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

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Quantitative assessments of 21st-century climate impacts on biodiversity typically predict high extinction risk^{1,2}, and their projections influence conservation decisions. Conversely, the palaeorecord shows strong sensitivity of species abundances and distributions to past glacial-interglacial climate changes³, but few clear instances of extinctions attributable to rising temperatures. However, few studies have incorporated paleoecological data into projections of future distributions and such work has been limited to few taxa. Here we project future changes in abundance and conservation status under a doubled-CO₂ scenario for 147 European and North American plant taxa using niche-based models calibrated against taxa-climate relationships for the past 21,000 years. Incorporating long-term data into niche-based models⁴ heightens both the magnitude of projected future changes of plant abundances and increases model accuracy in cross-validation tests. The larger projected changes in abundances and community turnover translate into different, and often more threatened, future IUCN conservation status for tree taxa. Long-term based models increases the conservation threat status of 48% and 81% taxa, and 35.5% and 29.3% are estimated to be in different IUCN categories when compared versus single-time models in North America and Europe respectively. However, no taxon is projected to disappear, suggesting resilience for these taxa despite large modeled changes in abundances and consistent with low extinction levels of plant taxa during the Late Quaternary. Long-term studies linking paleorecords⁵ and forecasting techniques has the potential to improve conservation assessments.

Climate change is projected to increase extinction risk and accelerate losses of biological diversity in the coming decades. However, extant species have persisted through past glacial-interglacial cycles, usually with major changes in abundance and distribution. Those dynamics, which are well described by the recent fossil record and highly relevant to envision what the future may bring to the biotic systems of the planet, remain

underutilized when building quantitative scenarios of biodiversity responses to future climate change^{6,7}. Future projections are typically based on correlative niche-based models, calibrated against species-climate relationships for the late 20th century, and have been critiqued⁸ for not representing species sensitivity and adaptive capacity⁸, for rarely using more responsive indicators such as changes in species abundances⁹, and for a lack of long-term perspective². Species responses to past climate changes offer an opportunity to assess and predict the resilience of Earth's biosphere to a rapidly warming world^{3,10,11}. Combining contemporary and paleoecological data on species-climate relationships under multiple states of the climate system may improve the projections of species abundances under scenarios of future climate change^{4,5,12,13,14} and thereby provide enhanced science-based input to conservation policies.

Our analyses of spatiotemporal shifts in plant abundances since the last deglaciation (the last 21,000 years; 21 ka) for 89 plant taxa in Europe and 58 in North America (see SI) predicts larger absolute changes in future abundance, both for taxa expanding or contracting, than those employing the single-time approach, 1ka (Fig 1A and 1B). Under the long-term approach, projected changes in absolute magnitude under a future doubled-CO₂ scenario are larger than for the single-time approach – for 91% and 82% of the taxa in Europe and North America respectively). If we translate the results of the long-term approach into conservation status, based on A3b IUCN criteria (15) (see Fig. 1C and D), no taxa are predicted to go extinct, but 15.8% and 26.7% of the analyzed plant taxa are estimated to be Critically Endangered (CR) in North America and Europe respectively (Figure 1). 35.5% and 29.3% of taxa in North America and Europe respectively are estimated to be in different IUCN categories when the long-term approach is compared versus the single-time approach (Fig 2; see SI for results based in a less accurate algorithm). The estimated future conservation status is therefore particularly sensitive to incorporating long-term dynamics. Moreover, because projected abundance changes tend to be larger for the long-term approach, incorporating long-term data heightens the projected conservation risk for many taxa. For species decreasing in abundance, the long-term approach tends to increase the conservation

threat level across both continents. When taxa of Least Concern are excluded, the long-term approach increases the conservation threatened status of 48% and 81% taxa in North America and Europe respectively (Fig 2). The conservation assessments for individual taxa should be interpreted cautiously because the relationship between pollen and plant abundances is positive but usually not 1:1 or linear; here we focus on aggregate results and differences between model experiments.

The long-term approach also provides more accurate predictions than the single-time approach, based on cross-validation analyses using a time period (8 ka) from the relatively warm early Holocene as a test (Fig 3, SI; see SI for a full description of validation results). The accuracy of the long-term approach persists even after correcting for sample size by a randomization procedure (Extended Data Fig. 1 and 2; and SI). Accuracy varies with plant abundance and tends to be higher for the most abundant taxa (Extended Data Fig. 3 and 4). The better performance of the long-term approach when projecting through time is consistent with the assumption that abundance records from multiple time periods may better infer the climatic component of the fundamental niche of species, including upper and lower thermal limits, than a realized climatic niche inferred from the static picture of a single time period^{4,16}.

The finding that adding long-term paleoecological records results in larger future projected changes in taxon abundances (and heightened extinction risk – but no projected extinctions – for decreasing taxa) is consistent with the profound changes in species abundances and distributions observed during the glacial-interglacial cycles of the Quaternary (and in earlier geological eras), recorded across multiple marine and terrestrial taxonomic groups and across continents and latitudes^{3,17}. These imply a future of even larger restructuring in species abundances and community composition than expected based on recent observations alone. Correlative niche-based CEMs that use abundance as the response variable are deeply rooted in Whittaker's gradient analysis¹⁸, yet assessments based on a single recent time period do not capture the large temporal

gradients in species abundances during periods of rapid climate change, and can truncate portions of species fundamental climatic niches¹⁹. Specifically, in this study, inferring climatic niches from the recent distribution of taxa does not account for the colder and drier conditions of the full-glacial period nor the more seasonal and rapidly changing climates of the late-glacial and early Holocene that populations experienced and survived, even at low abundances. Hence, incorporating long-term abundance data into quantitative models improves estimates of biotic sensitivity to climate change. Note that no taxon future abundance fully disappears across continental study areas, consistent with the rarity of plant extinctions during the warming phase of recent glacial-interglacial cycles²⁰.

Taxa occupying different portions of their fundamental climatic niche as climates change over time¹⁶ may explain the differences between long-term versus single-time approaches. Our results indicate significant shifts in realized climatic niches for some taxa through time, although climatic niches are broadly stable within taxa (Extended Data Fig. 5 and SI). Note also that our estimates of conservation status are conservative as our models assume a full dispersal scenario, whereas in reality many taxa are dispersal-limited. The climate change velocity for the twenty-first century, between 0.8 to 12.6 km/decade, is within the range of estimates of recent range shifts²¹ (16.9km/decade) but faster than estimates of plant distribution shifts during the last deglaciation: up to 2.7 km/decade in North America²² and 2.6 km/decade in Europe²³, although those estimates are sensitive to temporal resolution²², and our ability to accurately reconstruct past plant distributions²⁴.

Hence, when information about the profound effects of past climatic changes on taxa abundances and distributions, is incorporated into species distributional models, these distributional models predict more intense future dynamics than expected based on single-time studies. This suggests a scenario of 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 not necessarily accompanied by climate-driven waves of extinction. Combining data from multiple time periods accommodates past shifts in realized niches and thereby produces more robust descriptions of climatic niches along temporal gradients and future projections. Our modeling of abundance data leverages the greatest strength of micropaleontological records; prior work shows a strong positive monotonic relationship between pollen abundance and plant abundances at regional to continental scales (Supp Info). Challenges and uncertainties of combining modern and palaeodata to improve future predictions include evolutionary responses to past climate change, paleoclimatic simulations, non-analogue future climatic conditions (Extended Data Fig. 6), the physiological effects of increasing atmospheric CO₂ concentrations, and variable taxonomic resolution²⁷. More integrative efforts, for both historic resurveys of species distributions^{25,26} and paleoecological data⁸ for multiple taxonomic groups, are needed to better estimate the exposure, sensitivity and adaptive capacity of species to climate change.

Our approach hence allows more robust estimates of the future responses of species to climate change by incorporating information about their responses to past climate changes. 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 paleoclimatic simulations, the same approach can be implemented for forecasting other taxa trends including terrestrial vertebrates, insects, and freshwater and marine taxa. Moreover, novel and integrative research routes are much needed to include species historical responses to climate change, including those imprinted in the genes of extant and extinct species²⁸. Many challenges remain to accurately predicting the future of ecological species and communities²⁹, including species interactions under climate change³⁰, but the long-term paleoecological record and paleoclimatic data are one vital component to enhancing the robustness of predicted dynamics and better-grounded recommendations for conservation policies.

Methods summary

Here, we use the large and well-documented spatio-temporal shifts in plant abundances during the last deglaciation (the last 21,000 calendar years; 21 ka) to calibrate niche-based climate envelope models (CEMs) and apply them to estimate the future impacts of climate change for 89 plant taxa in Europe and 58 in North America. More specifically, we link the distributions of fossil pollen abundance to paleoclimatic simulations, from Hadley Centre Coupled Model, version 3, for 1ka time bins between 21,000 years ago and the present. We use the spatio-temporal patterns of pollen abundance and climatic conditions to build a taxa response surface spanning multiple time periods in order to provide a fuller representation of their fundamental climatic niche⁴ (long-term approach). Using this long-term approach we project the future abundance values of plant taxa for a climate change scenario for 2050, 560 ppmv, based on two varieties of species distribution models, boosted regression trees (BRTs; GAMs, Extended Data Fig 7) and general additive models (GAMs, Extended Data Fig 8). We estimate the number of taxa increasing or decreasing abundance in 2050 and estimate extinction risk from the A3b IUCN criterion for each taxa, which is based on projected reductions in population size¹⁵ We then compare those results against an models calibrated solely against data from the most recent single time period, 1 ka (single-time approach). We cross-validate the performance of both approaches (long-term and single-time) by leaving out one time period with relatively high Northern Hemisphere temperatures (8ka) and quantifying the predictive accuracy of both approaches for this time period. See SI for a full description of datasets, methods and supplementary results.

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

Supplementary information contains full Materials and Methods (from Section 1 to 13), sensitivity results and tables S1 to S5

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Author Contributions: DNB conceived and headed the overall project. DNB, SV, BH, SB, JW and CR provided the main conceptual and methodological inputs. SB and JW provided the fossil pollen databases. JS and PV provided the paleoclimatic simulations. BH performed the climate envelope model analysis. DNB performed the IUCN conservation status estimates and the model validation analysis. SV performed the niche overlap and non-analogue climatic conditions analysis. DNB conducted the analysis on the differences of CO₂ concentrations along different part periods and the effect of abundance on the magnitude of change among IUCN categories. DNB, SV, BH, SB, JW and CR wrote most of the manuscript, with input from BD, JS and PV.

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Figure 1. Location of the fossil pollen record and an extension in time of Hutchinson's niche concept.

a. Scientists have had drilling and studying distribution of plant abundances based on pollen fossil for the last decades. **b.** We compiled a database of pollen records, yellow dots, to encompass the spatio-temporal abundance trends for 147 taxa for the Late Pleistocene in North America and Western Europe. **c.** An extension of Hutchinson³¹ niche concept based on the niche-biotope duality, to accommodate a dynamic temporal niche. The biotope at a specific time period, t_0 , shows the geographical range of a theoretical taxa with populations of a varying abundance, as denoted by the size of the circles, across a climatic gradient, as denoted by the change in colors from blue to orange. The abundance and climatic conditions are projected into a climatic space, niche space, to quantify a niche featured by changing taxa abundances, as denoted by the different grey colours, across climatic space. **D.** We extend the Hutchinsonian niche concept into the temporal axis matching the palaeoabundances and palaeoclimatic conditions in biotope changing through different periods of time: $t_0, t_{-1}, t_{-2}, t_{-3} \dots t_{-x}$. It better estimates the full set of climatic conditions inhabited by taxa, or in other words, the relationship between abundance and climate change. The temporal niche of taxa can be projected into future climate change scenarios to estimate future conservation status.

Figure 2. Projected abundance changes and IUCN conservation status for 2050

A, B: Projected changes in abundance by 2050AD for 58 plant species in North America, and 90 plant species in Europe. Colors indicates decreasing (red), stable (grey) and increasing (blue) abundances, respectively. In North America, 43.1% of taxa are projected to increase median abundance across the region by 2050 ('winners'), 50% will decrease in abundance ('losers'), and 6.9% are projected to maintain their abundances (+/- 15% change in relative pollen abundances) (Fig. 1). For Europe, 43.3% are projected to be winners and 51.1% losers, and 4.4 % are projected to maintain their abundances. C, D: Proportion of taxa, represented by square area, by conservation status projected for 2050 under criterion A3b of IUCN Red List of Threatened Species, for North America (C) and Europe (D). Square color indicates IUCN categories of conservation status: blue for taxa of Least Concern, yellow for Vulnerable, orange for Endangered and red for Critically Endangered. Within each category, light colors show results based on the long-term approach and dark colors show results based on the single time period approach. The 15.8% of the analyzed plant taxa in North America could become Critically Endangered (CR), 17.5% Endangered (EN), 8.8% Vulnerable (VU), and 57.9% of Least Concern (LC). For Europe, we project that 26.7% of taxa could become Critically Endangered (CR), 11.1% Endangered (EN), 2.2% Vulnerable (VU), and 60% of Least Concern (LC). No taxa are predicted to go extinct.

Figure 3. Cross-validation analysis. Normalized root mean squared error (NRMSE) results for validation analysis for four different analytic methods, using either BRT or GAM models and either a single-time (blue) or long-term (yellow) data approach, for European and North American plant taxa. Model predictions for pollen abundances in these regions for 8 ka is compared to actual recorded abundances at this time. Boxes extend from the first to third quartiles. Whiskers extend to data points that are less than 1.5 times the range of the interquartile values. Outliers are represented by circles. N.B. one large outlier in the North American single-time GAM analysis is beyond the plotted range of values. Overall, BRT performs better than GAMs and long-term approach better than single-time.