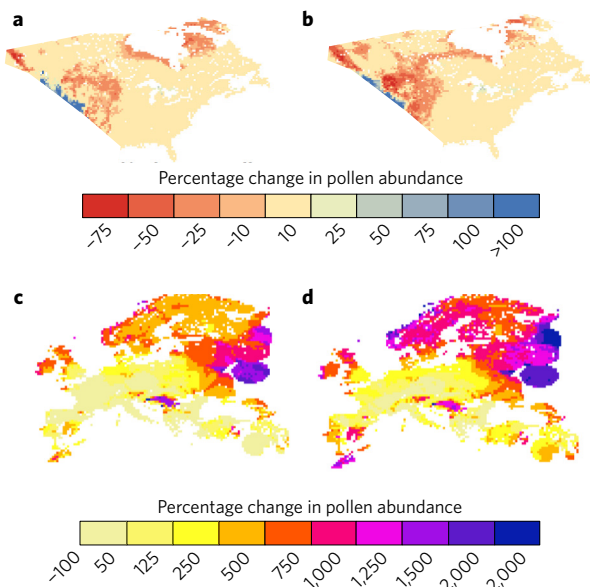
are projected to suffer the highest reductions in modelled relative abundance (Fig. 4).

Other challenges of combining modern data with palaeo-data to improve future predictions include: evolutionary responses to past climate change; uncertainties in palaeoclimatic simulations; non-analogue future climatic conditions (Supplementary Fig. 5); accurately modelling the past and future physiological effects of increasing atmospheric CO<sub>2</sub> concentrations; uncertainties in dating techniques; lack of demographic meta-population dynamics in CEMs<sup>28</sup>; and variable taxonomic resolution. More integrative efforts using historic resurveys of species distributions<sup>29</sup> and palaeoecological data<sup>9</sup> for multiple taxonomic groups would enable better model estimation of the exposure, sensitivity, and adaptive capacity of species to climate change. Given the increasing availability of palaeoecological data across large regions of the planet, including sedimentary ancient DNA for those taxa with scarce or no fossil remains, and more robust palaeoclimatic simulations, it is increasingly possible to implement this approach for forecasting a wide range of taxa such as terrestrial vertebrates, insects, and freshwater and marine taxa. On-going improvements in dating methods and high-resolution palaeorecords continue to improve our ability to quantify ecological responses to past





**Figure 3 | Cross-validation analysis.** Normalized root mean squared error, NRMSE, values for validation analysis for single-time (std) versus multi-temporal (pooled) approaches, for European and North American data sets, and for generalized additive model (GAM), boosted regression tree (BRT), random forest (RF), and a weighted mean ensemble (Ens). The boxes extend from the first to the third quartiles. The whiskers extend to data points that are  $>1.5$  times the range of the interquartile values. Outliers are represented by circles. Overall, RF and BRT slightly outperform other models and the multi-temporal approach outperforms single-time models, particularly for GAM. For both the European and North American data, NRMSE results differed significantly among the analytical approaches (Kruskal-Wallis chi-squared = 1,228.76, d.f. = 7,  $P < 0.001$ , Kruskal-Wallis chi-squared = 2,230.78, d.f. = 7,  $P < 0.001$ , respectively).



**Figure 4 | Modelled changes in relative pollen abundance for 2050.** Under a climate scenario driven by  $\text{CO}_2$  doubling, large parts of Europe and North America will maintain or increase the overall abundance of plant species. **a–d**, Single-time approach (**a,c**) and multi-temporal approach (**b,d**) projections. Legend classes represent deciles of the distribution of the percentage of change. The change in pollen relative abundance is estimated as the ratio, multiplied by 100, between future relative abundance and current relative abundance.

climate change. The plethora of new fossil data, historical resurveys, genetic evidence, and models is opening a new frontier for studying species historical responses to climate change, including those imprinted in the genes of extant and extinct species<sup>30</sup>. The framework we showcase here demonstrates how past biodiversity

dynamics can contribute to better-grounded and better-quantified recommendations for conservation policies for species facing global changes in their environment.

## Methods

Methods and any associated references are available in the [online version of the paper](#).

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## Author contributions

D.N.-B. conceived and headed the overall project. D.N.-B., S.V., B.G.H., S.C.B., J.W.W. and C.R. provided the main conceptual and methodological inputs. S.C.B. and J.W.W. provided the fossil pollen databases. J.S. and P.V. provided the palaeoclimatic simulations. B.G.H. performed the climate envelope model analysis. D.N.-B. performed the IUCN conservation status estimates and the model validation analysis. S.V. performed the niche-overlap and non-analogue climate analyses. D.N.-B. conducted the analysis on the differences of CO<sub>2</sub> concentrations across time and the effect of abundance on the magnitude of change among IUCN categories. D.N.-B., S.V., B.G.H., S.C.B., J.W.W. and C.R. wrote most of the manuscript, with input from B.D., J.S. and P.V.

## Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to D.N.-B.

## Competing financial interests

The authors declare no competing financial interests.

## Methods

We use spatial and temporal distributions of plant abundances and palaeoclimatic simulations since the Last Glacial Maximum (the last 21,000 calendar years; 21 ka) to calibrate niche-based climate envelope models (CEMs) and apply them to estimate future plant abundances and exposure to climate change impacts. For North America, fossil pollen data from 527 sites were downloaded from the Neotoma Paleoecology Database ([www.neotomadb.org](http://www.neotomadb.org)). The 546 European fossil pollen sites were previously compiled for use in environmental reconstructions<sup>31</sup>. This data set is largely based on the European Pollen Database, but extended to include sites in areas with sparse or no data.

We project the future abundance values of plant taxa for a 2050 climate change scenario for 560 ppmv CO<sub>2</sub>, based on three varieties of CEMs and a consensus solution: boosted regression trees (BRTs), general additive models (GAMs), random forest, and weighted mean consensus (EnsWA). We estimate the number of taxa increasing or decreasing in abundance in 2050 and estimate threat level according to the A3b IUCN criterion (see Supplementary Information), which is based on projected reductions in population size<sup>19</sup>. To estimate an approximate conservation status for the analysed taxa we used criterion A3 of the Red List of IUCN. Criterion A is designed to highlight taxa that have undergone a significant decline in the near past or are projected to experience a significant decline in the near future, and requires specifying whether the reduction is based on direct observation (A1, A2 and A4 only), or an index of abundance appropriate to the taxon, among other possible data sources (A3). Criterion A3 is based on population reductions projected or suspected to be met in the future 10 years or three generations (whichever is longer, but up to a maximum of 100 years). Here we use relative fossil pollen abundances as a proxy for plant abundances and the projected changes in modelled pollen abundances as an indicator of threat of population declines. We also explore the IUCN conservation status according to area-based assessment (see Supplementary Information). We explore agreement among model outcomes with respect to changes in taxon abundances (stable, increasing, or decreasing) across 16 sets of projections (Fig. 2) comparing the results for: single-time versus multi-temporal approaches; data sets (all modelled taxa versus only taxa with the most accurate models); cutoffs for the threshold defining stability ( $\pm 5\%$  versus  $\pm 15\%$ ); and choice of CEM (random forest versus weighted average ensemble). We also provide eight sets of projections for future IUCN conservation status based on combinations of single versus multi-temporal approaches, choice of CEM algorithm and the threshold of pollen change defining stability (see Supplementary Information).

We cross-validate three modelling algorithms (BRT, GAM and random forest), as well as an ensemble approach that is based on a weighted mean of the results of the three approaches (Fig. 3). For the ensemble approach, weighted means are calculated individually for each species, with the weighted contribution of each of the three modelling algorithm based on the validation results (Supplementary Information). Lack of temporal or independent data sets to validate future predictions has forced researchers to deeply explore the sensitivity of CEMs to conceptual and methodological assumptions, and to adopt techniques such as ensemble forecasting to provide central tendencies and total variability of future trends. Here we analyse sensitivity to model algorithm, using validation against observed abundance data in each millennium since the Last Glacial Maximum (Supplementary Information). In the rest of the paper, we report main results based on boosted regression trees, which was the algorithm with the highest predictive performance. For the purposes of this validation only, models based on long-term data were recalibrated after removing the data for the time period being tested, which ensures the predictions produced by models used in the validation were independent of the observed data that they were compared to. In summary, we cross-validate the performance of single-time and multi-temporal approaches across all possible time periods from 21,000 years ago through to 2,000 years ago in 1,000-year time steps after controlling by sample size. We also cross-validate model performance in adjacent time period data sets based on the time period immediately before the date of the test data (that is, 1,000 years before the test data time period). See Supplementary Information for a full description of data sets, protocols and supplementary results. Predictions were compared against actual pollen abundances using normalized root mean squared error (NRMSE) values, with lower values indicating more accurate models. The significance of difference in NRMSE scores of different modelling approaches (that is, long-term or single time period, BRT, GAM, random forest or ensemble) was tested using non-parametric approaches; that is, Kruskal–Wallis one-way analysis of variance, for overall differences, and paired Mann–Whitney rank sum tests, for pair-wise comparisons (with observations paired according to analytical method and time period tested).

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