

How will climate novelty influence ecological forecasts? Using the Quaternary to assess future reliability

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Abstract

Future climates are projected to be highly novel relative to recent climates. Climate novelty challenges models that correlate ecological patterns to climate variables and then use these relationships to forecast ecological responses to future climate change. Here, we quantify the magnitude and ecological significance of future climate novelty by comparing it to novel climates over the past 21,000 years in North America. We then use relationships between model performance and climate novelty derived from the fossil pollen record from eastern North America to estimate the expected decrease in predictive skill of ecological forecasting models as future climate novelty increases. We show that, in the high emissions scenario (RCP 8.5) and by late 21st century, future climate novelty is similar to or higher than peak levels of climate novelty over the last 21,000 years. The accuracy of ecological forecasting models is projected to decline steadily over the coming decades in response to increasing climate novelty, although models that incorporate co-occurrences among species may retain somewhat higher predictive skill. In addition to quantifying future climate novelty in the context of late Quaternary climate change, this work underscores the challenges of making reliable forecasts to an increasingly novel future, while highlighting the need to assess potential avenues for improvement, such as increased reliance on geological analogs for future novel climates and improving existing models by pooling data through time and incorporating assemblage-level information.

KEYWORDS

climate change, climate novelty, community-level modeling, ecological forecasting, no-analog climate, Quaternary, species distribution modeling

1 | INTRODUCTION

As 21st-century climates continue to shift to states outside the range of societal and scientific experience, our ability to forecast the effects of climate change diminishes (Beckage, Gross, & Kauffman, 2011). Periods of high climate novelty in the past—that is, times when some regions experienced “no-analog” climates that are not

comparable to the climates present anywhere today (Garcia, Cabeza, Rahbek, & Araújo, 2014; Radeloff et al., 2015)—have corresponded with the emergence of novel ecological systems, such as new communities and biomes (Finsinger, Giesecke, Brewer, & Leydet, 2017; Williams & Jackson, 2007; Williams, Shuman, Webb, Bartlein, & Leduc, 2004). The large magnitude of expected future climate change given anthropogenic warming is likely to result in novel climates in many regions of the world (Mahony, Cannon, Wang, & Aitken, 2017; Ordóñez, Williams, & Svenning, 2016; Williams, Jackson,

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& Kutzbach, 2007) and influence patterns of biodiversity for centuries to come (Walther, 2010; Walther et al., 2002). Although these changes are likely to have substantial consequences for the natural systems upon which societies depend, estimating ecological responses to future climate novelty remains a major challenge because contemporary observations alone provide incomplete insight into how the distribution and abundance of organisms may change under climatic conditions that do not presently exist (Fitzpatrick & Hargrove, 2009; Williams & Jackson, 2007).

Although the problem of making biodiversity forecasts to novel climates has been acknowledged (Fitzpatrick & Hargrove, 2009; Williams & Jackson, 2007), empirical models that relate species occurrence data to environmental variables in order to forecast future species distributions and ecological patterns are pervasive in global change ecology (Ferrier & Guisan, 2006; Guisan & Thuiller, 2005). Methods such as species distribution models (SDMs) are used to forecast range shifts and changes in species composition (Elith & Leathwick, 2009; Fitzpatrick, Gove, Sanders, & Dunn, 2008; Lawler et al., 2009), identify climate refugia and priorities for protection (Graham, VanDerWal, Phillips, Moritz, & Williams, 2010; Loarie et al., 2008; Mokany et al., 2017), and estimate extinction risk (Thomas et al., 2004; Urban, 2015). Forecasts from these correlative models may be particularly sensitive to climate novelty given their reliance on extrapolation of parameter values beyond those for which the model was developed and validated (Fitzpatrick & Hargrove, 2009; Hutson, 1977; Mainali et al., 2015; Owens et al., 2013; Randin et al., 2006; Zurell, Elith, & Schröder, 2012). Numerous studies have assessed the transferability of distribution models when projected to new times and places (Dobrowski et al., 2011; Feeley & Silman, 2010; Rapacciuolo et al., 2012; Rubidge, Monahan, Parra, Cameron, & Brashares, 2011; Veloz et al., 2012), but few have performed such tests across levels of climate change similar in magnitude to those expected this century or explicitly examined how model performance may change as climate novelty increases (Maguire et al., 2016).

We also have limited knowledge of how expected future climate novelty compares to that in the past. In terms of the magnitude and continental distribution of climate novelty, for example, are regions in North America with the most novel future climates the same regions that experienced high novelty during postglacial warming? Similarly, which aspects of climate (temperature, precipitation, etc.) tend to be associated with novel climates in the past vs. the future? Climate novelty can arise as a result of changes in one dimension of climate (e.g., maximum precipitation of the wettest quarter) or through changes in multiple climate dimensions simultaneously (Garcia et al., 2014; Ordonez et al., 2016). The variables contributing to climate novelty also are unlikely to remain constant through time and may differ between past and future climates (Williams & Jackson, 2007).

In a recent study, Maguire et al. (2016) used fossil pollen assemblages in eastern North America and paleoclimate simulations to (1) assess the predictive skill of SDMs and community-level models (CLMs) projected between multiple times in the past 21,000 years and (2) quantify relationships between model performance and

climate novelty. They showed that as past climate novelty increased, model performance rapidly declines and then levels off, regardless of modeling algorithm. However, CLMs, which incorporated assemblage-level information on taxon presence-absence, tended to outperform SDMs, which were fitted for individual taxa with no assemblage-level information. Maguire et al. (2016) only considered paleoclimatic simulations and did not explicitly assess the novelty of future climates relative to past climates nor did they attempt to estimate the expected decline in the predictive ability of ecological forecasting models over the coming decades. Thus, how the potential sensitivity of models to future climate novelty compares to past sensitivity remains unknown.

Here, we compare the expected novelty of future climates to those of the past based on a shared contemporary-period baseline, quantify which aspects of climate are most strongly associated with climate novelty in the past vs. in the future, and estimate how future climate novelty could influence the performance of ecological forecasts. We ask (1) How similar is future climate novelty predicted for North America relative to past climate novelty, in terms of magnitude, continental distribution, and drivers? (2) How might predictive skill of correlative distribution models change as future climate novelty increases? (3) How strongly does the sensitivity to future climate novelty vary among modeling approaches, given demonstrated differences in extrapolative performance for the past? Overall, we present an integrated view of climate novelty from 21,000 years ago to the near future across North America and the first quantified assessment of the potential effects of future climate novelty on predictive skill of SDMs and CLMs over the coming decades.

2 | MATERIALS AND METHODS

2.1 | Climate simulations

To determine the relative magnitude of past vs. future climate novelty and its implications for future ecological forecasting, we used a unified set of debiased and downscaled climate simulations for North America at 0.5° spatial resolution that span the Last Glacial Maximum (LGM) 22,000 years before present (BP) to the 21st century. These climate simulations, described by Lorenz, Nieto-Lugilde, Blois, Fitzpatrick, and Williams (2016), allow integrated modeling of past (22 ka BP to 1950 CE) and future (2020–2090 CE) ecological responses to climate change, and direct comparison of future and past climate novelty. The dataset contains two transient paleoclimatic simulations (CCSM3 and ECBilt), and 12 earth system models (ESMs) for two Representative Concentration Pathway (RCP) scenarios for the 21st century: RCP 4.5, a mid-range emissions scenario, and RCP 8.5, a high-range emissions scenario. Recent emission trajectories have been closest to RCP 8.5 (Global Carbon Project, 2016; www.globalcarbonproject.org). Results in the main text emphasize RCP 8.5 because findings were similar among scenarios, differing mainly in magnitude rather than pattern (i.e., RCP 4.5 showed less climate novelty than RCP 8.5).

We used the CCSM3 simulations for our paleoclimate variables as recommended by Lorenz et al. (2016). From the CCSM3 simulations, we extracted 200-year averages of paleoclimate from 21 to 0 ka BP, centered on 500-year time steps (e.g., the 1.5-ka BP climate variables are averaged across the years 1.6–1.4 ka BP). For the 21st century, the climate simulations represent 20-year monthly averages, calculated at 10-year intervals between 2020 and 2090 CE (i.e., 2020 = 2011–2030).

We used 500-year time steps and centennial averages for the paleoclimate simulations because we wanted the paleoclimate data to match the effective temporal resolution of multi-site pollen data syntheses (i.e., 500-year time steps), thereby ensuring our results remained comparable to those of Maguire et al. (2016). However, our choice of time step and averaging window differs substantially from those used for the future climate data and, therefore, could mask finer-scale temporal variability in climate (Fordham, Saltr , Brown, Mellin, & Wigley, 2018). To explore how different time steps and averaging windows may affect estimates of climate novelty, we also extracted paleoclimate data from 5,000 to 0 ka BP using the same parameters as for the future climate simulations (i.e., 20-year averages centered on decadal time steps).

Choice of reference time period to which all comparisons of past and future climate are made also can affect estimates of climate novelty. To maximize comparability of our climate novelty analyses (1) among the paleoclimate and future climate analyses and (2) between this paper and the prior work by Maguire et al. (2016), we use a single reference climatic dataset for all climate novelty assessments. This contemporary climate reference dataset is drawn from the CCSM3 simulations, which have been debiased and downscaled to observational data from the Climate Research Unit TS v3.20 (Harris, Jones, Osborn, & Lister, 2014; New, Hulme, & Jones, 1999) and NASA/GEWEX (Gupta et al., 2010; Zhang et al., 2013) as described in Lorenz et al. (2016). We defined the modern reference period as the average climate from 1850 to 1990 CE (the CCSM3 runs used here ended in 1990). The 150-year time extent of the modern climate reference represents a compromise between the 200-year time windows used for the past by Maguire et al. (2016) and the 20-year time windows used here to assess the decade-by-decade emergence of future novelty and expected declines in future ecological predictive ability. This contemporary average, centered on 1920 CE, also hence represents a broad 20th-century baseline that is the point of comparison for both past climates and for 21st-century climates. However, to explore how different baselines might alter our results, we also performed a portion of our analyses using a baseline centered on 1950 that only included the most recent 80 years from CCSM3. Following geological convention, we refer to the contemporary time period as “present” or 0 ka BP.

2.2 | Quantifying climate novelty

We quantified climate novelty (Radeloff et al., 2015) as the distance from past or future climates to their closest analog in the 0 ka BP

reference climate dataset describe above. For consistency, we used the same six minimally correlated bioclimatic variables (Pearson correlation coefficient <.75) used in Maguire et al. (2016). These are as follows: maximum temperature of the warmest quarter (qt_hgr_TMAX, °C), minimum precipitation of the driest quarter (qt_lwr_PRCP, mm), maximum precipitation of the wettest quarter (qt_hgr_PRCP, mm), annual summed actual evapotranspiration (an_sum_AET, mm), annual summed water deficit index (an_sum_WDI, mm), and annual average evapotranspiration ratio (an_avg_ETR, unitless). Annual summed water deficit index (an_sum_WDI) is calculated as potential evapotranspiration (PET)–precipitation, while an_avg_ETR is the ratio of AET to PET for each month, averaged across each year. To characterize climatic conditions through time and across assumptions regarding future climate, we extracted values for these variables across all time periods (21 ka BP to 2090 CE) and climate simulations for each ice-free climate grid cell in North America.

We used two methods of calculating climate distance to quantify climate novelty: standardized Euclidean distances and Mahalanobis distances. We report results in the main text based on Euclidean distances. To estimate climate novelty using Euclidean distances, we standardized (mean = 0, standard deviation = 1) the six climate variables using values from the full set of climate simulations for all times (past, present, and future periods), RCPs ($n = 2$), and ESMs ($n = 12$). Using these standardized variables, we calculated the six-dimensional Euclidean distance from each grid cell in North America for past or future climate to all grid cells in North America for the reference baseline climate at 0 ka BP. Climate novelty for each grid cell for a particular time in the past or future was then calculated as the minimum of all the resulting pairwise Euclidean distances from the climate at a grid cell in the past or future to the set of all climate grid cells in the 0 ka BP reference dataset (i.e., for a grid cell at location i at time t , we quantified climate novelty as the distance to its closest climate analog at 0 ka BP). Lastly, to summarize climate novelty for each time step as a whole, we calculated the median of these minimum Euclidean distances across all locations, resulting in a single median distance from each time in the past or future to the closest analog at 0 ka BP. Note that in the language of Williams et al. (2007), we are calculating “novel climates” in the past and “disappearing climates” for the future. However, following Radeloff et al. (2015) and Mahony et al. (2017), regardless of time period, we are assessing novelty of the climate system relative to the same calibration period (0 ka BP).

Our method of quantifying climate novelty differs from previous work (i.e., Maguire et al., 2016) in several ways. First, Maguire et al. (2016) used the first two principal components from a principal components analysis to calculate Euclidean distances. By calculating Euclidean distances using six standardized variables rather than just two principal components, we avoid biasing our subsequent analyses that quantified the drivers of climate novelty (see below). Second, Maguire et al. (2016) used the mean rather than the median distance as an overall metric of each time period's climate novelty. Given the skewed distributions of climate distances, using the median will result in more conservative estimates of novelty and less sensitivity to extreme pairwise minimum distances between some locations.

Lastly, correlations between the raw climate variables can artificially inflate standardized Euclidean distances (Mahony et al., 2017). By using the same six largely uncorrelated variables used by Maguire et al. (2016), we were able to limit these effects. However, to confirm that correlations between variables did not influence our results based on standardized Euclidean distances, we also quantified climate novelty using Mahalanobis distance. Mahalanobis distance accounts for correlations in the raw variables and calculates a unitless distance from a cloud of points (i.e., grid cells at 2090 CE) to all locations in a second set of points (e.g., the 0 ka BP grid cells of our baseline time period). To quantify climate novelty using Mahalanobis distance, we fit a Mahalanobis model using the climate simulations from a particular time period in the past or future (and a given RCP for the future) and predicted this model to the climate of the 0 ka BP reference period using the “mahal” function in the “dismo” package (Hijmans, Phillips, Leathwick, & Elith, 2017) in R (R Core Team, 2016). To characterize climate novelty for each time step, we calculated the median of the resulting Mahalanobis distances across the climates for all locations at that time step. Note that the results from standardized Euclidean distance and Mahalanobis distances are expected to differ given differences in the way these two methods were implemented (i.e., standardized distances were calculated using the entire climate space comprised of all past, present, and future values, whereas Mahalanobis distances were determined by fitting a model at each time individually and calculating distances to 0 ka BP).

In addition to using different methods to calculate climate distances, we also expanded the spatial domain used in Maguire et al. (2016). In Maguire et al. (2016), analyses were limited to the past and pollen sites in eastern North America, where data were available to fit and evaluate SDMs and CLMs. Here, we additionally consider climate novelty for all of North America at several time periods in both the past and future. Therefore, we calculated standardized Euclidean and Mahalanobis distances using two sets of reference locations: (1) all grid cells in North America ($n = 13,932$ grid cells at 0 ka BP), as described above, and (2) only those grid cells occupied by a fossil pollen site in eastern North America at 0 ka BP ($n = 173$ grid cells; see Maguire et al. (2016) for details). In all climate distance calculations, we removed grid cells from the analyses if they were under ice or water (e.g., during the last glaciation and during deglaciation) at a given time period. Thus, the spatial domain and the number of grid cells that contribute to calculation of the median minimum climate distance for each time period changes over time in the past. For future time periods, the number of grid cells was the same as for 0 ka BP. These analyses allow us to assess the representativeness and sensitivity of novelty and ecological inferences based on just the eastern North America pollen sites at 0 ka BP relative to the full North American domain.

2.3 | Estimates of the predictive skill of ecological forecasting models (SDMs and CLMs) as a function of future climate novelty

Maguire et al. (2016) fit and projected ecological forecasting models across different time periods over the past 21,000 years using five

paired SDM and CLM algorithms and determined whether SDMs or CLMs had an advantage in projecting species distributions and assemblage composition through time and across high magnitudes of past climate novelty. Their analyses were based on 19 fossil pollen taxa (at the generic, or in some cases the pollen-type, level) abundant through time in sedimentary cores across eastern North America. They evaluated the predictive skill of each SDM or CLM by training a model at one time (e.g., 5 ka BP), forecasting or hindcasting fossil pollen distributions to new times (e.g., 0 and 8 ka BP), and calculating two evaluation metrics using fossil pollen data for the forecasting/hindcasting period: (1) area under the curve (AUC; a measure of model discrimination) and (2) 1-Brier Score (a measure of model calibration). These metrics were then used to determine the empirical relationship between model skill and climate distance between the training and evaluation periods.

In order to estimate the expected robustness of ecological forecasts for the future by comparison with estimates of how model robustness changed with past climate novelty, we used the mean AUC and 1-Brier Scores across each of the five SDM or CLM algorithms from Maguire et al. (2016). However, we recalculated the climate distances in Maguire et al. (2016) using the methods described in the “Quantifying climate novelty” section above. This entailed recalculating climate distances from each grid cell containing a pollen site for the time period in which the SDM or CLM model was fitted to the set of grid cells containing a pollen site in the time period to which the model was projected. To determine the empirical relationship between model skill and climate distance for every combination of a model-fitting and model-projecting time period in the past, we fit a local polynomial regression (LOESS) using the “loess” function in R (R Core Team, 2016). This provided an empirical relationship to estimate how average performance of SDMs or CLMs changes with our updated estimates of climate distance. To estimate the effects of future climate novelty on the predictive skill of ecological forecasting models, we then used the LOESS regressions to predict AUC and 1-Brier scores for SDMs and CLMs forecasted to 21st-century climate scenarios, using the calculated climate distance for each decade, ESM, and RCP over the coming century. The resulting estimates of expected model performance under future climate novelty are most relevant for eastern North America and for the taxonomic groups modeled by Maguire et al. (2016). However, the performance-novelty relationship also provides insights more generally for other regions and taxonomic groups.

2.4 | Drivers of climate novelty

To examine the effects of individual climate variables on climate novelty, we quantified the relationships between climate distance and the amount of change in each climate variable (i.e., anomalies) between 0 ka BP and a time t in the past or future. We quantified the importance of each anomaly in contributing to overall climate novelty using Random Forests and associated variable importance routines as implemented in the “cforest” (Hothorn, Bühlmann, Dudoit, Molinaro, & Van Der Laan, 2005) and “varimp” (Strobl,

Boulesteix, Kneib, Augustin, & Zeileis, 2008) functions in the “party” package in R (R Core Team, 2016). For each time period, the response variable was the climate distance from time t to the nearest climate analog at 0 BP for each grid cell and the predictor variables were anomalies for each of the six climate variables between 0 ka BP and time t at each grid cell. To calculate anomalies for variables not bounded at zero (i.e., maximum temperature of the warmest quarter and annual summed water deficit index), we subtracted the 0 ka BP value from the value at time t . For minimum precipitation of the driest quarter, maximum precipitation of the wettest quarter, and annual summed actual evapotranspiration, we calculated anomalies by dividing the past/future value by the 0 ka BP value, adding one to avoid problems with dividing by zero:

$$\frac{Z_t + 1}{Z_{t=0} + 1}$$

where Z is the climate variable of interest. Lastly, for annual evapotranspiration ratio, we calculated anomalies by dividing the past/future value by the 0 ka BP value:

$$\frac{Z_t}{Z_{t=0}}$$

2.5 | Trajectory of climate change through time

To visualize the overall trajectory of climate change from the last glacial maximum (21 ka BP) to 2090 CE, we used the PCA on the comprehensive climate data from across North America for all time periods and plotted grid cells in PCA space using the first two principal components.

2.6 | Data availability

Fossil pollen data and downscaled climate simulations are available from Dryad (<https://doi.org/10.5061/dryad.hk400> and <https://doi.org/10.5061/dryad.1597g>, respectively).

3 | RESULTS

3.1 | North America

Over the coming century, climate novelty for all of North America steadily increases each decade, regardless of ESM (Figure 1b). The jump in novelty between 0 ka BP and 2020 CE highlights the projected future climate novelty relative to the 0 ka BP baseline and appears unrelated to smoothing induced by the 500-year time step and centennial averaging used for the paleoclimate data. By 2090 CE, climates across North America are projected to be as novel as climates were around 13 ka BP (Figure 1a), relative to contemporary climates and given the high emissions trajectory (RCP 8.5). For some ESMs (e.g., GFDL-CM3), future climate novelty will be higher than any time over the last 21,000 years. Understandably, the level of future climate novelty depends on greenhouse gas emissions. For

the RCP 4.5 scenario, climate novelty by 2090 CE stays within the range of climate novelty observed between ca. 8 and 21 ka BP, depending on ESM (Figure S5a,b).

The geographic pattern of climate novelty contrasts between the future and past (Figure 2). For the past, regions of high novelty are concentrated mainly in southcentral North America, with isolated patches along the western coast and in southern Mexico. The greatest climate distances occur at 18 ka BP (Figure 2a), but are relatively limited in spatial extent, whereas the most geographically extensive climate novelty occurs at 15 ka BP (Figure 2b). These geographic patterns correspond to spikes in median novelty near these times (Figure 1). In contrast, by 2050 CE (Figure 2e), and especially at 2090 CE (Figure 2f), highly novel climates become pervasive across North America, with highest novelty mainly limited to the Pacific Northwest.

In terms of drivers of novelty, for both past and future, climate novelty across North America is most strongly associated with changes in variables that reflect water balance: e.g., annual water deficit index (an_sum_WDI) and annual summed actual evapotranspiration (an_sum_AET) are prominent drivers of peak novelty in both past and future (Figure 3a). In the future climate simulations, changes in minimum precipitation of the driest quarter (qt_lwr_PRCP) are also a strong component of future climate novelty, while in the past climate simulations, maximum precipitation of the wettest quarter (qt_hgr_PRCP) and maximum summer temperature (qt_hgr_TMAX) were important contributors. However, the strength of the relationship was weaker for the future than the past (i.e., compare importance values plotted on the y-axes of Figure 3a).

3.2 | Fossil pollen sites in eastern North America

The findings reported above for all of North America generally hold for the subset of locations from eastern North America with long ecological time series (i.e. pollen sites) that can be used to test the performance of ecological forecasting models as a function of past climate novelty. At the 0 ka BP fossil pollen sites, past climate novelty rapidly increases at ca. 13 ka BP and peaks between 16 and 19 ka BP, during deglaciation and the Bølling–Allerød warm period (Figure 1c). At 2090 CE, climate novelty for RCP 8.5 will be similar to the magnitude of climate novelty seen ca. 13 and 20 ka BP; however, at these sites, projected climate novelty in the future is generally not as high as peak climate novelty in the past (Figure 1d). Findings were similar, but more muted, for RCP 4.5 (Figure S5c,d).

As reported for all of North America, the drivers of climate novelty in eastern North America were similar in the past and future (Figure 3b), with the notable exception of maximum summer temperature. In the past, the prominent drivers of peak climate novelty are associated with changes in water balance and precipitation, as well as with temperature (i.e., maximum precipitation of the wettest quarter (qt_hgr_PRCP) and maximum summer temperature (qt_hgr_TMAX) at 15 ka BP, and maximum precipitation of the wettest quarter (qt_hgr_PRCP) and annual summed actual evapotranspiration (an_sum_AET) at 18 ka BP; Figure 3b). Peak novelty by the

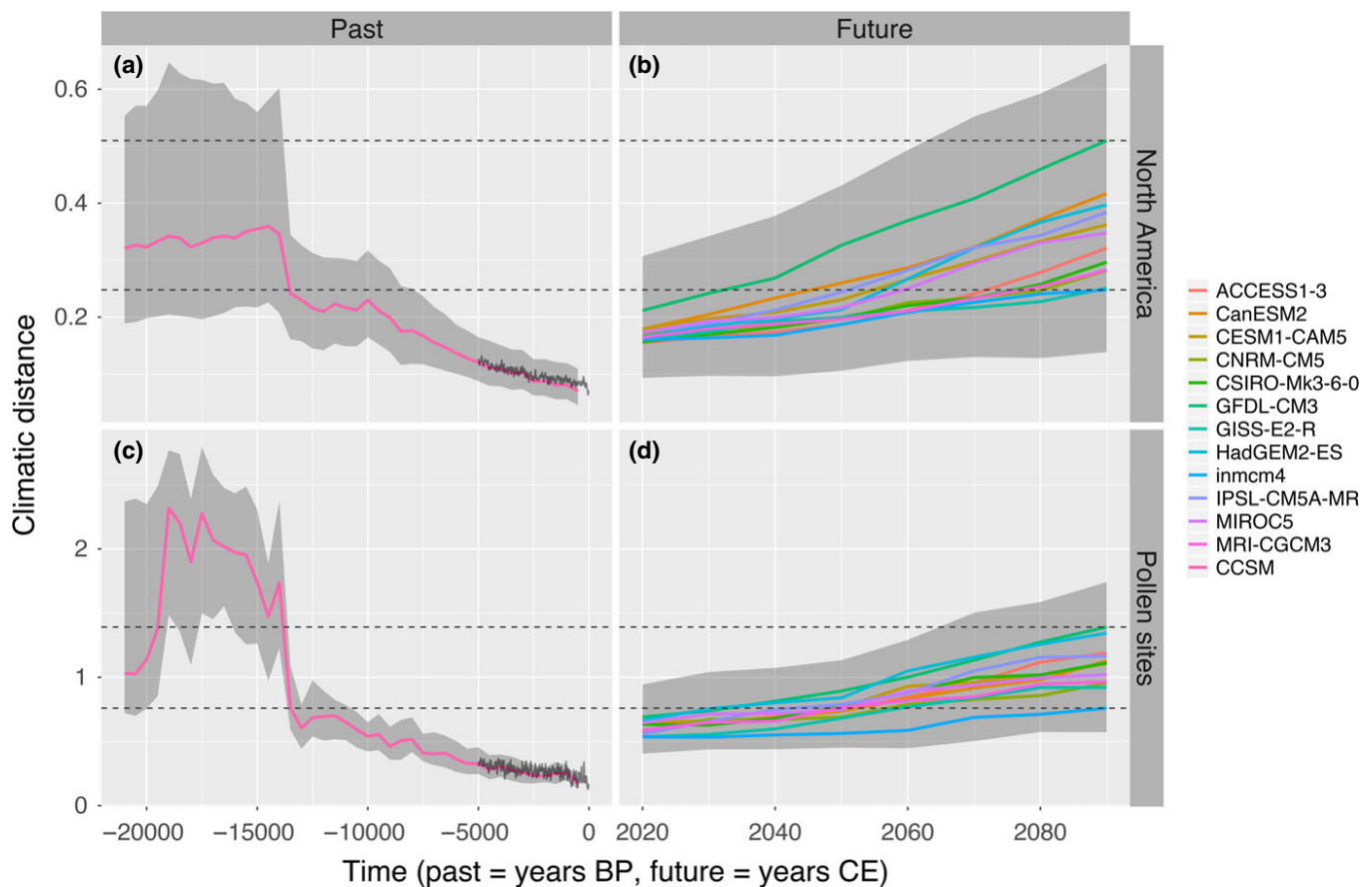


FIGURE 1 Comparison of past and future (RCP 8.5) climate novelty for all of North America and 0 ka BP pollen sites in eastern North America. Colored lines represent the median standardized Euclidean climate distance across all locations (i.e., all pixels in North America or pollen sites in eastern North America) from each time in the (a, c) past or (b, d) future to the closest analog at the 0-ka BP baseline. Shading indicates the range of values between the 25th and 75th quartiles. The dark gray solid line in (a, c) indicates climatic distances calculated from the subset of paleoclimate data extracted from 0 to 5 ka BP using a decadal time step and 20-year averaging window. Horizontal dashed lines indicate the range of future novelty at 2090 CE across the 12 ESMs. See Figure S1 for results using Mahalanobis distance and Figure S5 for results for RCP 4.5

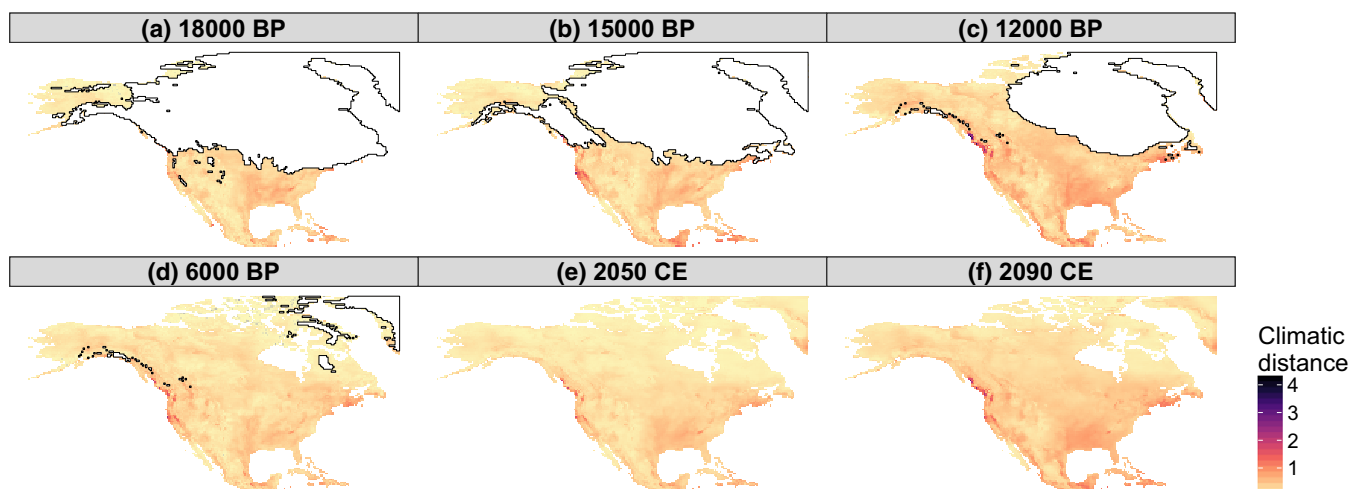


FIGURE 2 Spatial pattern of past and future (RCP 8.5) climate novelty through time. For each pixel, the map shows the standardized Euclidean climate distance from each time period in the past or future to its closest analog at 0 BP, with future maps showing the mean novelty across the 12 ESMs. See Figures S10a–S15a for larger versions of these maps and Figures S2 and S10b–S15b for maps based on Mahalanobis distances

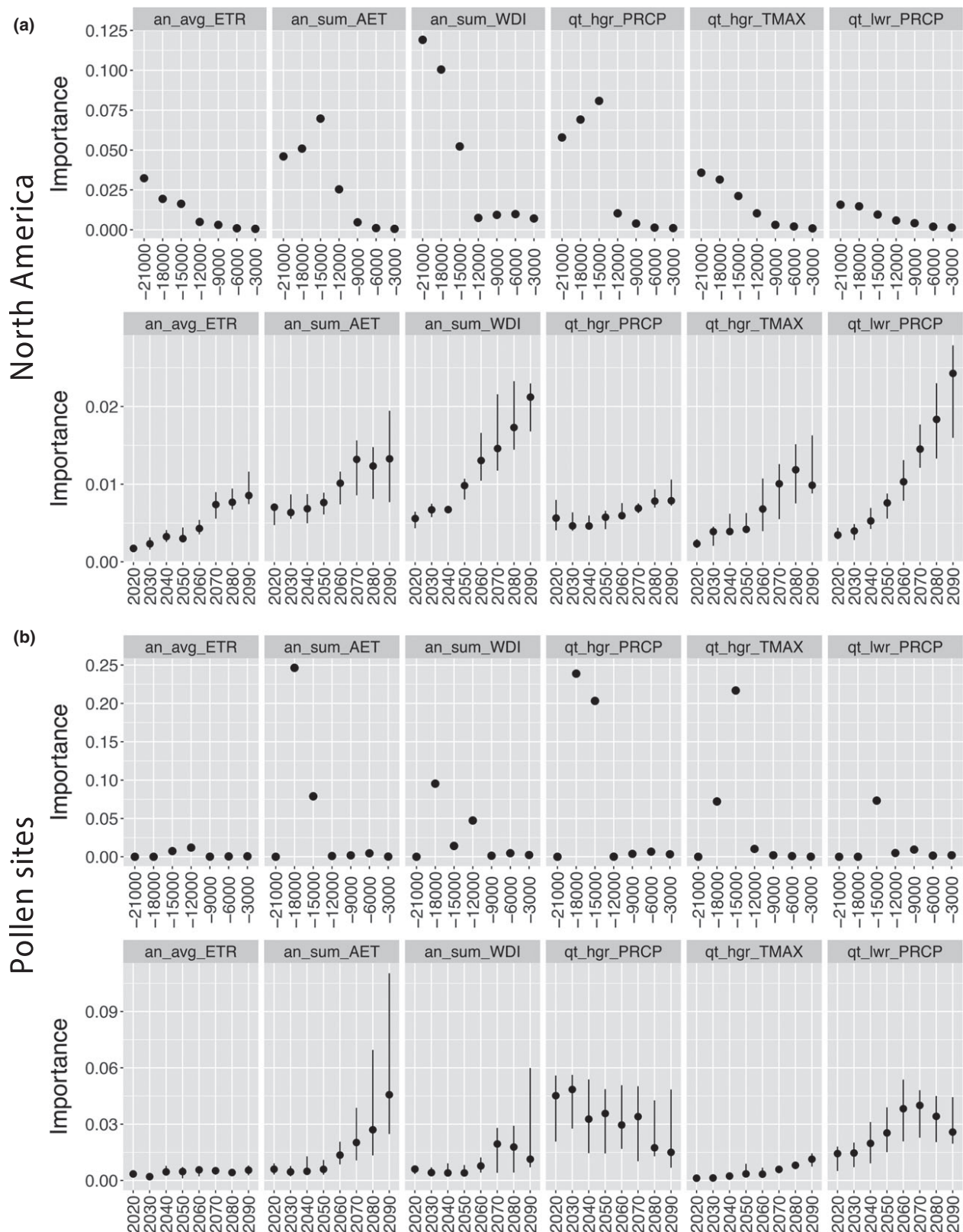


FIGURE 3 Contribution of climate variables to past and future (RCP 8.5) climate novelty for (a) all of North America and (b) at 0 ka BP pollen sites in eastern North America calculated using standardized Euclidean climate distance. In all plots, time runs forward from left to right. For future climate novelty, points represent the median across the 12 ESMs, while bars indicate the bootstrapped 95% confidence interval. Note that the y-axis scale varies between the past and future time periods. an_avg_ETR = mean yearly evapotranspiration ratio; an_sum_AET = annual summed actual evapotranspiration; an_sum_WDI = annual summed water deficit index; qt_hgr_PRCP = maximum precipitation of the wettest quarter; qt_hgr_TMAX = maximum temperature of the warmest quarter; qt_lwr_PRCP = minimum precipitation of the driest quarter. See Figure S3 for results based on Mahalanobis distances

end of the 21st century is also associated with changes in precipitation (maximum precipitation of the wettest quarter (qt_hgr_PRCP) and minimum precipitation of the driest quarter (qt_lwr_PRCP)) and water balance (annual summed actual evapotranspiration (an_sum_AET); Figure 3b). As for all of North America, variable importance was lower for the future than the past.

Consistent with the findings of Maguire et al. (2016), model predictive skill declines with increasing magnitude of climate novelty in the past (Figure 4a,c). Depending on the goodness-of-fit metric used, the decline was rapid and then leveled off (AUC; Figure 4a) or was approximately linear (Brier Score; Figure 4c). Accordingly, as climate changes and novelty increases, the predictive skill of ecological forecasting models is expected to steadily decrease over the coming decades (Figure 4b,d). However, SDMs and CLMs vary in their sensitivity to past, and therefore, future increases in novelty. On average, CLMs tended to be consistently more skillful than SDMs, particularly at higher levels of climate novelty (Brier score; Figure 4c). The differences between SDMs and CLMs are more muted with the AUC statistic, but also show marginally better performance of CLMs at higher climate novelty. For most future times and regardless of the method used to calculate climate novelty, CLMs are expected to perform as well as or better than SDMs (Figures 4b,d and S4b,d), even if emissions are limited to the RCP 4.5 pathway (Figures S7 and S8).

4 | DISCUSSION

The goals of this study were to compare past and future climate novelty relative to present climates, identify changes in which aspects of climate are most strongly associated with climate novelty, and estimate the implications of future climate novelty for the predictive skill of ecological forecasts. We found that in coming decades, climate novelty may exceed that experienced during the past 21,000 years, although findings differed across spatial domains, ESMs, and RCPs (Figures 1, 2, and S5). For example, when the spatial domain is limited to fossil pollen sites in eastern North America, climate novelty in the past and future (RCP 8.5) tends to be greater than that for all of North America, but future climate novelty is within the range of values experienced in the past. High climate novelty in the past in eastern North America is associated with the formation of novel communities (Williams & Jackson, 2007; Williams, Shuman, & Webb, 2001). Our finding that climate novelty is expected to be lower in the future than it was in the past suggests that novel communities may not be as likely to form in this region in the future, all else being equal. In contrast, when the spatial domain is all of North America, future (RCP 8.5) climate novelty may exceed past climate novelty for some ESMs (for the Mahalanobis distance measure of climate novelty, future novelty may exceed that in the past for both regions, Figure S1). Not surprisingly, the level of future climate novelty depends on greenhouse gas emissions: if future emissions are limited (e.g., RCP 4.5), climate novelty by 2090 CE stays within the range of climate novelty observed in the past, especially in eastern North America (Figures S5 and S6).

Climate novelty arises due to changes in climatic conditions that produce novel combinations of temperature, precipitation, and their interaction (Williams & Jackson, 2007). For both the past and future, and regardless of region, changes in variables that reflect water balance and precipitation tended to be more strongly associated with climate novelty than temperature (Figures 3 and S3), suggesting some commonality in past and present components of climate novelty. Nevertheless, the ultimate *drivers* of climate change and novelty differ between past and future: past climates were driven by orbital forcings, greenhouse gas variations resulting from carbon cycle feedbacks, and changes in ice cover, leading to a change from a glacial state at the LGM to the warmer interglacial (Clark et al., 2012; Denton et al., 2010), while changes in future climate and novelty are driven mainly by anthropogenic greenhouse gas emissions and lead to a transition from a warm present to a hot future (Stocker et al., 2013; Figure S9).

Climate novelty is measured relative to a reference time and place, and therefore, any assessment of novelty will be sensitive to the choice of reference baseline (Radeloff et al., 2015). The choice of a reference time period is a nontrivial decision in this era of changing climates and is an instance of the larger issue of nonstationary, shifting baselines in environmental sciences and decision-making (Jackson et al., 2001; Milly et al., 2008). Here, we have used the average climate from 1850 to 1990 CE from CCSM3 as the reference baseline. We chose this baseline (the most recent 150 years from the CCSM3 SynTrace run) to maximize comparability to the paleoclimatic simulations and the prior work by Maguire et al. (2016). This choice of 1850–1990 CE effectively sets the recent past as the baseline for assessing novelty and excludes recent decades of warming. Hence, this reference climate is likely to enhance the calculated future climate novelty more than would a reference period centered on more recent times (e.g., the WorldClim dataset (Fick & Hijmans, 2017) often used in ecological forecasting uses average climate for 1970–2000 CE to characterize current climate). The moderate levels of climate novelty at 2020 CE (Figure 1) are, in part, a reflection of a reference baseline set in the recent past, and this enhanced climate novelty should also translate into a more pronounced decrease in model performance (Figure 4b,d) than if a more recent climatic baseline was used. However, our testing of a different baseline centered on 1950 that included the only most recent 80 years from CCSM3 produced virtually no change in our conclusions. Regardless of region, future climate novelty was only about 2% less on average (results not shown) than for the 150-year baseline centered on 1920. Similarly, our results using the same time step and averaging window for both the past 5 ka BP and future (dark solid line, Figures 1a,c; S1a,c; S5a,c; and S6a,c) confirm that the jump in climate novelty between 0 BP and 2020 cannot be attributed to smoothing or other effects associated with the centennial averaging window and 500-year time step used for the paleoclimate data.

Although using a more recent reference baseline reduces the calculated level of future climate novelty somewhat, it overlooks the fact that many species distributions may contain strong memory and legacy effects and may be better matched to the climates of the

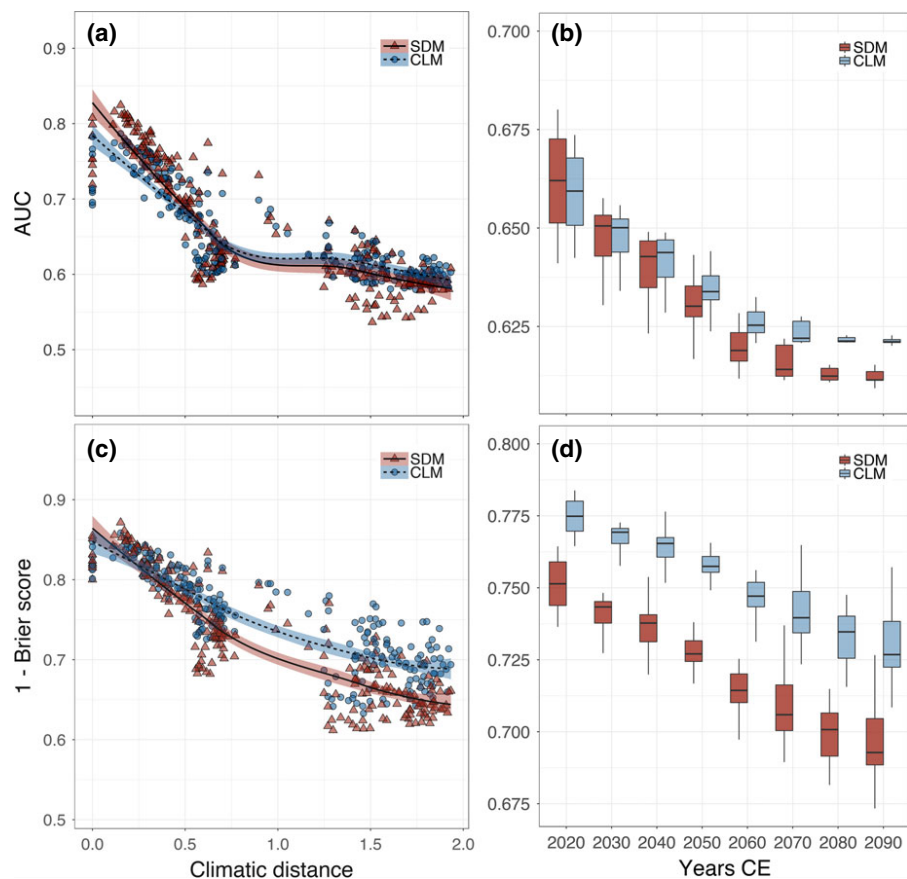


FIGURE 4 Mean fitted and expected predictive skill of (red) SDMs and (blue) CLMs vs. the standardized Euclidean climate distance measure of climate novelty. (a) AUC and (c) 1-Brier Score vs. past climate distance for models fit using fossil pollen data. (b) Expected mean AUC and (d) 1-Brier Score for SDMs and CLMs given increases in future (RCP 8.5) climate novelty predicted from the LOESS regressions in panels (a) and (c). In all panels, values are averaged across the five SDM or CLM modeling algorithms from Maguire et al. (2016). Boxplots in (b, d) indicate variation across the 12 ESMs

20th century (or earlier) than to those of the more recent decades. This is especially true for long-lived sessile organisms such as trees: their distributions are likely to be in increasing disequilibrium with climate and so average climate during the last few decades may not reliably characterize true climatic requirements (Goring & Williams, 2017; Svenning & Sandel, 2013). A more recent climatic baseline may be more appropriate for organisms that (1) are better suited to rapidly tracking their climatic niche and (2) have good observational data for recent decades.

Overall, at each decade further into the future, the climate system is expected to move further away from baseline conditions. What does this expected increase in future climate novelty imply for our ability to forecast accurately species distributions and assemblages? Our results suggest that forecasts will be only slightly better than random (i.e., $AUC = 0.5$) by the end of the 21st century, impeding our ability to estimate accurately species distributions and assemblages using correlative approaches. CLMs offer a marginal improvement over SDMs, although they also suffer from declines in predictive performance with increases in climate novelty. The extent to which the performance of SDMs and CLMs reported in Maguire et al. (2016) reflects the spatially, temporally, and taxonomically homogenized nature of the fossil pollen data requires further study.

Climate is not the only aspect of the earth system that will differ in the future, and the combined effect of rapidly changing climates, invasive species, population loss, dispersal lags, and land-cover change will also influence predictions of future ecological patterns. Hence, predictive skill is likely to be further lowered when these other factors are considered. Nonetheless, many first-order patterns in projected climate change are robust and can be used as the basis for planning. Although high climate novelty may hinder our ability to forecast the specific nature of biological responses, projections of the magnitude of compositional change of species assemblages have been found to be relatively robust (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013). Climate novelty is a real challenge, but it should not be a paralyzing one.

Several avenues exist to improve ecological forecasting in the face of climate novelty. One is to pool ecological data from multiple time periods to better encompass the climatic niche of species (Nogués-Bravo et al., 2016), with a critical need to focus on past warm periods that may be partial analogs for warm future climates. How best to pool data through time to avoid biasing models to particular time periods is a subject of ongoing study. Another solution is to rely more on mechanism and less on correlation for forecasting future ecological responses, whenever possible. However, all

mechanistic models rely to some degree on parameterization against observational data, so they do not entirely avoid the novelty challenge, and their predictions are not necessarily superior to empirical models (Fordham et al., 2018; Kearney, Wintle, & Porter, 2010; Shabani, Kumar, & Ahmadi, 2016). A third solution is to refine correlative models by selecting predictor variables and ecologically realistic response curves based on biological knowledge (Guevara, Gerstner, Kass, & Anderson, 2018) and by including abundance or population dynamics not just presence-absence, which may provide richer and better-constrained estimates of species distributions and their governing processes (Howard, Stephens, Pearce-Higgins, Gregory, & Willis, 2014). A final solution is to rely on models such as CLMs or joint species distribution models (Clark, Gelfand, Woodall, & Zhu, 2014) that better incorporate information about species co-occurrences and implicitly include the processes that drive these patterns. CLMs still suffer from relatively low accuracy when projected to the most novel climates (Figure 4b,d), but, because they simultaneously model multiple co-occurring taxa, they can buffer against idiosyncratic or artefactual modeled future changes in individual taxon-climate relationships, which may account for their superior performance over single-species algorithms (Maguire et al., 2016). In contrast, the better performance of SDMs for recent, less novel times comes at the expense of lower skill when predicting to highly novel climates. Regardless, of the solution(s) implemented, it is imperative that, at minimum, studies identify where (in geographic space) models are extrapolating outside of the training data, as has been automated in some algorithms (e.g., Elith, Kearney, & Phillips, 2010).

Overall, the speed and magnitude of climate change projected for the coming decades are beyond those experienced over the past 10,000 years (Marcott, Shakun, Clark, & Mix, 2013) and will likely severely alter earth's support systems (Barnosky et al., 2012; Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Hence, a key scientific objective is to predict accurately the distributions of species and communities given future climate change so that we can facilitate adaptation, mitigate impacts, and manage the closely interdependent human-natural systems. Prior work has identified regions expected to experience high novelty in the future. This study demonstrates that the effect on ecological forecasting is large and of similar or greater magnitude to the novel climate regimes that emerged during the late Quaternary. Scientific progress relies on identifying critical unknowns, then working to constrain them via better understanding of the relevant patterns and processes. The behavior of ecological systems in highly novel climates remains a critical unknown and source of uncertainty in ecological forecasting. The prospect of increasing climatic novelty serves as a major motivator for improving ecological forecasting models and for better constraining such models with ecological data from across a wide range of temporal scales and earth system states.

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REFERENCES

- Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., ... Smith, A. B. (2012). Approaching a state shift in Earth's biosphere. *Nature*, 486, 52–58. <https://doi.org/10.1038/nature11018>
- Beckage, B., Gross, L. J., & Kauffman, S. (2011). The limits to prediction in ecological systems. *Ecosphere*, 2, 125.
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>
- Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 9374–9379. <https://doi.org/10.1073/pnas.1220228110>
- Clark, J. S., Gelfand, A. E., Woodall, C. W., & Zhu, K. (2014). More than the sum of the parts: Forest climate response from joint species distribution models. *Ecological Applications*, 24, 990–999. <https://doi.org/10.1890/13-1015.1>
- Clark, P. U., Shakun, J. D., Baker, P. A., Bartlein, P. J., Brewer, S., Brook, E., ... Williams, J. W. (2012). Global climate evolution during the last deglaciation. *Proceedings of the National Academy of Sciences of the United States of America*, 109, E1134–E1142. <https://doi.org/10.1073/pnas.1116619109>
- Denton, G. H., Anderson, R. S., Toggweiler, J. R., Edwards, R. L., Schaefer, J. M., & Putnam, A. E. (2010). The last glacial termination. *Science*, 328, 1652–1656. <https://doi.org/10.1126/science.1184119>
- Dobrowski, S. Z., Thorne, J. H., Greenberg, J. A., Safford, H. D., Mynsberge, A. R., Crimmins, S. M., & Swanson, A. K. (2011). Modeling plant ranges over 75 years of climate change in California, USA: Temporal transferability and species traits. *Ecological Monographs*, 81, 241–257. <https://doi.org/10.1890/10-1325.1>
- Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1, 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Feeley, K. J., & Silman, M. R. (2010). Biotic attrition from tropical forests correcting for truncated temperature niches. *Global Change Biology*, 16, 1830–1836. <https://doi.org/10.1111/j.1365-2486.2009.02085.x>
- Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, 43, 393–404. <https://doi.org/10.1111/j.1365-2664.2006.01149.x>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Finsinger, W., Giesecke, T., Brewer, S., & Leydet, M. (2017). Emergence patterns of novelty in European vegetation assemblages over the past 15 000 years. *Ecology Letters*, 20, 336–346. <https://doi.org/10.1111/ele.12731>
- Fitzpatrick, M. C., Gove, A. D., Sanders, N. J., & Dunn, R. R. (2008). Climate change, plant migration, and range collapse in a global biodiversity hotspot: The Banksia (Proteaceae) of Western Australia. *Global*

- Change Biology*, 14, 1337–1352. <https://doi.org/10.1111/j.1365-2486.2008.01559.x>
- Fitzpatrick, M., & Hargrove, W. (2009). The projection of species distribution models and the problem of no-analog climate. *Biodiversity and Conservation*, 18, 2255–2261. <https://doi.org/10.1007/s10531-009-9584-8>
- Fordham, D. A., Bertelsmeier, C., Brook, B. W., Early, R., Neto, D., Brown, S. C., ... Araújo, M. B. (2018). How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology*, 24, 1357–1370. <https://doi.org/10.1111/gcb.13935>
- Fordham, D. A., Saltr , F., Brown, S. C., Mellin, C., & Wigley, T. M. L. (2018). Why decadal to century timescale palaeoclimate data are needed to explain present-day patterns of biological diversity and change. *Global Change Biology*, 24, 1371–1381. <https://doi.org/10.1111/gcb.13932>
- Garcia, R. A., Cabeza, M., Rahbek, C., & Ara jo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, 1247579. <https://doi.org/10.1126/science.1247579>
- Goring, S. J., & Williams, J. W. (2017). Effect of historical land-use and climate change on tree-climate relationships in the upper Midwestern United States. *Ecology Letters*, 20, 461–470. <https://doi.org/10.1111/ele.12747>
- Graham, C. H., VanDerWal, J., Phillips, S. J., Moritz, C., & Williams, S. E. (2010). Dynamic refugia and species persistence: Tracking spatial shifts in habitat through time. *Ecography*, 33, 1062–1069. <https://doi.org/10.1111/j.1600-0587.2010.06430.x>
- Guevara, L., Gerstner, B. E., Kass, J. M., & Anderson, R. P. (2018). Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. *Global Change Biology*, 24, 1511–1522. <https://doi.org/10.1111/gcb.13992>
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Gupta, S. K., Kratz, D. P., Stackhouse, P. W. Jr, Wilber, A. C., Zhang, T., & Sothcott, V. E. (2010). Improvement of surface longwave flux algorithms used in CERES processing. *Journal of Applied Meteorology and Climatology*, 49, 1579–1589. <https://doi.org/10.1175/2010JAMC2463.1>
- Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations—the CRU TS3. 10 Dataset. *International Journal of Climatology*, 34, 623–642. <https://doi.org/10.1002/joc.3711>
- Hijmans, R. J., Phillips, S. J., Leathwick, J. R., & Elith, J. (2017). *dismo: Species distribution modeling*. R package version 1.1-4. Retrieved from <https://CRAN.R-project.org/package=dismo>
- Hothorn, T., B hlmann, P., Dudoit, S., Molinaro, A., & Van Der Laan, M. J. (2005). Survival ensembles. *Biostatistics*, 7, 355–373. <https://doi.org/10.1093/biostatistics/kxj011>
- Howard, C., Stephens, P. A., Pearce-Higgins, J. W., Gregory, R. D., & Willis, S. G. (2014). Improving species distribution models: The value of data on abundance. *Methods in Ecology and Evolution*, 5, 506–513. <https://doi.org/10.1111/2041-210X.12184>
- Hutson, W. H. (1977). Transfer functions under no-analog conditions: Experiments with Indian Ocean planktonic foraminifera. *Quaternary Research*, 8, 355–367. [https://doi.org/10.1016/0033-5894\(77\)90077-1](https://doi.org/10.1016/0033-5894(77)90077-1)
- Jackson, J. B., Kirby, M. X., Berger, W. H., Bj rndal, K. A., Botsford, L. W., Bourque, B. J., ... Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–637. <https://doi.org/10.1126/science.1059199>
- Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, 3, 203–213. <https://doi.org/10.1111/j.1755-263X.2010.00097.x>
- Lawler, J. J., Shafer, S. L., White, D., Kareiva, P., Maurer, E. P., Blaustein, A. R., & Bartlein, P. J. (2009). Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, 90, 588–597. <https://doi.org/10.1890/08-0823.1>
- Loarie, S. R., Carter, B. E., Hayhoe, K., McMahon, S., Moe, R., Knight, C. A., & Ackerly, D. D. (2008). Climate change and the future of California's endemic flora. *PLoS One*, 3, e2502. <https://doi.org/10.1371/journal.pone.0002502>
- Lorenz, D. J., Nieto-Lugilde, D., Blois, J. L., Fitzpatrick, M. C., & Williams, J. W. (2016). Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100 AD. *Scientific Data*, 3, 160048. <https://doi.org/10.1038/sdata.2016.48>
- Maguire, K. C., Nieto-Lugilde, D., Blois, J. L., Fitzpatrick, M. C., Williams, J. W., Ferrier, S., & Lorenz, D. J. (2016). Controlled comparison of species- and community-level models across novel climates and communities. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152817. <https://doi.org/10.1098/rspb.2015.2817>
- Mahony, C. R., Cannon, A. J., Wang, T., & Aitken, S. N. (2017). A closer look at novel climates: New methods and insights at continental to landscape scales. *Global Change Biology*, 23, 3934–3955. <https://doi.org/10.1111/gcb.13645>
- Mainali, K. P., Warren, D. L., Dhileepan, K., McConnachie, A., Strathie, L., Hassan, G., ... Parmesan, C. (2015). Projecting future expansion of invasive species: Comparing and improving methodologies for species distribution modeling. *Global Change Biology*, 21, 4464–4480. <https://doi.org/10.1111/gcb.13038>
- Marcott, S. A., Shakun, J. D., Clark, P. U., & Mix, A. C. (2013). A reconstruction of regional and global temperature for the past 11,300 years. *Science*, 339, 1198–1201. <https://doi.org/10.1126/science.1228026>
- Milly, P. C., Betancourt, J., Falkenmark, M., Hirsch, R. M., Kundzewicz, Z. W., Lettenmaier, D. P., & Stouffer, R. J. (2008). Stationarity is dead: Whither water management? *Science*, 319, 573–574. <https://doi.org/10.1126/science.1151915>
- Mokany, K., Jordan, G. J., Harwood, T. D., Harrison, P. A., Keppel, G., Gilfedder, L., ... Ferrier, S. (2017). Past, present and future refugia for Tasmania's palaeoendemic flora. *Journal of Biogeography*, 44, 1537–1546. <https://doi.org/10.1111/jbi.12927>
- New, M., Hulme, M., & Jones, P. (1999). Representing twentieth-century space-time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, 12, 829–856. [https://doi.org/10.1175/1520-0442\(1999\)012<0829:RTCSTC>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<0829:RTCSTC>2.0.CO;2)
- Nogu s-Bravo, D., Veloz, S., Holt, B. G., Singarayer, J., Valdes, P., Davis, B., ... Rahbek, C. (2016). Amplified plant turnover in response to climate change forecast by Late Quaternary records. *Nature Climate Change*, 6, 1115–1119. <https://doi.org/10.1038/nclimate3146>
- Ordonez, A., Williams, J. W., & Svenning, J.-C. (2016). Mapping climatic mechanisms likely to favour the emergence of novel communities. *Nature Climate Change*, 6, 1104–1109. <https://doi.org/10.1038/nclimate3127>
- Owens, H. L., Campbell, L. P., Dornak, L. L., Saupe, E. E., Barve, N., Sober n, J., ... Peterson, A. T. (2013). Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling*, 263, 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.04.011>
- R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Radeloff, V. C., Williams, J. W., Bateman, B. L., Burke, K. D., Carter, S. K., Childress, E. S., ... Usinowicz, J. (2015). The rise of novelty in ecosystems. *Ecological Applications*, 25, 2051–2068. <https://doi.org/10.1890/1471-1781.1>
- Randin, C. F., Dirnb ck, T., Dullinger, S., Zimmermann, N. E., Zappa, M., & Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, 33, 1689–1703. <https://doi.org/10.1111/j.1365-2699.2006.01466.x>
- Rapacciuolo, G., Roy, D. B., Gillings, S., Fox, R., Walker, K., & Purvis, A. (2012). Climatic associations of British species distributions show

- good transferability in time but low predictive accuracy for range change. *PLoS One*, 7, e40212. <https://doi.org/10.1371/journal.pone.0040212>
- Rubidge, E. M., Monahan, W. B., Parra, J. L., Cameron, S. E., & Brashares, J. S. (2011). The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. *Global Change Biology*, 17, 696–708. <https://doi.org/10.1111/j.1365-2486.2010.02297.x>
- Shabani, F., Kumar, L., & Ahmadi, M. (2016). A comparison of absolute performance of different correlative and mechanistic species distribution models in an independent area. *Ecology and Evolution*, 6, 5973–5986. <https://doi.org/10.1002/ece3.2332>
- Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., ... Midgley, P. M. (2013). Climate change 2013: The physical science basis. *Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5)*. Cambridge Univ Press, New York.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC Bioinformatics*, 9, 307. <https://doi.org/10.1186/1471-2105-9-307>
- Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100, 1266–1286. <https://doi.org/10.3732/ajb.1200469>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348, 571–573. <https://doi.org/10.1126/science.aaa4984>
- Veloz, S. D., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary: Implications for 21st-century predictions by species distribution models. *Global Change Biology*, 18, 1698–1713. <https://doi.org/10.1111/j.1365-2486.2011.02635.x>
- Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2019–2024. <https://doi.org/10.1098/rstb.2010.0021>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Williams, J., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475–482. <https://doi.org/10.1890/070037>
- Williams, J. W., Jackson, S. T., & Kutzbach, J. E. (2007). Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 5738–5742. <https://doi.org/10.1073/pnas.0606292104>
- Williams, J. W., Shuman, B., & Webb, T. III (2001). Dissimilarity analyses of Late-Quaternary vegetation and climate in eastern North America. *Ecology*, 82, 3346–3362.
- Williams, J. W., Shuman, B. N., Webb, T., Bartlein, P. J., & Leduc, P. L. (2004). Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs*, 74, 309–334. <https://doi.org/10.1890/02-4045>
- Zhang, T., Stackhouse, P. W., Gupta, S. K., Cox, S. J., Mikovitz, J. C., & Hinkelman, L. M. (2013). The validation of the GEWEX SRB surface shortwave flux data products using BSRN measurements: A systematic quality control, production and application approach. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 122, 127–140. <https://doi.org/10.1016/j.jqsrt.2012.10.004>
- Zurell, D., Elith, J., & Schröder, B. (2012). Predicting to new environments: Tools for visualizing model behaviour and impacts on mapped distributions. *Diversity and Distributions*, 18, 628–634. <https://doi.org/10.1111/j.1472-4642.2012.00887.x>

SUPPORTING INFORMATION

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