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# Climate Change and the Emergence of No-Analog Forest Assemblages in North America

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## ABSTRACT

Future climate change is expected to result in tree species shifting their geographic distributions in ways that could reorganize species into assemblages with no contemporary analog. These projected no-analog forests raise concern as their ecological function could similarly shift, which may challenge established conservation and management efforts. Here, we implement a community-level modelling approach to identify the key climatic and topographic drivers of forest composition in North America, and then use these models to predict the distribution of "disappearing" and "novel" forest assemblages in future climate. We applied this modelling technique to both the taxonomic and phylogenetic composition of forest trees, to identify where species turnover may be greatest, and whether species are likely to be replaced with close relatives. Our work shows that approximately 11.9% of contemporary North American forests have low predicted similarity to future forests, and 26.2% of future forests could be compositionally novel compared with contemporary forests, but there was substantial geographic variability in the magnitude of these metrics across the continent. High-elevation regions in the west tend to be nearest to their closest compositional analog, suggesting these regions may be most likely to realize the future predicted composition. This work provides a new approach to understanding how forest composition may shift in future climates in a way that avoids the need for individual species predictions and extends climate-matching approaches with meaningful biological data.

## 1 | Introduction

Climate shifts over the coming decades are projected to result in novel combinations of temperature and precipitation that will require species to shift their geographic ranges and reorganize into assemblages that may have no contemporary or past analog (Williams, Jackson, and Kutzbach 2007; Williams and Jackson 2007). Just as future climate change will result in some climatic regimes disappearing from the landscape, and novel climates potentially emerging in their place, biological communities are likely to follow a similar trajectory, as has been observed for tree assemblages experiencing rapid climate change during the Pleistocene (Williams, Shuman, and Webb III 2001). Although novel species assemblages and climates are not a new phenomenon in deep time (Jackson 2013), the pace of their current emergence with realized and anticipated rates of climate change represent unique challenges for conservation and management. Disappearing assemblages (i.e., contemporary assemblages without future analogs) may warrant special conservation attention especially if these assemblages have unique ecological function, have special cultural significance, or provide habitat for rare, endangered, or otherwise important species. Likewise, the emergence of novel assemblages (i.e., future assemblages without contemporary analogs) could challenge

established management techniques as species responses to management practices may change when occupying unique biotic and climatic conditions.

No-analog assemblages are expected to emerge from combinations of resident species maintaining portions of their current range, and the immigration and emigration of other species between regions (stayers and movers in the parlance of Hobbs et al. 2018). While predicting taxonomic change through time is useful for understanding strict compositional changes, not all taxonomic shifts are likely to be ecologically meaningful. For instance, the replacement of one species with a closely related species that occupies a similar functional niche may be less likely to result in a shift in ecosystem function than if species are replaced by distantly related or evolutionarily distinct species. In North America, for instance, the replacement of congeneric species that are known to hybridize (e.g., some *Populus*, *Salix*, *Betula*, and *Quercus* species) is unlikely to dramatically transform ecosystem function, whereas replacement of angiosperms with gymnosperms, or vice versa, which diverged hundreds of millions of years ago, and differ intrinsically in numerous functional traits (Augusto et al. 2015; Zhang et al. 2017), could fundamentally alter ecosystem function. Although not all traits are phylogenetically conserved, and many are impacted by local environmental conditions, many important functional traits are nevertheless similar among closely related species (Ávila-Lovera, Winter, and Goldsmith 2023; Davies et al. 2013; Swenson and Enquist 2007). Furthermore, the growing recognition that forest phylogenetic composition affects a bevy of community characteristics (e.g., microorganism and pest assemblages, nutrient cycling, and forest productivity; Gougherty and Davies 2022; Hao et al. 2018; Valencia et al. 2022) suggests accounting for phylogenetic change may prove more ecologically insightful than strict taxonomic change.

Quantifying compositional change, whether taxonomic or phylogenetic, however, presents numerous challenges as it requires synthesizing the distributions of dozens or hundreds of species across large geographic areas. Previous work that has attempted to quantify compositional change frequently use a "predict first, assemble later" approach (D'Amen et al. 2017) where models are built for individual species, projected to the future, and then these individual predictions are used to infer compositional change (Graham et al. 2017; Peters et al. 2022; Rathore, Roy, and Karnatak 2022; Stralberg et al. 2009). Although this approach has proven insightful in numerous disparate systems, it is contingent on creating many individual distribution models, which may be challenging to fit for scattered, rare, or endangered species (the latter of which are frequently of management concern), and often do not account for biotic interactions, like competition and facilitation, that can be inferred from species (non-)co-occurrence in community-level models (Ferrier and Guisan 2006). Furthermore, it can be challenging to propagate the uncertainty generated from predictions from potentially hundreds of models, frequently ensembled from disparate algorithms with various underlying assumptions. Alternatively, species assemblage changes and biotic novelty have sometimes been inferred using strictly climate metrics, such as climate velocity, climatic similarity/novelty, or shifting isoclines (Carroll et al. 2015; Ordonez, Williams, and Svenning 2016; Ordonez et al. 2024). Although strictly climate-based approaches relax the need for making many individual species models, the lack of biotic information in these approaches limits their inference, as species assemblages may shift nonlinearly over multiple climatic gradients, and climatic and biotic velocities may diverge during periods of rapid climate change (Ordonez and Williams 2013). Furthermore, identifying the actual climatic variables relevant for compositional changes is likely to be challenging when biological information is not included in the modelling framework. Ultimately, in these cases where the goal is to predict compositional differences, it may be the most straightforward to model species composition directly, rather than relying on many models for individual species.

Here, we apply the concepts of "novel" and "disappearing" climates (sensu Williams, Jackson, and Kutzbach 2007) to forest tree assemblages to map which contemporary forest assemblages may have no future analog, and which future assemblages may have no contemporary analog. We apply this approach to both the taxonomic and phylogenetic composition of forests to understand how forest novelty may be moderated by evolutionarily similar species. To implement our approach, we modelled tree assemblages in North America using generalized dissimilarity models (GDM; Ferrier et al. 2007), and used the models to make predictions in three ways to quantify local compositional change, and disappearing and novel forest assemblages (Figure 1). Local compositional change quantifies the change required for forests to keep pace with local climate change, whereas metrics of disappearing forest assemblages quantify how similar contemporary forests are to the most analogous future forest, and novel forest assemblages quantify how similar future forests are to the most analogous contemporary forests. We summarized results by mapping predictions within ecoregions (from Omernik and Griffith 2014; Figure S1) and tested the sensitivity of accounting for geographic distances (Figure S2). Our approach provides a way to assess how forest composition may respond to climate change without the need for parameterizing individual species distribution models, and in a way that advances climatic novelty metrics with meaningful biological data.

## 2 | Methods

### 2.1 | Overview and Tree Distribution Data

To implement our approach, we used tree distribution data to calculate metrics of taxonomic and phylogenetic compositional differences, and then modelled compositional differences as a function of climatic and topographic differences between sites. We then used these models to predict compositional shifts for future climates to identify regions that could be compositionally similar or different between contemporary and future climates (Figure 1). We used tree abundance data compiled as part of the updated Silvics of North America, which combined forest inventories from the United States, Canada, and Mexico to a common 20-km grid (Prasad et al. 2024). For the United States and Mexico, species relative importance was calculated as the ratio of the sum of individual species' basal area and the number of stems, relative to all species in the plot. For Canada, where the inventory consisted of 2 × 2 km photo plot grids, the percent species composition corresponding to relative importance values was summarized and averaged across 20 × 20 km grids to

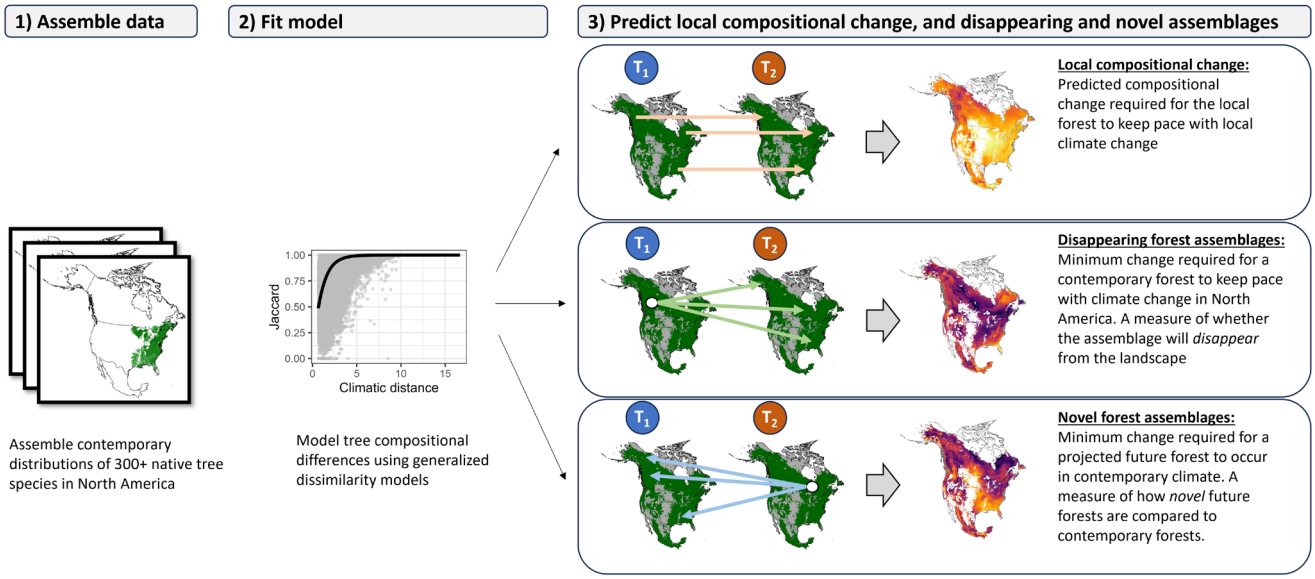


**FIGURE 1** | Workflow for modelling tree assemblages and predicting compositional change in response to climate change.

achieve equivalence with US and Mexican RIVs. Details for synonymizing the inventories can be found in Prasad et al. (2024). For Mexico, we focused solely on species that also occurred in the United States, as Mexico is a transition zone between temperate and tropical climates. Thus, our analyses are most directly relevant for the temperate tree assemblages in North America. In total, our analyses included 302 native North American tree species.

## 2.2 | Compositional Dissimilarity

We used the Jaccard index to calculate forest taxonomic differences and mean phylogenetic distance (MPD) to calculate phylogenetic differences. The Jaccard index was chosen as it is robust to multiple types of sampling and numeric errors and is an easily interpretable metric of shared species between forest assemblages. Phylogenetic differences were calculated using a phylogenetic tree created from the V.PhyloMaker package (Jin and Qian 2019) in R (R Core Team 2023), which prunes a supertree based on our species of interest, and appends unsampled species within the inclusive genus. The mean phylogenetic distance was calculated with the picante package (Kembel et al. 2010) and is calculated as the MPD between the individual species of two communities. MPD is low when communities share many closely related species, and high when two communities are composed of distantly related species. Because the model (described below) requires the response to be between 0 and 1, we rescaled the phylogenetic distances to the maximum possible value of the phylogeny, to ensure all model runs were on a consistent scale. Because calculating taxonomic and phylogenetic distance between each pair of 20-km cells in North America was computationally prohibitive we randomly selected 1000 points, without replacement, from across North America to calculate forest taxonomic and phylogenetic differences and iterated this process 10 times. In total, these 10 models included nearly 5 million compositional comparisons between pairs of forested sites, a number that was large enough for meaningful interpretation and simultaneously avoided computational bottlenecks.

## 2.3 | Model & Predictions

We used GDM, a type of nonlinear matrix regression, to model forest taxonomic and phylogenetic differences as a function of climate and topographic differences at forested sites (Ferrier et al. 2007). GDM uses I-splines to transform individual climate variables, such that the difference between transformed climate variables at pairs of sites sum to an aggregate climatic distance that increases monotonically with compositional dissimilarity (Mokany et al. 2022). Crucially, once the model is fit, the response metric (in our case, Jaccard index or MPD) can be predicted between any pair of sites with the corresponding climate data. The model was fit with the gdm package (Fitzpatrick et al. 2022) in R (R Core Team 2023). Climate variables in the model were extracted from the AdaptWest dataset (AdaptWest Project 2022; Mahony et al. 2022; Wang et al. 2016) and aggregated to the 20-km grid of the tree distribution data. Contemporary climate (1991–2020) and topographic variables included slope (using the terra package; Hijmans 2024), and seasonal averages of summer and winter precipitation and summer and winter temperature. Future climate data were based on eight general circulation models—ACCESS-ESM1.5, CNRM-ESM2-1, EC-Earth3, GFDL-ESM4, GISS-E2-1-G, MIROC6, MPI-ESM1.2-HR, and MRI-ESM2—for a high emission scenario (shared socioeconomic pathway 8.5) at the end of the century (2071–2100). Climate variables from these eight GCMs were averaged before the predictions, described below, were conducted. Although contemporary summer and winter temperature (used in model fitting) were relatively strongly correlated across the continent ($r = 0.88$), variable differences between sites are most relevant for GDM. Following Mokany et al. (2022), maximum correlation between any pair of variable differences ranged from 0.61 to 0.67 (mean: 0.64 across 10 model iterations) between summer and winter temperature—indicating only moderate

correlation in variable differences. Variable importance and significance were tested using the gdm.varImp function (using default parameters), which fits a GDM to 50 permutations of the data table, and compares model fit when variables are and are not permuted. Importance is calculated as the percent change in deviance explained when a variable is permuted (vs. when it is not), and significance is calculated by comparing deviance explained when a variable is not permuted to model deviance explained across the 50 permutations.

Because the topology of the phylogeny has been shown to impact the fit (and hence, predictions) of GDMs (Rosauer et al. 2014), we tested the effect of coarsening the phylogenetic resolution on model fit. To do so, we selected 21 thresholds along the phylogeny as a proportion of the largest phylogenetic distance (from 0.05 to 0.95 by 0.05 increments, and including 0.01 and 0.99), and whenever the distance between two species was less than the threshold, the phylogenetic distance was assigned to 0. At smaller values of the threshold (e.g., near 0.01) this had the effect of grouping closely related species together, whereas at larger values (e.g., 0.99), this had the effect of grouping all angiosperms and all gymnosperms together. We then fit a GDM for each of these threshold values and compared deviance explained. We found that coarsening the resolution of the phylogeny had no appreciable improvement on deviance explained when compared to an equivalent taxonomic model fit with the same data. We present the results of this test in the Supporting Information (Figure S3) but maintain focus in the main text on the un-coarsened phylogenetic model.

After fitting the GDMs, we used it to make predictions in three ways (Figure 1). First, we predicted forest compositional differences between each cell in North America in contemporary climate and the same cell in future climate. This metric quantifies the local change in forest composition through time and represents how much a forest composition would need to change to keep pace with local shifts in climate ("Local compositional change," Figure 1). Next, we used the model to predict forest compositional difference between each cell in North America in contemporary climate and each cell in North America in future climate ("Disappearing assemblages," Figure 1). For these predictions, we then identified the minimum predicted value and mapped the distance and intensity of the predicted Jaccard index or MPD value. This metric quantifies how similar contemporary forests are to the most similar predicted future forest. Higher values of this metric indicate a greater likelihood of the forest assemblages having no future analog, or "disappearing" from the landscape, due to shifts in species climatic habitat. Finally, we implemented the same procedure but predicted the compositional differences between cells in future climate and cells in contemporary climates ("Novel assemblages," Figure 1). This metric represents how similar future forests may be to contemporary forests. Higher values of this metric indicated a greater likelihood of future forest assemblages being novel compared with contemporary forests. Each of the three predictions above was done for each of the 10 GDM model iterations, which were averaged prior to finding the local compositional change, and metrics of disappearance and novelty. Prior to identifying the minimum values, we also removed the intercept from the predicted values, which helped to ensure the predictions were comparable across models, and not driven by the different random samples drawn for the 10 model runs. We constrained each prediction to only the current forested areas in North America, so as not to predict forest assemblages where forests do not currently occur. Forested areas were derived from the North American land cover dataset from the North American Land Change Monitoring System (NALCMS) Group, aggregated to our 20-km resolution (Commission for Environmental Cooperation 2023). Any 20-km cell with at least one forested pixel was included in the predictions. Although we acknowledge forests are likely to expand in some regions in the future, by using a broad standard for whether a 20-km cell is considered forested (i.e., cover $\geq$0.25%), we implicitly account for future local forest spread and tree migration *infilling* (Prasad et al. 2020), without making additional assumptions about where forests may appear in future climates. We summarized results by mapping predictions within ecoregions (Figure S1, Omernik and Griffith 2014) and identified instances when the most analogous sites were in different ecoregions.

In addition to assessing the geographic pattern of the raw dissimilarity metrics, we also calculated a derived metric, meant to capture the extent to which forests could escape local compositional change by potentially relocating elsewhere on the continent. This metric was calculated as (local—disappearing metric)/local and indicates the proportion difference between the predicted local compositional change and predicted change at the most analogous site. Higher values indicate a greater "benefit" of relocation to the site that minimizes compositional change, compared with remaining at the contemporary site.

While using the absolute minimum value of dissimilarity, regardless of the geographic distance to the site, is standard when finding the closest climate analog, and is useful when just climate data are used, integrating biological data presents additional challenges. Specifically, predicting a compositional analog hundreds or thousands of kilometers away may not be particularly meaningful if the species in that assemblage have no realistic chance of reaching that location. Furthermore, using the absolute minimum dissimilarity over large geographic areas may be prone to single-cell outliers. Indeed, in some initial model runs, we found numerous instances where the lowest predicted value was hundreds of kilometers further from the focal cell, than the second lowest value (Figure S2). Thus, in these cases, it may be useful to account for both geographic distance and assemblage differences when identifying the most analogous site. For this reason, in addition to using the strict minimum, described above, we also used a metric that simultaneously minimizes geographic distance and compositional dissimilarity when identifying the most analogous site. Other similar works have set maximum geographic search distances for identifying the most analogous site to address this issue (Gougherty, Keller, and Fitzpatrick 2021; Williams, Jackson, and Kutzbach 2007), but these require setting arbitrary geographic thresholds. To implement our procedure, after predicting the compositional dissimilarity metric (i.e., Jaccard or MPD) between a focal cell and all other cells, we calculated a Euclidean distance between each cell and a nonexistent hypothetical cell that minimized both the Jaccard index and geographic distance from the focal cell (see Figure S2 for a visual representation). We then selected the cell with the minimum Euclidean distance as the nearest cell that minimized compositional dissimilarity and geographic

distance. To ensure both the geographic distance and Jaccard index contributed to the Euclidean distance, each was scaled to a mean of zero and standard deviation of one. Results below focus on these "geographically informed" compositional analogs as they are less sensitive to individual outlier pixels and, in numerous regions, yielded a compositional analog much nearer to the focal cells. We present similar maps on the basis of the absolute minimum in the Supporting Information.

It should be noted that although GDMs have previously been used to make similar spatiotemporal predictions with tree genetic data (Gougherty, Keller, and Fitzpatrick 2021) and plant composition data in Queensland, Australia (Ferrier, Harwood, and Williams 2012), the dissimilarity predictions should not be considered a metric of how much forests will change, per se, but rather the approximate amount of change necessary to maintain the contemporary relationship between climate and forest assemblages. Although it is possible the climate–biodiversity relationship may be nonstationary over time, previous work on fossil pollen datasets shows similar patterns of compositional turnover along climate gradients when compared to contemporary survey data (Nieto-Lugilde et al. 2015). This suggests the contemporary climate–biodiversity relationship is a useful baseline to use for predictions. Nevertheless, it is important not to over-interpret small predicted compositional changes as modelled shifts in composition along environmental gradients could be due to sampling errors, species misidentifications, or stochasticity among nearby plots used in model fitting. Thus, even though many forests may be predicted to have some compositional change, only those at the higher end of the gradient should be considered novel. Data and code used to fit models are available at Gougherty (2024).

## 3 | Results

### 3.1 | Model Performance and Variable Importance

GDMs had a strong ability to predict taxonomic shifts along climatic gradients. On average, deviance explained, across 10 model iterations, was 66.0% (range: 64.9%–67.6%), and the model revealed that winter and summer temperature were the primary drivers of forest taxonomic composition, whereas precipitation variables and slope contributed less to overall model performance (Figures S4 and S5). Nevertheless, each of the five variables was significant ($p < 0.05$) in each of the 10 model iterations. In contrast, models of forest phylogenetic composition performed substantially poorer, with an average deviance explained of 26.8% (range: 23.8%–29.2%). Summer temperature was the primary driver of forest phylogenetic composition, followed by summer precipitation—the remaining variables had effectively no importance in the models. Although temperature variables were the most important in both the taxonomic and phylogenetic models, the importance was considerably higher for the phylogenetic model than for the taxonomic model (Figure S4). This seems likely due to taxonomic composition shifting along multiple climate axes, such that permuting any particular variable can be compensated by other climate variables. Summer temperature and summer precipitation were each significant ($p < 0.05$) in each of the 10 phylogenetic model iterations, but of the remaining variables, only slope was significant in one of the models. Winter precipitation and winter temperature were either not significant or not tested because they had no contribution to the unpermuted model.

### 3.2 | Predicted Compositional Shifts in North America

Predicted compositional differences varied substantially throughout the forested regions in North America. In aggregate, local compositional change was predicted to be high throughout the continent, whereas metrics of assemblage disappearance and novelty were more variable (Figures 2 and 3). Regions with the greatest potential for reducing the need for local compositional change were found in the center of the continent, in particular in central Canada, and Midwest and Northeastern United States (Figure S6). Across North America, 11.9% of forests had high possibility of disappearing (Jaccard index $> 0.5$)—indicating the most analogous site would share fewer than 50% of species with the contemporary assemblage—whereas 26.2% of forests had high compositional novelty. Below, we characterize the regionalization of the predicted compositional change in three of the main forested regions in North America—eastern temperate forests, high elevation western forests, and northern boreal forests—which align with the major precipitation (east–west) and temperature (north–south) gradients across the continent.

### 3.3 | Eastern, Western and Northern Forests

Forests in eastern North America had among the highest levels of local compositional change, and the greatest possibility of disappearing and novel forest assemblages (Figures 2 and 3; Figure S7). Local taxonomic compositional difference was consistently high throughout the region, frequently with a Jaccard index $> 0.75$ indicating future assemblages would share less than 25% of species with contemporary assemblages. Metrics of both disappearing and novel assemblages were also high in parts of eastern North America, in particular in the southeast United States. Forests further north in the upper Midwest and northeast United States had notably lower predicted compositional change, indicating future climates could support compositional analogs for these forests in the future. When shifts were assessed between ecoregions, many contemporary forests in the eastern United States were predicted to be compositionally similar to other forests in the same ecoregion (Figures 4 and 5; Figure S8), but there were also evident shifts to more northern ecoregions, in particular to the "Northern Forest" ecoregion that extends from the upper Great Lakes region to Central Canada—consistent with an overall northward trajectory for many forest assemblages in the east (Figure 5). When assessed in the reverse direction, a substantial amount of forested area had its nearest analog in the Great Plains—suggesting drier continental forests maybe represent future eastern forests. Interestingly, the geographic pattern of dissimilarly was quite different when phylogenetic relationships were included (Figure S9). Forests in the southeast, in particular, had comparably low local compositional change, low possibility of disappearing, and novel phylogenetic assemblages relative to the continent as a whole. Although local predicted compositional differences tended to

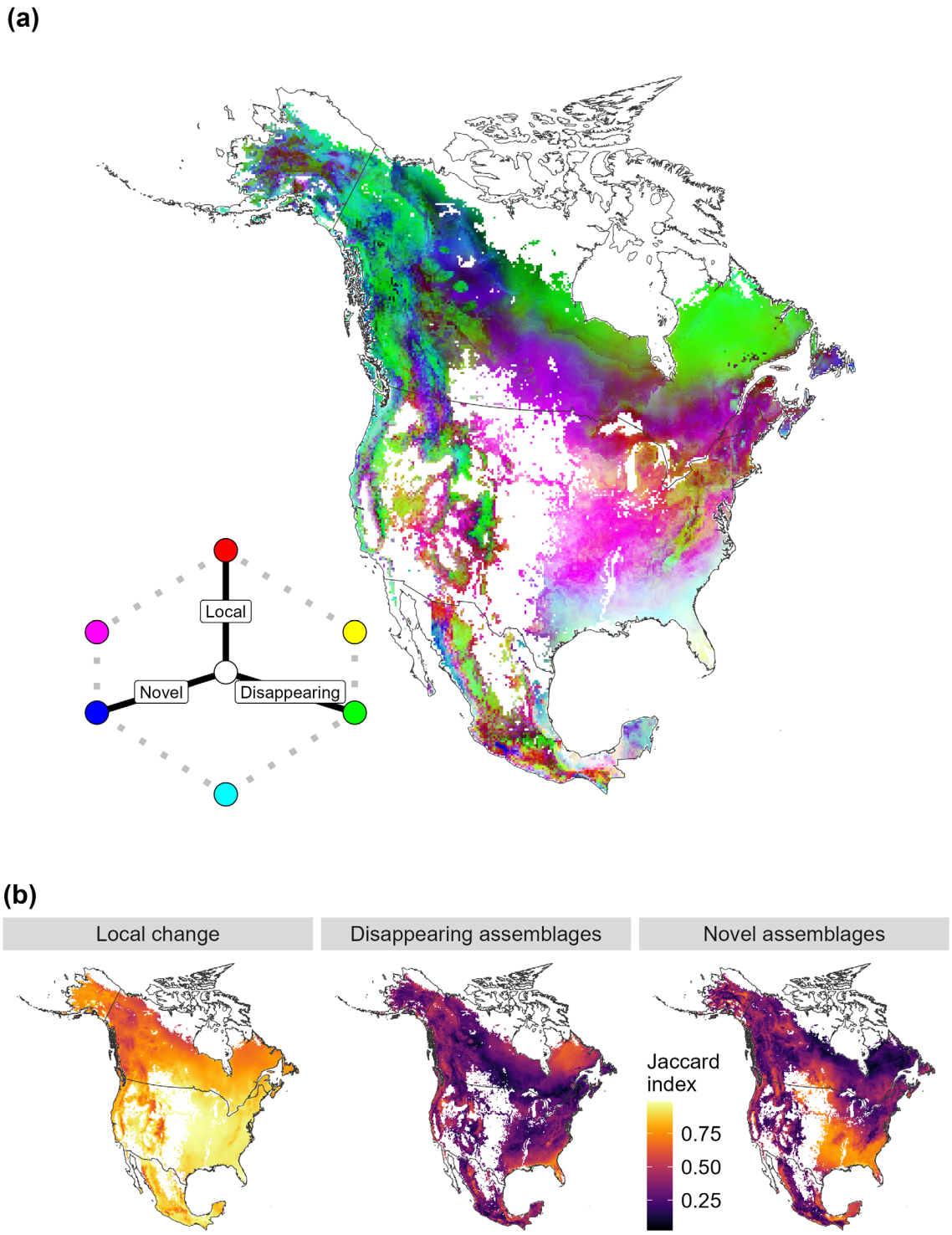


**FIGURE 2** | (a) Red-green-blue image of (b) local taxonomic dissimilarity (red axis) and metrics of taxonomic assemblage disappearance (green) and novelty (blue) between current (1991–2020) and future climates (2071–2100). Maps in (b) show the geographically informed minimum Jaccard values (see Figure S2). Individual maps in (b) were scaled to their quantiles to assign color intensities in (a). Brighter colors (closer to white) in (a) indicate high levels along each of the three dissimilarity metrics, whereas darker colors (closer to black) indicate lower values.

increase with latitude in eastern North America, there was a general lack of strong gradients in disappearing and novel assemblages, suggesting most forests will have a close phylogenetic analog in the future. Taken together, the taxonomic and phylogenetic metrics suggest that forests in the south will likely require shifts in tree composition to keep pace with climate change, but that these species could, given the uncertainty in the phylogenetic model, be closely related to the species already present in those forests.

Like eastern forests, local compositional change was predicted to be high throughout forests in western North America and these areas were interspersed with regions of lower predicted change, especially in some of the high-elevation regions

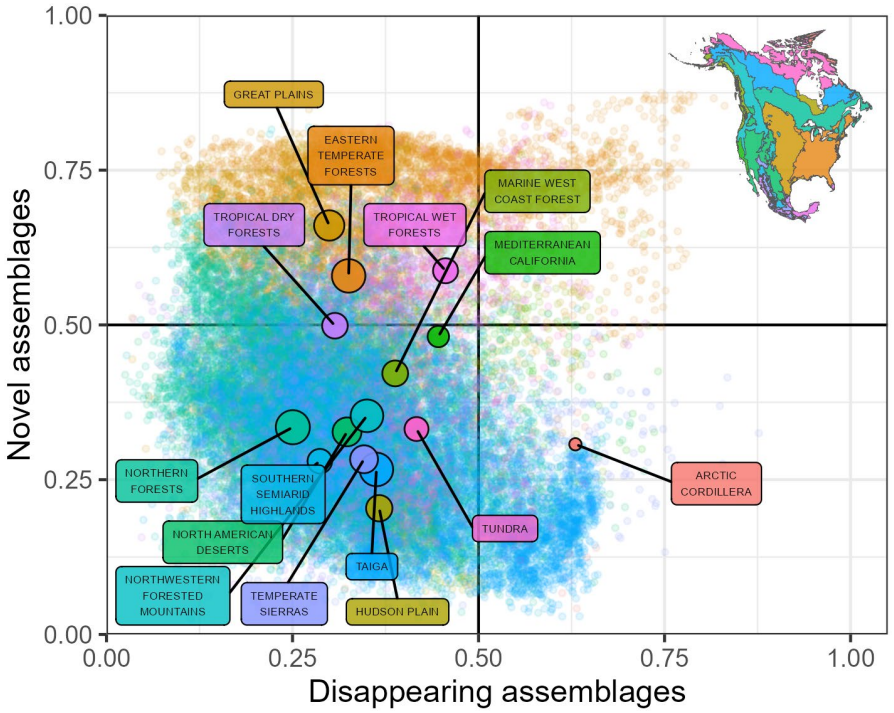


**FIGURE 3** | Metrics of disappearing and novel forest assemblages in North America. Each small point is an individual pixel and larger, labelled points are averages within ecoregions, proportional to forested area within the respective ecoregion. Several pixels that fell along a shoreline in the Water ecoregion are not shown. Lines at 0.5 represent high predicted compositional differences, where points in the upper right quadrant indicate a high possibility of disappearing and novel forest assemblages, whereas points in the bottom left indicate a lower possibility of disappearing or novel assemblages. Points and labels match the colors of the ecoregions in the inset map.

of the Rocky and Sierra Nevada Mountains. Regions with a high possibility of disappearing and novel forest assemblages were apparent throughout western North America, but these areas tended to be sporadic, especially compared with the more continuous areas of compositional change predicted in southeastern forests (Figure 2). Distances to the most similar compositional analogs tended to be lower compared with the east, (Figure 6). Shifts between ecoregions were also less apparent than in the east, but shifts occurred among forests in the North American desert, which frequently had their most analogous future composition in the northwest forests (Figure 4). Like eastern forests, the possibility of disappearing and novel phylogenetic assemblages was low throughout the region, frequently near zero—indicating that many contemporary forests could have a close phylogenetic analog in the future (Figure S9). Although there was a similar lack of gradients in metrics of disappearing and novel assemblages, like the east, some high elevation areas in the US and Canadian Rocky Mountains had slightly elevated likelihood of disappearance, suggesting these high elevation areas may have a slightly elevated likelihood of compositional change compared with many of the surrounding forests.

Among the main forested areas in North America, northern forests had among the lowest levels of local compositional change, and lower possibility of disappearing and novel assemblages; however, there were areas of higher predicted change (Figure 2). The likelihood of disappearing assemblages was particularly high in northern Canadian Atlantic region and mountainous regions in the northwest. In contrast, compositional novelty was low along the northern forest edge—likely because these forests can draw from a large area south of their contemporary location (Figures 2 and 5). Assessed within ecoregions, there were substantial shifts into more northern forests consistent with an overall northward trajectory for many forests, like described above. A large proportion of northern forest, for instance, had their nearest compositional analog in taiga (Figures 4 and 5; Figure S8), and likewise, a considerable portion of contemporary forest in taiga had their nearest analog in tundra. Like eastern and western forests, predicted phylogenetic composition shift was low throughout most of the northern forests. Exceptions however were evident in Alaska which had relatively high novelty, suggesting future forests in these regions may be phylogenetically distinct compared with forests in contemporary North America (Figure S9).

## 4 | Discussion

Forest assemblage responses to future climates will be contingent on local species populations being able to adapt or acclimate to new climatic conditions and/or the ability to migrate to suitable habitats. Shifting climates in North America are likely to necessitate nearly all forests to undergo some compositional change to keep pace with future climate change, and our continental-scale analysis indicates that for some North American forests, the compositional changes could be substantial, even if migration potential is unconstrained. Forests with large predicted compositional differences may warrant special conservation attention and further study to understand the factors driving compositional change (e.g., changes in richness and turnover) as even relatively minor shifts in forest compositions

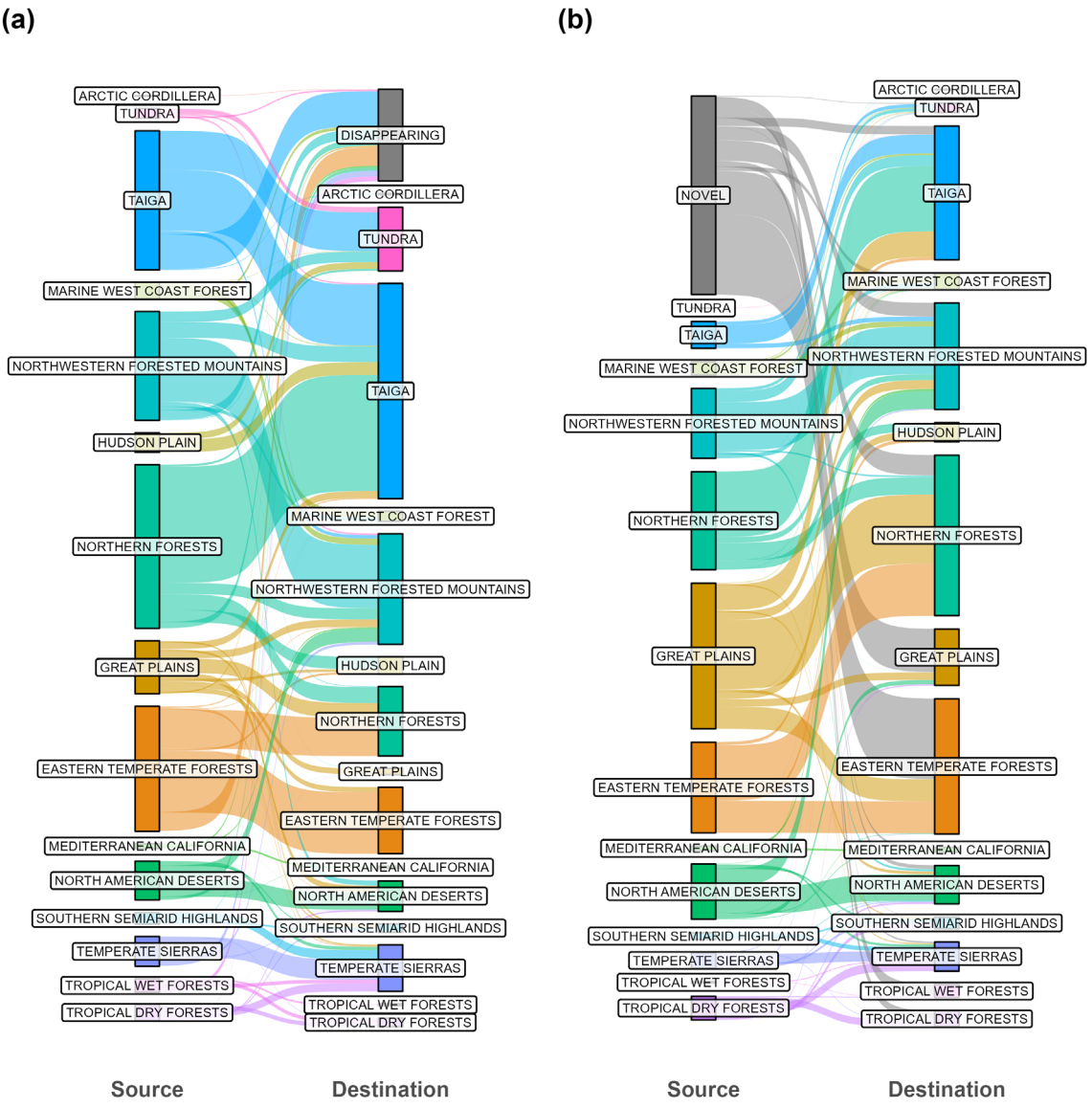


**FIGURE 4** | Sankey plot showing flows between ecoregions for locations that minimize compositional dissimilarity (a) from contemporary (1991–2020) to future climate (2071–2100), and (b) from future to contemporary climate. Note the "Source" in (a) represents the same set of forested pixels as the "Destinations" in (b). Several pixels that fell along a shoreline in the Water ecoregion are not shown. "Disappearing" and "Novel" pools represent predictions when the compositional difference was relatively high (Jaccard index > 0.5). See Figure S8 for an identical plot without these pools.

could have downstream effects on other taxa, including wildlife, microorganisms, and understory species, that rely on particular forest assemblages for habitat and nutrition. This work explores a new way of understanding and quantifying forest compositional changes, in a way that is biologically meaningful and without the need for classifying species assemblages or disaggregating assemblages to their constituent species.

### 4.1 | Forest Assemblage Shifts in Future Climates

Although predicted compositional change was high in many forests throughout the continent, there were numerous regions that may represent unique vulnerabilities, and potentially opportunities, in future climates. Forests in the southeastern United States, in particular, had among the highest levels of predicted compositional change in North America, regardless of whether predictions were done in forward or reverse directions. Numerous unique characteristics of this region likely make its forests particularly vulnerable to compositional shifts in future climates. First, forests in the southern United States have among the highest levels of tree diversity in North America, a large number of endemic species (Jenkins et al. 2015), and the region is a global hotspot for multiple tree genera, including two of the most speciose genera in North America—pines and oaks (Lyu et al. 2022; Nobis, Traiser, and Roth-Nebelsick 2012). High tree diversity and endemicity in these forests likely result in substantial compositional turnover over short geographic/climatic distances, such that small climatic changes over the coming decades could result in the loss and/or gain of many individual species resulting in novel assemblages. The geography of the southeastern region likely also influences the possibility of shifting compositions. As most compositional analogs are found north of their current location, the lack of temperate

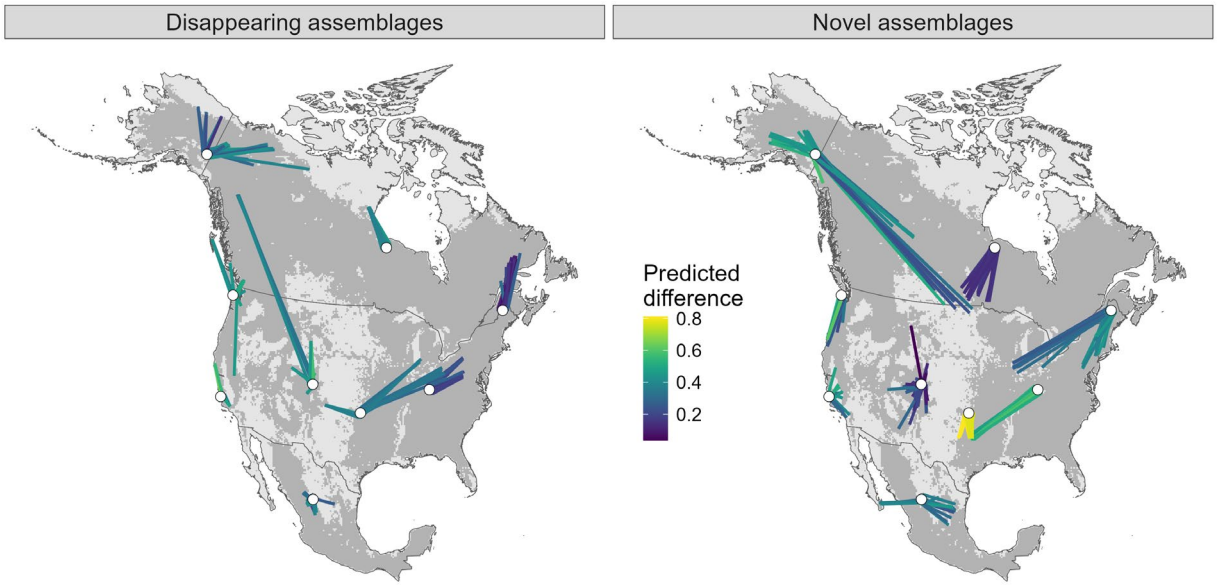


**FIGURE 5** | Locations of nearest future and contemporary compositional analogs for nine randomly selected points (with 75-km buffer) stratified in nine of the main forested Level-1 ecoregions (see Figure S1) in North America. Lines are colored by the predicted compositional difference (Jaccard index) between contemporary (1991–2020) and future climates (2071–2100), and dark gray areas are forests.

forests directly south of the region (not including the much drier forests of Mexico) constrain the availability of forests that could be preadapted to the future climates of this region. Consistent with this pattern, areas with the most forests south of their contemporary locations (i.e., the northern edge of forests in North America) have among the lowest levels of predicted compositional change. Likewise, the unique subtropical climate of the southeast, due in part to the influence of the Gulf of Mexico, likely also contributes to the possibility of compositional shifts as the climates further north may have suitable future temperature but lack adequately similar precipitation regimes. The confluence of climate, geography, and species diversity in the southeast portend great uncertainty whether contemporary assemblages can be maintained in this region.

Many forested areas in the northern parts of North America were predicted to have close compositional analogs in future climates, but these analogs were frequently a great distance from the contemporary forests (hundreds to thousands of kilometers away), which raises significant concern whether the species that make up these forests could actually reach their closest analog locations. In some regions in southern Alaska, where the nearest analog is > 1000 km away, for instance, some sort of intervention would likely be needed for the constituent species to reach the analog location. For many areas, such intervention is likely not feasible, but in cases where populations or species can be moved—as in assisted migration programs, or when sourcing climate-adapted seeds (Adams et al. 2024)—identifying where populations could be placed in similar assemblages could improve the likelihood of surviving and thriving in future climates. By considering forest changes from the community perspective, the integrated nature of species biotic and abiotic determinants are embedded (Louthan, Doak, and Angert 2015) and results regarding the community assemblage level of ecological organization provide insights about the maintenance of those dynamics.

### 4.2 | Phylogeny

Somewhat surprisingly, the phylogenetic model, which accounted for species shared evolutionary history, performed substantially worse than the taxonomic model, which only included information on species occurrences. Although we generally expected the inclusion of phylogeny would improve the model, this appeared not to be the case—for multiple possible reasons. First, because much of North America lies in a temperate climatic zone, the region may be too narrow in geographic or climatic extent to capture species phylogenetic turnover, which may be more emergent at multi-continental or global scales. While extending the geographic extent of the models seems promising and could better elucidate the drivers of phylogenetic composition, global models of phylogenetic composition are likely to be much less valuable for management or conservation. The temperate forests of Europe and Asia share many of the tree genera of North America and are likely phylogenetically similar to forests in North America, but identifying a future phylogenetic analog on a different continent is not particularly useful when local action is required to respond to climate change. The issue of geographic scale is also evident at the continental extent in our analysis—that is, in North America, very closely related species can inhabit very different climates. Pines are a good example of this in North America, where nearly every region has some sort of pine-dominated forest—though the species themselves differ. The wide distribution of other genera (e.g., *Quercus*, *Acer*, *Salix*) present in many parts of North America, have a similar homogenizing effect on forest phylogenetic compositions that acts to reduce the phylogenetic signal along climate gradients. Although phylogenetic gradients may be apparent at broad scales that capture global evolutionary dynamics, it is also possible that phylogenetic gradients could emerge at narrower geographic scales. Limiting analysis to a single latitudinal or elevational transect, for instance, could better distinguish warm and cold-adapted species, and capture the phylogenetic

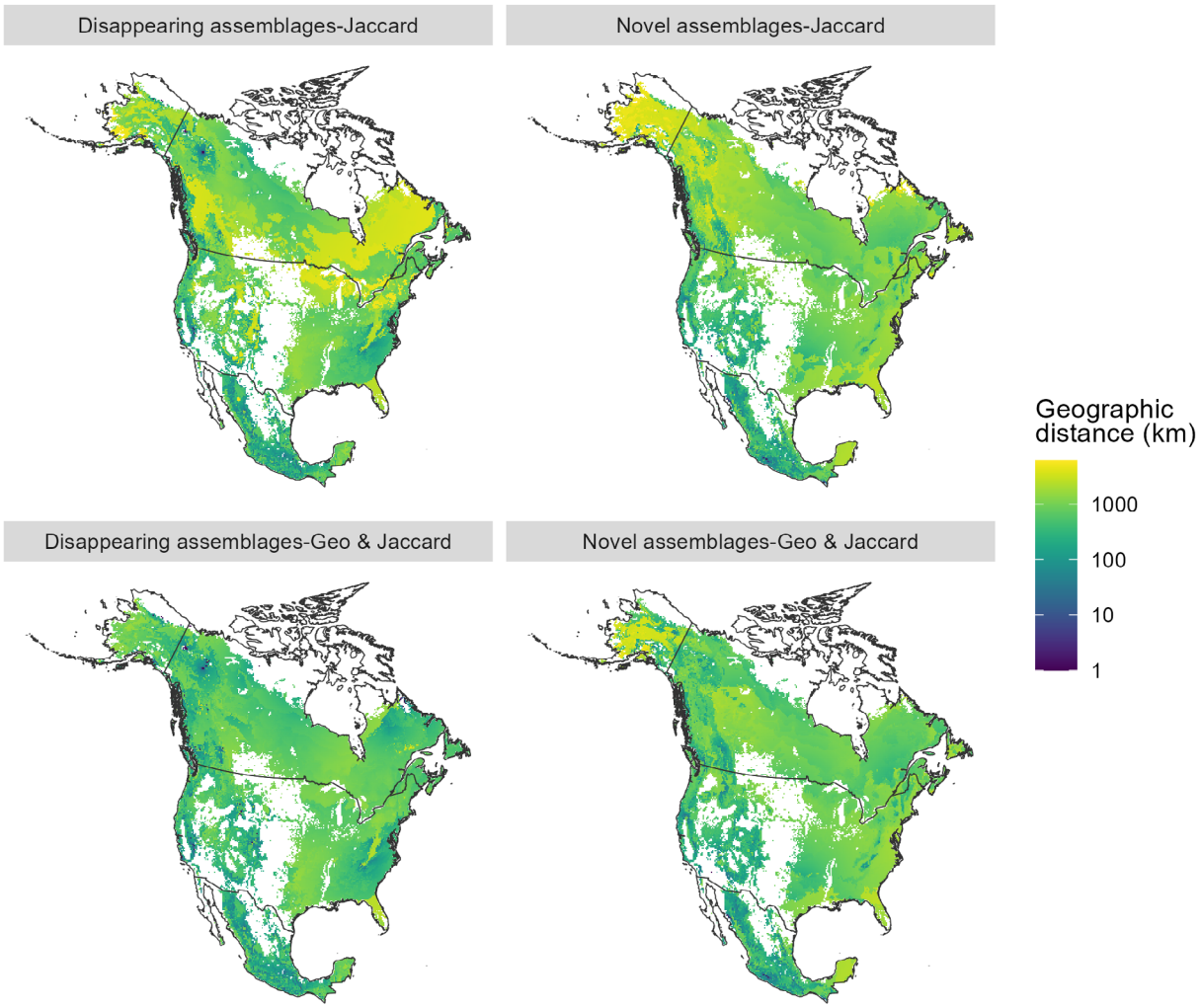


**FIGURE 6** | Geographic distances to locations that minimize compositional dissimilarity, when predicted from contemporary (1991–2020) to future (2071–2100) climate ("Disappearing assemblages"), and from future to contemporary climate ("Novel assemblages"). Maps in the top row are distances to the location with the strict minimum dissimilarity, whereas maps in the bottom row also account for geographic distances to the locations that minimize dissimilarity (geographically informed, see also Figure S2). Note the scale is $\log_{10}+1$ transformed.

signal in thermal tolerances (Lancaster and Humphreys 2020). However, previous work on pollen assemblages has shown that the relationship between phylogenetic composition and climate gradients has shifted over time (Pradhan, Nieto-Lugilde, and Fitzpatrick 2021). If the associations between phylogenetic composition are transient and nonstationary over time and/or space, this could partially explain why our phylogenetic model performed poorly compared with the taxonomic model.

### 4.3 | Caveats, Implications & Next Steps

Although our approach provides insights into how forest composition may change in response to future climates, there are numerous caveats that should be considered when interpreting the metrics of compositional change. First, our models assume forest composition is primarily governed by climate. Although this is a reasonable assumption at broad geographic scales—given that the constituent tree species distributions are frequently limited by climate at macroscales—other factors, such as fire, pest outbreaks, soils, and biotic interactions, can also play a role at a variety of spatial scales. When identifying more regional compositional analogs is desired, it may be worth including some of these non-climate effects, which could improve the inference and realism of the models. Second, tree species, being long-lived organisms that can take decades to reach maturity, will not respond instantaneously to climate change, and thus any shifts in community composition are likely to be lagged (Alexander et al. 2018; Bertrand et al. 2011). Although these sorts of maturity and migration considerations can be accounted for, to some extent, with individual species distribution models, they present more of a challenge for the type of community composition model done here. Thus, it is crucial to highlight that our metrics should not be a considered a measure of how much community composition *will* change, per se, but rather is best interpreted as a measure of the disruption of the contemporary climate–biodiversity relationship that could manifest as a shift in community composition in future climates. Finally, it is important to acknowledge that our model assumes forest communities are currently at equilibrium with climate. Although this is a basic assumption of most distribution modelling approaches, recent work has shown North American tree species tend to underfill

their potential ranges and some may be at disequilibrium in the contemporary climate (Sandel 2019; Seliger et al. 2021). This adds an additional layer of uncertainty, especially as disequilibrium appears to be higher among species with smaller range sizes, but we note GDMs built on contemporary forest inventory data have been shown to have a good ability to predict tree assemblage changes through time (Nieto-Lugilde et al. 2015), which bolsters the use of a space-for-time substitution to measure these climate change impacts.

Forest assemblages play an important role in the distributions of other taxa that utilize forests, so the possibility of some forest assemblages disappearing and other novel assemblages emerging are likely to have downstream effects for other, forest-utilizing, species. The impacts of disappearing and novel forests are likely to be strongest for species with strong associations with particular tree species or forest assemblages, whereas more generalist species may be largely unaffected by shifting forest compositions. Species reliant on oaks—which provide important food sources for wildlife and insect herbivores (Mcshea et al. 2007; Narango, Tallamy, and Shropshire 2020)—provide one such example, where the replacement of oaks with other tree species could have disproportionate effects on other forest-utilizing species. Beyond individual species, the reliance of whole assemblages on forest assemblages portends considerable uncertainty whether novel forest assemblages could result in novel assemblages of other species. In North America, of particular concern is the southeastern United States—which had among the highest levels of predicted compositional forest change in the continent—as it is home to high levels of diversity and/or endemicity of mammals, birds, amphibians, and reptiles (Jenkins et al. 2015). Although more work is needed to determine whether novel forest assemblages could result in novel assemblages of other taxa, quantifying macroscale links between forest assemblages and assemblages of other taxa, while controlling for climate variability, could improve our understanding of joint-taxa vulnerabilities to shifting climates.

Although our approach offers important macroscale insights on how forest compositions may shift with climate change, it can still be improved. At the forest community scale, understanding trait distributions may provide important information for ecosystem stability (de Bello et al. 2021). Integrating actual trait data in these sorts of models could more directly inform shifts in ecosystem function compared with either taxonomic or phylogenetic compositions. Many functional traits are phylogenetically conserved, and assessing trait composition could result in similar issues to those described for phylogenetic composition, but given that some phylogenetically conserved traits are also responsive to climate (Liu et al. 2024; Zhang et al. 2011) could provide a way forward. Intraspecific trait information collected over large geographic areas, in particular, could improve our understanding of shifting ecosystem function (Moran, Hartig, and Bell 2016) and could contribute to our understanding of how phenotypic plasticity and epigenetic responses could buffer species against climate change. Likewise, accounting for adaptive genetic variability in these sorts of models could offer a mechanistic understanding of how or why traits may shift in future climates. Although similar approaches have been applied to adaptive genetic variability of individual tree species (Fitzpatrick and Keller 2015; Gougherty, Keller, and Fitzpatrick 2021), these could be extended to the adaptive variability of whole forest communities to understand forest adaptive capacity to future climate change—especially if a common set of locally adapted genes could be identified across species (Whiting et al. 2024). Although more work needs to be done to compare and validate these techniques, they have the potential to extend our inference beyond climate novelty metrics to more explicitly address how forest assemblages may respond to future climates.

## 5 | Conclusions

Future climate shifts will put demands on species to shift their ranges in ways that could disrupt forest assemblages, such that some contemporary assemblages may be at high risk of disappearing from the landscape with some novel assemblages emerging. Our work shows that although nearly all forests in North America may need to undergo some compositional change to keep pace with climate change, future climates are suitable for many contemporary forest assemblages. Forest in the southeast United States had particularly high levels of predicted change, which raises considerable concern as it is a continental hotspot of diversity and endemicity of trees and multiple forest-utilizing taxa. Our approach for understanding future compositional changes advances climate novelty metrics with meaningful biological data that offers new insights into how forests may need to change in future climates.

### Author Contributions

**Andrew V. Gougherty:** conceptualization, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Anantha M. Prasad:** data curation, resources, writing – review and editing. **Matthew P. Peters:** data curation, resources, writing – review and editing. **Stephen N. Matthews:** data curation, resources, writing – review and editing. **Bryce T. Adams:** resources, visualization, writing – review and editing.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data and code that support the findings of this study are openly available in FigShare at https://doi.org/10.6084/m9.figshare.26381593. Tree distribution maps are available in the USDA Research Data Archive at https://doi.org/10.2737/RDS-2024-0020. Climate data are available from AdaptWest at https://adaptwest.databasin.org/pages/adaptwest-climatena/ (version 7.3).

### References

Adams, B. T., A. Royo, C. Kern, et al. 2024. "Identifying Climatically-Compatible Seedlots for the Eastern US: Building the Predictive Tools and Knowledge to Enable Forest Assisted Migration." *Frontiers in Forests and Global Change* 7: 1449340. https://doi.org/10.3389/ffgc.2024.1449340.

AdaptWest Project. 2022. "Gridded Current and Projected Climate Data for North America at 1km Resolution, Generated Using the ClimateNA v7.3 Software."

Alexander, J. M., L. Chalmandrier, J. Lenoir, et al. 2018. "Lags in the Response of Mountain Plant Communities to Climate Change." *Global Change Biology* 24, no. 2: 563–579. https://doi.org/10.1111/gcb.13976.

Augusto, L., A. De Schrijver, L. Vesterdal, A. Smolander, C. Prescott, and J. Ranger. 2015. "Influences of Evergreen Gymnosperm and Deciduous Angiosperm Tree Species on the Functioning of Temperate and Boreal Forests." *Biological Reviews* 90, no. 2: 444–466. https://doi.org/10.1111/brv.12119.

Ávila-Lovera, E., K. Winter, and G. R. Goldsmith. 2023. "Evidence for Phylogenetic Signal and Correlated Evolution in Plant–Water Relation Traits." *New Phytologist* 237, no. 2: 392–407. https://doi.org/10.1111/nph.18565.

Bertrand, R., J. Lenoir, C. Piedallu, et al. 2011. "Changes in Plant Community Composition Lag Behind Climate Warming in Lowland Forests." *Nature* 479, no. 7374: 517–520. https://doi.org/10.1038/nature10548.

Carroll, C., J. J. Lawler, D. R. Roberts, and A. Hamann. 2015. "Biotic and Climatic Velocity Identify Contrasting Areas of Vulnerability to Climate Change." *PLoS One* 10, no. 10: e0140486. https://doi.org/10.1371/journal.pone.0140486.

Commission for Environmental Cooperation. 2023. "Land Cover of North America at 30 Meters, 2020." http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2020/.

D'Amen, M., C. Rahbek, N. E. Zimmermann, and A. Guisan. 2017. "Spatial Predictions at the Community Level: From Current Approaches to Future Frameworks." *Biological Reviews* 92, no. 1: 169–187. https://doi.org/10.1111/brv.12222.

Davies, T. J., E. M. Wolkovich, N. J. B. Kraft, et al. 2013. "Phylogenetic Conservatism in Plant Phenology." *Journal of Ecology* 101, no. 6: 1520–1530. https://doi.org/10.1111/1365-2745.12154.

de Bello, F., S. Lavorel, L. M. Hallett, et al. 2021. "Functional Trait Effects on Ecosystem Stability: Assembling the Jigsaw Puzzle." *Trends in Ecology & Evolution* 36, no. 9: 822–836. https://doi.org/10.1016/j.tree.2021.05.001.

Ferrier, S., and A. Guisan. 2006. "Spatial Modelling of Biodiversity at the Community Level." *Journal of Applied Ecology* 43, no. 3: 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x.

Ferrier, S., T. D. Harwood, and K. J. Williams. 2012. "Queensland's Biodiversity Under Climate Change: Ecological Scaling of Terrestrial Environmental Change." CSIRO Climate Adaptation Flagship Working Paper 12B.

Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. "Using Generalized Dissimilarity Modelling to Analyse and Predict Patterns of Beta Diversity in Regional Biodiversity Assessment." *Diversity and Distributions* 13, no. 3: 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x.

Fitzpatrick, M., K. Mokany, D. Nieto-Lugilde, and S. Ferrier. 2022. "Gdm: Generalized Dissimilarity Modeling." R Package Version 1.5.0–9.1. https://CRAN.R-project.org/package=gdm.

Fitzpatrick, M. C., and S. R. Keller. 2015. "Ecological Genomics Meets Community-Level Modelling of Biodiversity: Mapping the Genomic Landscape of Current and Future Environmental Adaptation." *Ecology Letters* 18, no. 1: 1–16. https://doi.org/10.1111/ele.12376.

Gougherty, A. 2024. "Data From "Climate Change and the Emergence of No-Analog Forest Assemblages in North America."" figshare. p. 1575394 Bytes. https://doi.org/10.6084/M9.FIGSHARE.26381593.

Gougherty, A. V., and T. J. Davies. 2022. "Host Phylogenetic Diversity Predicts the Global Extent and Composition of Tree Pests." *Ecology Letters* 25, no. 1: 101–112. https://doi.org/10.1111/ele.13908.

Gougherty, A. V., S. R. Keller, and M. C. Fitzpatrick. 2021. "Maladaptation, Migration and Extirpation Fuel Climate Change Risk in a Forest Tree Species." *Nature Climate Change* 11, no. 2: 166–171. https://doi.org/10.1038/s41558-020-00968-6.

Graham, L. J., B. G. Weinstein, S. R. Supp, and C. H. Graham. 2017. "Future Geographic Patterns of Novel and Disappearing Assemblages Across Three Dimensions of Diversity: A Case Study With Ecuadorian Hummingbirds." *Diversity and Distributions* 23, no. 8: 944–954. https://doi.org/10.1111/ddi.12587.

Hao, M., C. Zhang, X. Zhao, and K. von Gadow. 2018. "Functional and Phylogenetic Diversity Determine Woody Productivity in a Temperate Forest." *Ecology and Evolution* 8, no. 5: 2395–2406. https://doi.org/10.1002/ece3.3857.

Hijmans, R. J. 2024. "Package 'terra'." R Package Version 1.7–71. https://CRAN.R-project.org/package=terra.

Hobbs, R. J., L. E. Valentine, R. J. Standish, and S. T. Jackson. 2018. "Movers and Stayers: Novel Assemblages in Changing Environments." *Trends in Ecology & Evolution* 33, no. 2: 116–128. https://doi.org/10.1016/j.tree.2017.11.001.

Jackson, S. T. 2013. "Perspective: Ecological Novelty Is Not New." In *Novel Ecosystems*, 61–65. Chichester, UK: John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118354186.ch7.

Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. "US Protected Lands Mismatch Biodiversity Priorities." *Proceedings of the National Academy of Sciences* 112, no. 16: 5081–5086. https://doi.org/10.1073/pnas.1418034112.

Jin, Y., and H. Qian. 2019. "V.PhyloMaker: An R Package That Can Generate Very Large Phylogenies for Vascular Plants." *Ecography* 42, no. 8: 1353–1359. https://doi.org/10.1111/ecog.04434.

Kembel, S. W., P. D. Cowan, M. R. Helmus, et al. 2010. "Picante: R Tools for Integrating Phylogenies and Ecology." *Bioinformatics* 26, no. 11: 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Lancaster, L. T., and A. M. Humphreys. 2020. "Global Variation in the Thermal Tolerances of Plants." *Proceedings of the National Academy of Sciences* 117, no. 24: 13580–13587. https://doi.org/10.1073/pnas.1918162117.

Liu, H., Q. Ye, M. R. Lundgren, et al. 2024. "Phylogeny and Climate Explain Contrasting Hydraulic Traits in Different Life Forms of 150 Woody Fabaceae Species." *Journal of Ecology* 112, no. 4: 741–754. https://doi.org/10.1111/1365-2745.14266.

Louthan, A. M., D. F. Doak, and A. L. Angert. 2015. "Where and When Do Species Interactions Set Range Limits?" *Trends in Ecology & Evolution* 30, no. 12: 780–792. https://doi.org/10.1016/j.tree.2015.09.011.

Lyu, L., F. Leugger, O. Hagen, et al. 2022. "An Integrated High-Resolution Mapping Shows Congruent Biodiversity Patterns of Fagales and Pinales." *New Phytologist* 235, no. 2: 759–772. https://doi.org/10.1111/nph.18158.

Mahony, C. R., T. Wang, A. Hamann, and A. J. Cannon. 2022. "A Global Climate Model Ensemble for Downscaled Monthly Climate Normals Over North America." *International Journal of Climatology* 42, no. 11: 5871–5891. https://doi.org/10.1002/joc.7566.

Mcshea, W. J., W. M. Healy, P. Devers, et al. 2007. "Forestry Matters: Decline of Oaks Will Impact Wildlife in Hardwood Forests." *Journal of Wildlife Management* 71, no. 5: 1717–1728. https://doi.org/10.2193/2006-169.

Mokany, K., C. Ware, S. N. C. Woolley, S. Ferrier, and M. C. Fitzpatrick. 2022. "A Working Guide to Harnessing Generalized Dissimilarity Modelling for Biodiversity Analysis and Conservation Assessment." *Global Ecology and Biogeography* 31, no. 4: 802–821. https://doi.org/10.1111/geb.13459.

Moran, E. V., F. Hartig, and D. M. Bell. 2016. "Intraspecific Trait Variation Across Scales: Implications for Understanding Global Change

Responses." *Global Change Biology* 22, no. 1: 137–150. https://doi.org/10.1111/gcb.13000.

Narango, D. L., D. W. Tallamy, and K. J. Shropshire. 2020. "Few Keystone Plant Genera Support the Majority of Lepidoptera Species." *Nature Communications* 11, no. 1: 5751. https://doi.org/10.1038/s41467-020-19565-4.

Nieto-Lugilde, D., K. C. Maguire, J. L. Blois, J. W. Williams, and M. C. Fitzpatrick. 2015. "Close Agreement Between Pollen-Based and Forest Inventory-Based Models of Vegetation Turnover." *Global Ecology and Biogeography* 24, no. 8: 905–916. https://doi.org/10.1111/geb.12300.

Nobis, M. P., C. Traiser, and A. Roth-Nebelsick. 2012. "Latitudinal Variation in Morphological Traits of the Genus Pinus and Its Relation to Environmental and Phylogenetic Signals." *Plant Ecology and Diversity* 5, no. 1: 1–11. https://doi.org/10.1080/17550874.2012.687501.

Omernik, J. M., and G. E. Griffith. 2014. "Ecoregions of the Conterminous United States: Evolution of a Hierarchical Spatial Framework." *Environmental Management* 54, no. 6: 1249–1266. https://doi.org/10.1007/s00267-014-0364-1.

Ordonez, A., F. Riede, S. Normand, and J.-C. Svenning. 2024. "Towards a Novel Biosphere in 2300: Rapid and Extensive Global and Biome-Wide Climatic Novelty in the Anthropocene." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 379, no. 1902: 20230022. https://doi.org/10.1098/rstb.2023.0022.

Ordonez, A., and J. W. Williams. 2013. "Climatic and Biotic Velocities for Woody Taxa Distributions Over the Last 16 000 Years in Eastern North America." *Ecology Letters* 16, no. 6: 773–781. https://doi.org/10.1111/ele.12110.

Ordonez, A., J. W. Williams, and J.-C. Svenning. 2016. "Mapping Climatic Mechanisms Likely to Favour the Emergence of Novel Communities." *Nature Climate Change* 6: 1104–1109. https://doi.org/10.1038/nclimate3127.

Peters, M. P., S. N. Matthews, A. M. Prasad, and L. R. Iverson. 2022. "Defining Landscape-Level Forest Types: Application of Latent Dirichlet Allocation to Species Distribution Models." *Landscape Ecology* 37, no. 7: 1819–1837. https://doi.org/10.1007/s10980-022-01436-6.

Pradhan, K., D. Nieto-Lugilde, and M. C. Fitzpatrick. 2021. "Relationships Between Climate and Phylogenetic Community Structure of Fossil Pollen Assemblages Are Not Constant During the Last Deglaciation." *PLoS One* 16, no. 7: e0240957. https://doi.org/10.1371/journal.pone.0240957.

Prasad, A., J. Pedlar, M. Peters, et al. 2020. "Combining US and Canadian Forest Inventories to Assess Habitat Suitability and Migration Potential of 25 Tree Species Under Climate Change." *Diversity and Distributions* 26, no. 9: 1142–1159. https://doi.org/10.1111/ddi.13078.

Prasad, A. M., M. P. Peters, J. H. Pedlar, et al. 2024. "Habitat and Migration Dynamics of North American Tree Species Under Climate Change."

R Core Team. 2023. "R: A Language and Environment for Statistical Computing [Computer Software]." R Foundation for Statistical Computing. https://www.R-project.org/.

Rathore, P., A. Roy, and H. Karnatak. 2022. "Predicting the Future of Species Assemblages Under Climate and Land Use Land Cover Changes in Himalaya: A Geospatial Modelling Approach." *Climate Change Ecology* 3: 100048. https://doi.org/10.1016/j.ecochg.2022.100048.

Rosauer, D. F., S. Ferrier, K. J. Williams, G. Manion, J. S. Keogh, and S. W. Laffan. 2014. "Phylogenetic Generalised Dissimilarity Modelling: A New Approach to Analysing and Predicting Spatial Turnover in the Phylogenetic Composition of Communities." *Ecography* 37, no. 1: 21–32. https://doi.org/10.1111/j.1600-0587.2013.00466.x.

Sandel, B. 2019. "Disequilibrium in Trait-Climate Relationships of Trees and Birds." *Frontiers in Ecology and Evolution* 7: 1–11. https://doi.org/10.3389/fevo.2019.00138.

Seliger, B. J., B. J. McGill, J.-C. Svenning, and J. L. Gill. 2021. "Widespread Underfilling of the Potential Ranges of North American Trees." *Journal of Biogeography* 48, no. 2: 359–371.

Stralberg, D., D. Jongsomjit, C. A. Howell, et al. 2009. "Re-Shuffling of Species With Climate Disruption: A No-Analog Future for California Birds?" *PLoS One* 4, no. 9: e6825.

Swenson, N. G., and B. J. Enquist. 2007. "Ecological and Evolutionary Determinants of a Key Plant Functional Trait: Wood Density and Its Community-Wide Variation Across Latitude and Elevation." *American Journal of Botany* 94, no. 3: 451–459. https://doi.org/10.3732/ajb.94.3.451.

Valencia, E., F. de Bello, T. Galland, et al. 2022. "Effects of Functional and Phylogenetic Diversity on the Temporal Dynamics of Soil N Availability." *Plant and Soil* 472, no. 1: 629–640. https://doi.org/10.1007/s11104-021-05277-1.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. "Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America." *PLoS One* 11, no. 6: e0156720. https://doi.org/10.1371/journal.pone.0156720.

Whiting, J. R., T. R. Booker, C. Rougeux, et al. 2024. "The Genetic Architecture of Repeated Local Adaptation to Climate in Distantly Related Plants." *Nature Ecology & Evolution* 8, no. 10: 1933–1947. https://doi.org/10.1038/s41559-024-02514-5.

Williams, J. W., and S. T. Jackson. 2007. "Novel Climates, No-Analog Communities, and Ecological Surprises." *Frontiers in Ecology and the Environment* 5, no. 9: 475–482. https://doi.org/10.1890/070037.

Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 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, no. 14: 5738–5742.

Williams, J. W., B. N. Shuman, and T. Webb III. 2001. "Dissimilarity Analyses of Late-Quaternary Vegetation and Climate in Eastern North America." *Ecology* 82, no. 12: 3346–3362.

Zhang, M., C. Ji, J. Zhu, X. Wang, D. Wang, and W. Han. 2017. "Comparison of Wood Physical and Mechanical Traits Between Major Gymnosperm and Angiosperm Tree Species in China." *Wood Science and Technology* 51, no. 6: 1405–1419. https://doi.org/10.1007/s00226-017-0954-1.

Zhang, S.-B., J. W. F. Slik, J.-L. Zhang, and K.-F. Cao. 2011. "Spatial Patterns of Wood Traits in China Are Controlled by Phylogeny and the Environment." *Global Ecology and Biogeography* 20, no. 2: 241–250. https://doi.org/10.1111/j.1466-8238.2010.00582.x.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section.