

# Late Quaternary climate legacies in contemporary plant functional composition

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## Abstract

The functional composition of plant communities is commonly thought to be determined by contemporary climate. However, if rates of climate-driven immigration and/or exclusion of species are slow, then contemporary functional composition may be explained by paleoclimate as well as by contemporary climate. We tested this idea by coupling contemporary maps of plant functional trait composition across North and South America to paleoclimate means and temporal variation in temperature and precipitation from the Last Interglacial (120 ka) to the present. Paleoclimate predictors strongly improved prediction of contemporary functional composition compared to contemporary climate predictors, with a stronger influence of temperature in North America (especially during periods of ice melting) and of precipitation in South America (across all times). Thus, climate from tens of thousands of years ago influences contemporary functional composition via slow assemblage dynamics.

## KEYWORDS

climate change, disequilibrium, exclusion, functional diversity, functional trait, Holocene, immigration, lag, legacy, Pleistocene

## 1 | INTRODUCTION

Shifts in the functional composition of plant communities can indicate variation in ecosystem functioning and ecosystem services (Chapin et al., 2000; Díaz & Cabido, 2001; Hooper et al., 2005; Jetz et al., 2016). Forecasting the two major components of functional composition, functional trait means (FM), and functional diversity (FD) (Villéger, Mason, & Moullot, 2008), is therefore of central interest. Insights into geographic variation in the contemporary functional composition of plant communities (Violle, Reich, Pacala, Enquist, & Kattge, 2014) comes from field surveys (Asner et al., 2014; Baraloto et al., 2010; De Bello, Lepš, & Sebastià, 2006), macroecological approaches (Campbell & McAndrews, 1993; Lamanna et al., 2014; Šimová et al., 2015; Swenson et al., 2012), and remote sensing approaches (Asner, Martin, Knapp, et al., 2017; Asner, Martin, Tupayachi, & Llactayo, 2017; Jetz et al., 2016). However, little is known about changes in these functional trait patterns over longer time scales (Blonder, Royer, Johnson, Miller, & Enquist, 2014; Polly et al., 2011; Thuiller et al., 2008). There is also growing evidence that paleoclimate has directly and indirectly structured contemporary species composition and functional composition (Ordonez & Svenning, 2016; Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015). It has been unclear how these paleoclimate effects on species composition translate to differences in functional composition, because even species assemblages in disequilibrium with contemporary climate may have equilibrium functional relationships with contemporary climate (Fukami, Martijn Bezemer, Mortimer, & Putten, 2005).

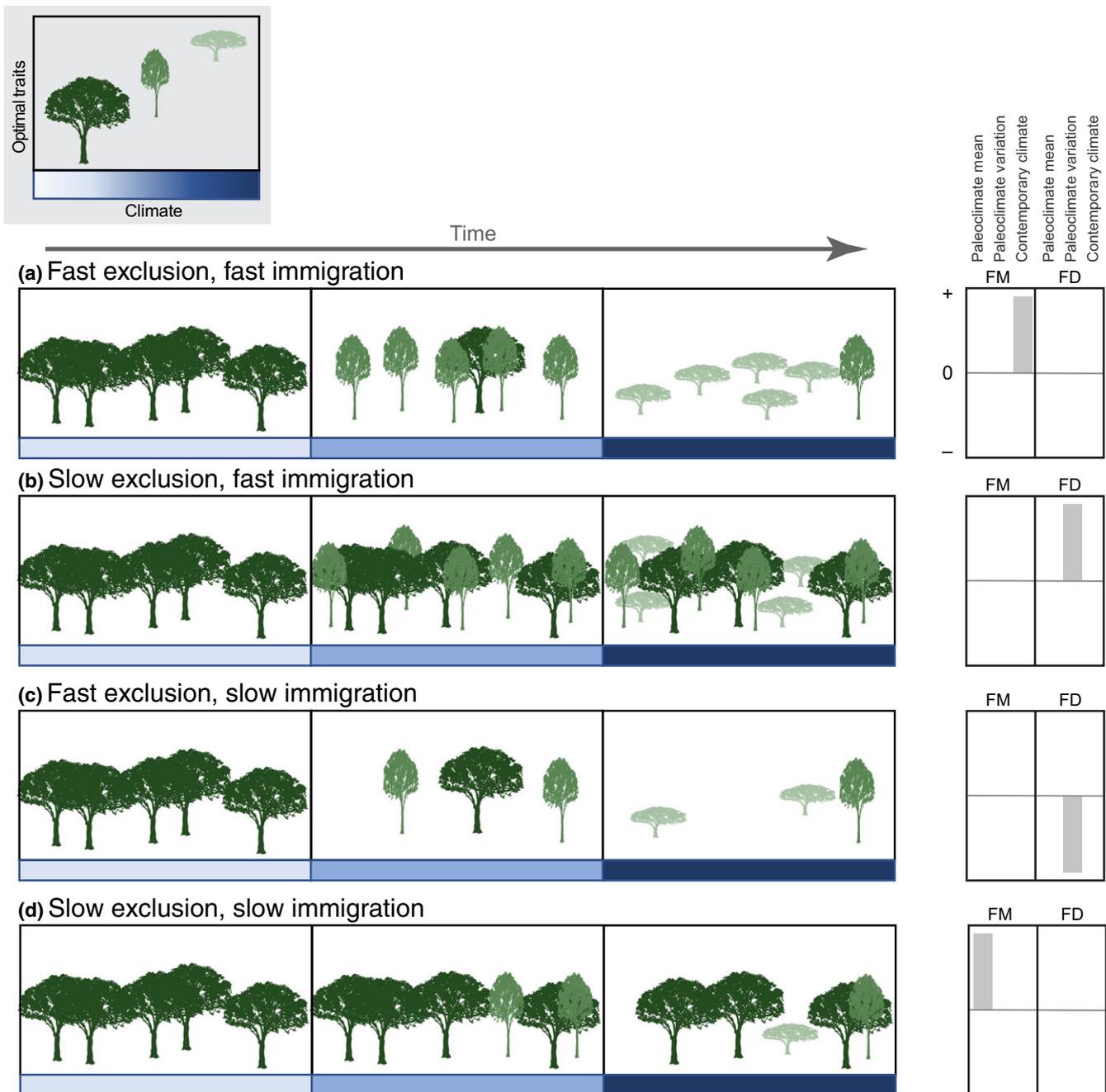
A core hypothesis of plant functional ecology is that contemporary environments determine contemporary functional composition (Enquist et al., 2015; Grime, 1974; Raunkjær, 1907; Schimper, 1898; Von Humboldt & Bonpland, 1807 (tr. 2009)). Many studies have shown relationships between FMs or FD and contemporary environmental variables, e.g. Cornwell and Ackerly (2009), Moles et al. (2014), suggesting equilibrium with contemporary environmental conditions is plausible. However, paleoclimate may also have had a strong influence on contemporary functional composition at large spatial scales (Svenning et al., 2015). A mismatch could exist between contemporary climate and contemporary FMs and FD because of disequilibrium in species' geographic ranges and lack of more appropriate species in the regional pool (Davis & Shaw, 2001; Enquist et al., 2015). Mechanisms that could lead to differing degrees of lagged responses of FMs and FD, and thus disequilibrium, include differential rates of exclusion and immigration driven by variation in dispersal limitation, longevity, and species interaction strengths that are associated with certain functional traits (Davis, 1984; Eiserhardt, Borchsenius, Plum, Ordonez, & Svenning, 2015; Enquist et al., 2015; Svenning & Sandel, 2013; Webb, 1986). Evidence for disequilibrium in functional composition is growing. For example, instability in climate in the Late Quaternary may have influenced contemporary functional composition in Europe (Mathieu & Jonathan Davies, 2014; Ordonez & Svenning, 2015, 2017; Svenning et al., 2015) and in the Americas (Ordonez & Svenning, 2016).

Paleoclimate influences on plant species composition are better known. For example, many tropical forests and temperate understory assemblages have compositions lagging contemporary climate changes at  $10^1$ – $10^3$  year timescales (Campbell & McAndrews, 1993; Cole, Bhagwat, & Willis, 2014; DeVicor, Julliard, Couvet, & Jiguet, 2008; La Sorte & Jetz, 2012). At  $10^3$ – $10^5$  year timescales, the European flora (Svenning & Skov, 2007) and North American plant range size distributions (Morueta-Holme et al., 2013) show strong signals of slow recovery from cover of ice sheets due to late-Quaternary glaciation. At  $10^5$ – $10^6$  year timescales, African and Madagascan palm distributions are predicted by Pliocene precipitation patterns (Blach-Overgaard, Kissling, Dransfield, Balslev, & Svenning, 2013; Rakotoarinivo et al., 2013). Last, at  $10^6$ – $10^7$  year timescales, Cenozoic climate change and land connectivity shifts have resulted in cold tolerance-driven extinction of some temperate trees (Eiserhardt et al., 2015), and have limited the dispersal and radiation of certain clades (Morley, 2011; Woodruff, 2010).

Here we first test a hypothesis (Hypothesis 0) that paleoclimate has additional predictive power for functional composition beyond that provided by contemporary climate. We do so by determining whether FMs or FD are best predicted by contemporary climate alone or by contemporary climate and paleoclimate together.

We also test four hypotheses for how paleoclimate and contemporary climate could influence contemporary FMs and FD (Figure 1). The hypotheses explore fast versus slow processes for exclusion and immigration of species under linear change in a mean climate value (Blonder et al., 2017). “Fast” and “slow” are terms used to indicate temporal rates of change in species composition and functional traits relative to the rate of climate change; mechanisms underlying exclusion and immigration could include ecological processes such as environmental filtering, competition, or dispersal or evolutionary processes such as speciation, adaptation, or extinction. These hypotheses are thus relevant over intervals where changes in climate can be treated as linear. They also all assume an underlying linear trait-environment relationship that would be obtained in the equilibrium limit.

In Hypothesis 1 (Figure 1a), if exclusion of species with inappropriate traits for a novel climate is fast and if immigration of more appropriate species is fast, then contemporary climate mean – contemporary FM relationships will exist. In Hypothesis 2 (Figure 1b), if exclusion of species with inappropriate traits is slow and if immigration of more appropriate species is fast, paleoclimate temporal variation – contemporary FD relationships will be positive because more species with appropriate traits are continually added to the assemblage without loss of other species. In Hypothesis 3 (Figure 1c), if exclusion of species with inappropriate traits is fast but if immigration of appropriate species is slow, then paleoclimate temporal variation – contemporary FD relationships will be negative because species with inappropriate traits become lost from an assemblage without replacement by other species. In Hypothesis 4 (Figure 1d), if exclusion is slow and if immigration is slow, then paleoclimate mean – contemporary FM relationships will exist because of temporally lagged losses and gains of suitable species.



**FIGURE 1** Four hypothetical scenarios for the relationship between contemporary functional traits and climate change. Inset panel shows the assumed equilibrium trait–environment relationship. (a) Hypothesis 1, fast exclusion and fast immigration: species will track contemporary climate, and there will be a strong contemporary climate mean – functional trait mean relationship. (b) Hypothesis 2, slow exclusion but fast immigration: many species that were at one time suitable still remain part of the assemblage, and there will be a positive relationship between paleoclimate temporal variation and functional diversity. (c) Hypothesis 3, fast exclusion but slow immigration: only species that were at all times suitable will be able to enter the assemblage, and there will be a negative relationship between paleoclimate temporal variation and functional diversity. (d) Hypothesis 4, slow exclusion and slow immigration: species will fail to track contemporary climate, and there will be a strong paleoclimate mean – functional trait mean relationship [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

These four hypotheses provide nonexclusive predictions of relationships between climate and functional trait patterns. More than one of these patterns could be simultaneously observed, depending on the dynamics of climate over a long period comprising multiple approximately linear changes. That is, predictions of relationships

between e.g. paleoclimate variation and contemporary FD do not preclude observation of relationships between paleoclimate mean and contemporary FMs.

Here, we ask: (a) whether paleoclimate means and temporal variation improve predictions of contemporary FMs and FD (Hypothesis

0), and (b) which of the proposed hypotheses (Hypothesis 1 – Hypothesis 4) are consistent with empirical patterns of contemporary FMs and FD. We derived gridded maps of contemporary FMs and FD (as convex hull volume (Cornwell, Schwilk, & Ackerly, 2006)) across the Americas by merging species-mean trait data with maps of species distributions. We used five plant functional traits that are representative of major ecological strategy axes (Díaz et al., 2016; Westoby & Wright, 2006), and predictive of species sorting along environmental gradients (Moles et al., 2014; Šimová et al., 2015, 2018). We then coupled these estimates with contemporary and paleoclimate maps at timescales spanning the Last Interglacial (120 ka) to the present. We chose climate axes of mean annual temperature and annual precipitation because of their established trait-environment relationships (Moles et al., 2014), and their ability to be reconstructed by general circulation models.

## 2 | MATERIALS AND METHODS

### 2.1 | Species distribution maps

We obtained occurrence data for New World plants from the BIEN database (version 3.0, access date 26 February 2017, <https://www.biendata.org>) (Enquist, Condit, Peet, Schildhauer, & Thiers, 2016; Maitner et al., 2018). Following Morueta-Holme et al. (2013), we selected only data that represented geo-validated and noncultivated occurrences, and standardized all taxonomic names (Boyle et al., 2013). Occurrence points were nonrandomly distributed, with higher observation densities in the continental United States and in Central America/northwestern South America.

To reduce biases from spatial variation in sampling intensity, we estimated species' geographic ranges using convex hulls (Elith & Leathwick, 2009). Convex hulls can be estimated without using climate variables for niche modeling, avoiding any potential circularity in our analyses that would be caused by (for example) a maximum entropy model calibrated on contemporary climate variables. We generated range polygons from latitude/longitude coordinates for species with more than three non-collinear observation points. For species with three or fewer observations (6,886/74,491 species = 9.2%), we assumed that the species was present only in the 100 × 100-km grid cell(s) containing the observation. We rasterized predictions over the Western Hemisphere on a 100 × 100-km grid cell equal area projection centered at 80°W, 15°N.

### 2.2 | Functional trait data

We selected five functional traits representing major ecological strategy axes for growth, survival, and reproduction (Díaz et al., 2016; Westoby & Wright, 2006). These included specific leaf area, plant height, seed mass, stem specific density, and leaf nitrogen. Trait data were obtained from the TRY database (<https://www.try-db.org>, accession date 19 June 2013) (Kattge et al., 2011), covering 45,507 species (7,051 genera). A list of data references is in Supporting Information Table S1. Because many taxa were missing some

observations of certain variables, a phylogenetic gap-filling approach (Schrodte et al., 2015) was used to estimate missing values; then for a fraction of taxa that were present in the occurrence data but not present in the TRY data (59,423 species, 3,343 genera), missing values were filled with genus means estimated from the TRY data. This approach likely results in less bias than omitting data for species without exact matches to trait data.

We also categorized each species by its growth habit. Using a New World database (Engemann et al., 2016), we classified species as woody (29,676 species) or non-woody (44,324 species). Analyses were carried out for either all or only woody species to distinguish potentially different climate drivers on traits between growth forms (Díaz et al., 2016; Šimová et al., 2018).

### 2.3 | Functional trait mapping

We used the distribution maps to estimate the species composition within each grid cell. We then matched this species list against the functional trait data to estimate the distribution of log-transformed traits within each grid cell. To reduce undersampling biases, we then removed from the analysis all cells with richness of species with nonmissing trait values <100 (a value chosen to be small, in this case representing the 7% quantile of the all species data, and which primarily removes extreme-latitude cells in Greenland and Ellesmere Island in the northern hemisphere, and Tierra del Fuego in the southern hemisphere) (Supporting Information Figure S1). This procedure was repeated for woody species.

To estimate FMs, we calculated the average trait value across all species occurring within the cell, based on overlapping range maps. To simplify these five axes, we calculated a “FM PC1”, defined as the score along the first principal component of the five mapped trait axes. This axis explained 83.5% of the variation in traits for the woody species subset and 74.5% of the variation for all species, and corresponds to increasing plant height, seed mass, and stem specific density, as well as decreasing SLA and leaf nitrogen content (Supporting Information Figure S2).

To estimate FD, we first calculated the five-dimensional convex hull volume across log-transformed values of each trait value occurring within the cell (Villéger et al., 2008). Second, we corrected this estimate because convex hull volumes often scale linearly with sample size, and because the fraction of species per grid cell with available trait measurements (“trait coverage”) was variable (78% mean, 10% s.d). To correct for the sample size effect in FD, we built a null model. We calculated the convex hull volume of random samples of the full trait dataset with species richness varying from 100 to 10,000 in steps of 100 (“FD<sub>true</sub>”), then subsampled each to a trait coverage value varying from 0.05 to 1.0 in steps of 0.05, and then recalculated the convex hull volume based on this subsample (“FD<sub>observed</sub>”). We repeated the convex hull volume calculation 10 times for each combination of species richness and trait coverage. We then built a linear model to predict FD<sub>true</sub> on the basis of linear terms of FD<sub>observed</sub>, species richness, and trait coverage, as well as 2-way and 3-way interactions between these variables. This model

explained 95.8% of the variation in  $FD_{true}$ . We therefore applied this model to  $FD_{observed}$  in the empirical data to yield a corrected estimate of  $FD_{true}$  (hereafter, FD) that accounted for variation in trait coverage.

$FD_{observed}$  and species richness are positively correlated, because as species richness increases within a grid cell,  $FD_{observed}$  can only stay constant or increase. Thus, it may be difficult to separate effects of paleoclimate-related processes on FD from effects on species richness. To partially address this issue, we also repeat all analyses for another composite variable  $FD_{res}$ , defined as the residuals of a regression of the corrected estimate of FD ( $FD_{true}$ ) on species richness. Thus positive values of  $FD_{res}$  indicate FD values higher than expected based on a random assemblage with the same species richness, while negative values indicate values lower than expected.

## 2.4 | Contemporary climate data

We obtained contemporary climate predictions (1979–2013 AD averages) for mean annual temperature (MAT) and mean annual precipitation (MAP) from the CHELSA dataset version 1.2 (available at <https://chelsea-climate.org/>) (Karger et al., 2017). The climate dataset is based on a quasi-mechanistic statistical downscaling of the ERA (European Re-Analysis) interim global circulation model with a GPCP (Global Precipitation Climatology Centre) bias correction, and incorporating topoclimate (Karger et al., 2017). This approach avoids biases inherent to interpolation between weather stations with uneven coverage of geographic and climate space. We then re-projected the 1-arcsecond resolution data to the same grid as the species distribution maps.

## 2.5 | Paleoclimate data

We obtained paleoclimate data from the HadCM3 general circulation model. The HadCM3 model consists of a coupled atmospheric, ocean, and sea ice model with noninteractive vegetation, with an atmospheric resolution of  $2.5^\circ$  latitude  $\times$   $3.75^\circ$  longitude. The model was driven by variations in orbital configuration, greenhouse gases, ice-sheet topography, and coincident sea level changes and bathymetry since 120 ka. Simulations included the effects of abrupt “fresh-water” pulses and the resulting abrupt climate changes that occurred during at 17 ka (Heinrich event) and 13 ka (Younger Dryas). Boundary conditions and spin-up are fully described in Hoogakker et al. (2016), Singarayer and Valdes (2010). Data were available at time points beginning 0–120 ka in 1 kyr slices from 1–22 ka, in 2 kyr slices from 22–84 ka, and in 4 kyr slices from 84–120 ka (example time slices in Figure 2, all time slices in Supporting Information Figures S3 and S4).

Model output was reprojected to the same coordinate system and resolution as the contemporary species distribution maps. This approach assumes a negligible impact of temporal variation in sea level on the vast majority of pixels and is the best compromise given that only contemporary functional composition data were available. Paleoclimate maps are close to contemporary climate maps during

the Holocene, and diverge strongly during the Pleistocene, as measured by mean absolute deviation between contemporary and paleoclimate pixel values (Supporting Information Figure S5).

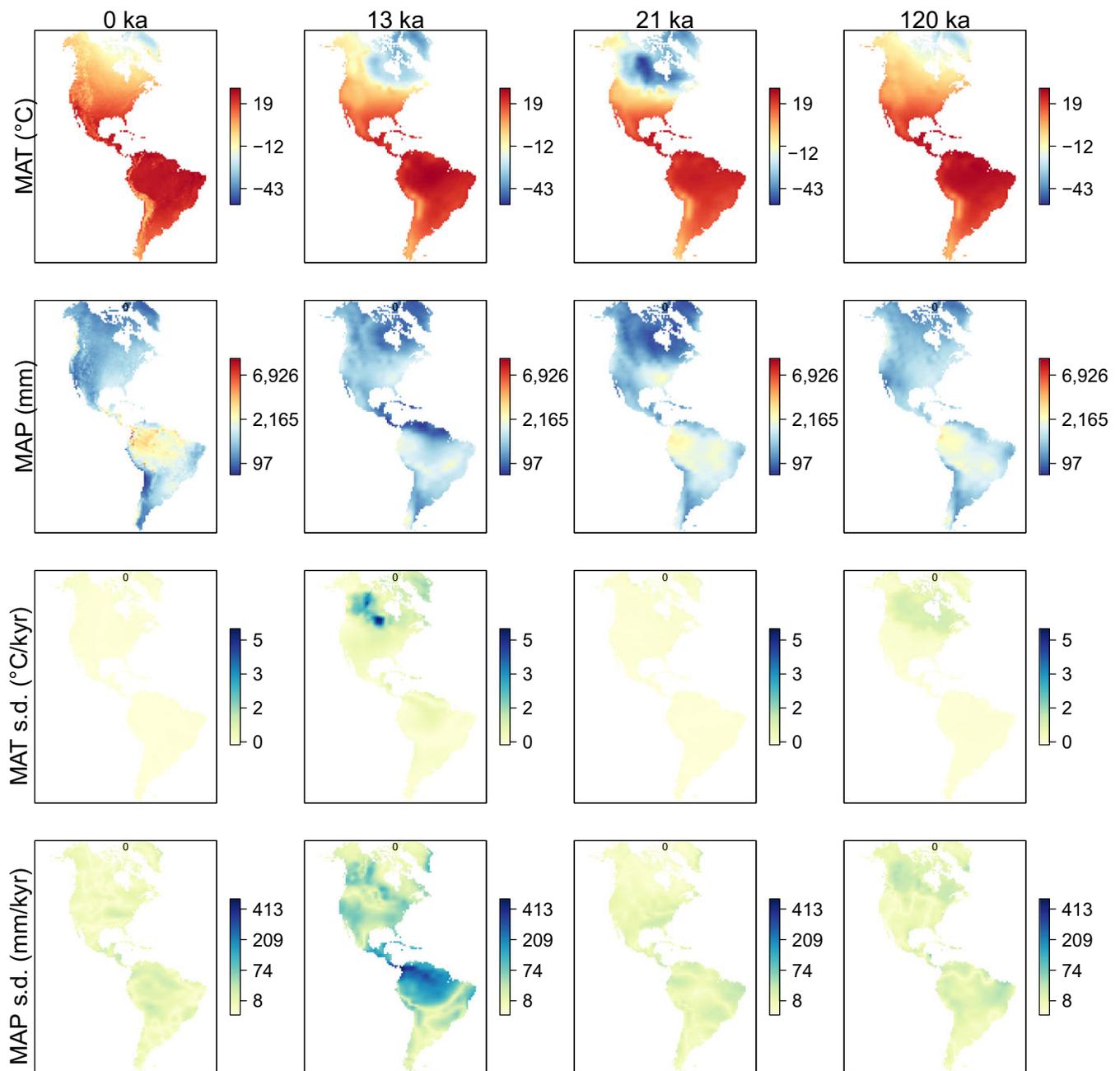
## 2.6 | Statistical analysis

To prepare climate data for analysis, we first square-root transformed contemporary and paleoclimate MAP data to improve normality. We calculated a temporal mean value at  $x$  ka, for  $x$  in 0 to 120, as well as a temporal standard deviation at  $x$  ka within each grid cell using a moving window approach, i.e. over values within the interval  $[x - k, x + k]$ . These temporal standard deviations were then standardized by divided by the total temporal range of the moving window. Temporal standard deviations thus have units of either  $^\circ\text{C}/\text{kyr}$  (temperature) or  $\text{mm}/\text{kyr}$  (precipitation). We used a value of  $k = 1$  where possible, but  $k = 4$  in some cases where HadCM3 data had coarser resolution (i.e. closer to 120 ka). Edge cases at 0 and 120 ka were calculated treating out-of-range data as missing. Contemporary climate was used for values at 0 ka, while paleoclimate was used for values at 1–120 ka.

We then rescaled all contemporary and paleoclimate predictor variables by z-transforming each relative to their grand mean and standard deviation (over all pixels and years) for each variable type from the HadCM3 model (MAT and MAP mean values and temporal standard deviation of MAT and MAP). This approach standardizes values across both variable types and models relative to estimates of their ranges across study interval. Thus, a value of +1 in a MAT layer indicates that this cell has a value that is 1 standard deviation larger than the mean value relative to all values seen in all locations over the 0–120 ka interval.

We used partial least squares (PLS) regression to determine the best predictors of FMs, FD, and  $FD_{res}$  in independent analyses. We conducted PLS regressions separately for North America and South America (split at the Panama/Colombia border) because of their different glaciation histories (Ehlers, Gibbard, & Hughes, 2011). The PLS approach accounts for the statistical nonindependence of large numbers of predictors by finding the rotation of the predictor matrix that best overlaps with the response vector, and identifies the latent factors (components) that correspond to these rotations (Geladi & Kowalski, 1986). The PLS components describe the independent contribution of each predictor variable to the response variable and are ordered by their explanatory capacity such that the first component (PLS1) by definition explains the most variation in the data. Thus, the approach can identify independent effects of multiple correlated predictors (i.e. separating the effects of contemporary and paleoclimate, even if they are sometimes correlated with each other). We built models that simultaneously incorporated up to six classes of predictors: contemporary climate mean values, paleoclimate temporal mean values, and paleoclimate temporal standard deviations (metrics of paleoclimate variation) for each of MAT and MAP.

We also performed a separate set of PLS analyses in order to assess biases from climate changes occurring at times and locations where plants may not have grown. Although predicting ice sheet



**FIGURE 2** Example contemporary climate and HadCM3 general circulation model temporal mean values for annual temperature (MAT) and annual precipitation (MAP) as well as for temporal standard deviations of MAT and MAP for the present day (0 ka), and for intervals beginning at 13 ka (Younger Dryas), 21 ka (Last Glacial Maximum), and 120 ka (Last Interglacial). Colors are scaled and transformed (see Materials and Methods), with labels indicating values back-transformed to original units. The full analysis includes a larger number of temporal mean values at intervals spaced between 0–120 ka

spatial coverage at each time and location would be ideal, we instead masked out pixels at all times and places where there was ice cover during the Last Glacial Maximum (21 ka) (corresponding to pixels in the black polygon in Figure 2i). This choice was motivated by the currently limited knowledge of temporally-resolved ice sheet dynamics during the full extent of study period (Kleman et al., 2010; Kleman, Fastook, Ebert, Nilsson, & Caballero, 2013).

We tested Hypothesis 0 for each of FMs, FD, or  $FD_{res}$  by comparing root mean square error of prediction (RMSEP) values for PLS

models that included contemporary climate ( $n = 2$  total predictors) and/or paleoclimate values ( $n = 250$  total predictors). Because RMSEP necessarily decreases with number of PLS components, we compared RMSEP values after fixing the number of PLS components in each model. This approach is more appropriate than model selection methods based on Akaike Information Criterion comparisons (Li, Morris, & Martin, 2002) because it is difficult to calculate degrees of freedom in PLS in order to correctly penalize likelihood values (Krämer & Sugiyama, 2011).

In this PLS framework, Hypotheses 1–4 can be distinguished by regression of contemporary FMs, FD, or  $FD_{res}$  on contemporary climate mean values, paleoclimate mean values over multiple times, and paleoclimate temporal variation over multiple times. We assessed the importance of each PLS component via the percentage of variance explained by the component. The effect of each variable at each time for FMs, FD, or  $FD_{res}$  can be interpreted as the PLS component's loading coefficient explaining the most variance in each model, with positive loading coefficients indicating that higher than average (over the 0–120 ka interval) values of this predictor yield higher than average values of the response variable. We also defined an overall effect for each class of predictor as the maximum absolute loading coefficient for that predictor type along each axis across all times.

All analyses were carried out with the R statistical environment (version 3.3.3). Occurrence data were obtained with the “BIEN” package (Maitner et al., 2018). Map rescaling and reprojection were carried out with the “raster” (Hijmans & Van Etten, 2014) and “maptools” (Bivand & Lewin-Koh, 2013) packages. Convex hulls were calculated with the “geometry” package (Habel, Grasman, Gramacy, Stahel, & Sterratt, 2015). PLS regression was carried out within the “pls” package (Mevik & Wehrens, 2007). All georeferenced data products underlying this analysis are available in Supporting Information File S1.

## 3 | RESULTS

### 3.1 | Contemporary functional trait patterns

Mapped FMs for all species for the five focal functional traits showed strong spatial gradients. Mean estimates of specific leaf area were highest in temperate/boreal North America (Figure 3a). Maximum plant height and seed mass were highest in the eastern Amazon basin (Figure 3b,c). Stem specific density was highest in the Amazon basin (Figure 3d). Leaf nitrogen content was highest in western North America and the southern South America (Figure 3e), all leading to similar latitudinal tropical-temperate-boreal gradients in FMs for PC1 (Figure 3f). FD was high throughout the tropics and into southeastern North America (Figure 3g), and  $FD_{res}$  was high in southeastern North America, Central America, and the Caribbean, as well as along the northeastern and eastern coasts of South America (Figure 3h). Species richness was highest in Central America and the western Amazon basin (Figure 3i). All of these results were qualitatively consistent when restricted to woody species only (Supporting Information Figure S6).

### 3.2 | Overall predictive power of paleoclimate

We found that models that incorporated paleoclimate and contemporary climate had higher predictive power than models that incorporated only contemporary climate (Figure 4). When comparing models with the same number of PLS components, the contemporary + paleoclimate models usually had equivalent or lower

root mean square error of prediction (RMSEP) than the contemporary climate models. For example, for FD calculated with data for all species and HadCM3 climate data, using 1 PLS component, RMSEP was 9% lower in North America and 20% lower in South America; when using data for woody species, RMSEP was 14% lower in North America and 20% lower in South America. Similar results held for all other response variables, other methodological choices, and 2 PLS components (Supporting Information Figure S7).

### 3.3 | Paleoclimate and contemporary climate predictors of contemporary functional composition

We present results for the HadCM3 paleoclimate model using all species, as results are representative across all modeling choices.

For FD in North America, we found that the first PLS component explained 57% of the variation in the data (Figure 5a). This component represented large effects ( $> 0.1$  in absolute standard deviations) for paleo MAT mean value (+0.11), paleo MAT temporal standard deviation (−0.20), and for paleo MAP temporal standard deviation (+0.11). There were no large effects from contemporary MAT or MAP mean values. These effects were strongest immediately after the Last Glacial Maximum (~20 ka) and the Last Interglacial (~120 ka).

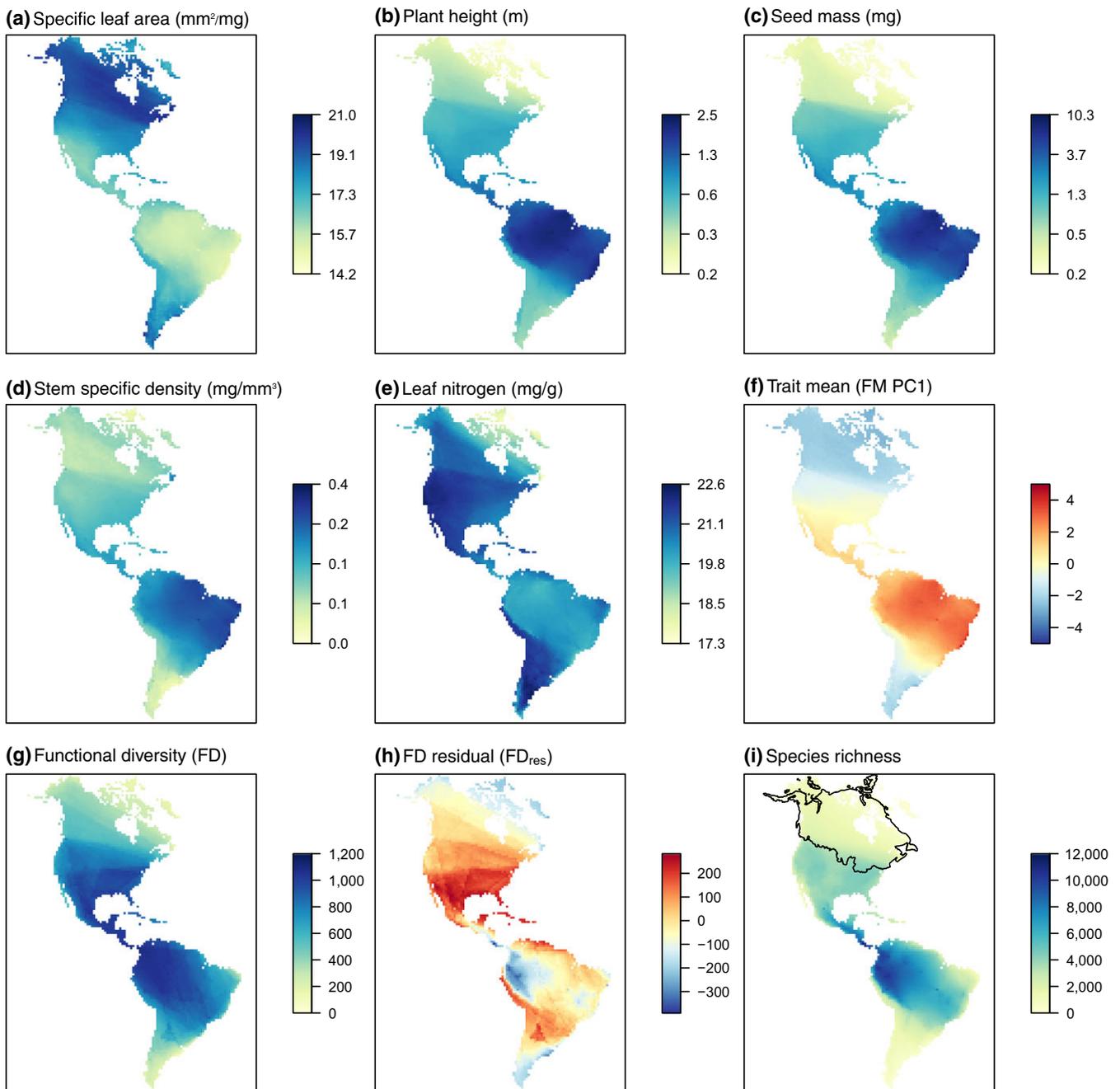
For FD in South America, we found that the first PLS component explained 60% of the variation in the data (Figure 5b). This component represented large effects for contemporary MAP mean value (+0.13), paleo MAP mean value (+0.10), and paleo MAP temporal standard deviation (+0.28). There was no large effect from any MAT predictor. Paleo MAP temporal standard deviation was most important at time periods beginning at 17 and 13 ka, corresponding to abrupt change from a Heinrich event and the Younger Dryas respectively.

Results for FMs and  $FD_{res}$  were similar to those for FD. One exception occurred in South America, where estimates for  $FD_{res}$  were opposite in sign (Supporting Information Figure S8). Results for higher PLS components are not reported, as explained variation for each was individually low (e.g. at most 7%–13% for PLS2 across all response variables using the HadCM3 data and all species across response variables). Model residuals for North and South America for varying numbers of components are shown in Supporting Information Figure S9.

All of the above results were qualitatively similar when restricting data to woody-only species (Supporting Information Figure S10). Analyses were also qualitatively similar when excluding pixels covered by ice sheets at the Last Glacial Maximum. Results for these analyses are presented in Supporting Information Figure S11.

## 4 | DISCUSSION

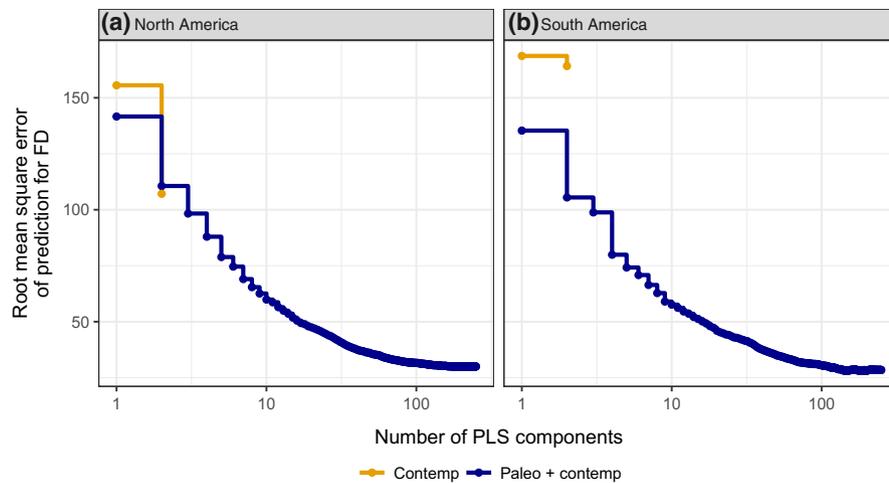
We identified spatially and temporally variable effects of paleoclimate on contemporary functional trait patterns, independent from those of contemporary climate. Across methodological choices,



**FIGURE 3** Estimated plant species assemblage characteristics, based on data for all species. Distributions of functional trait means (FMs) for five functional traits (each colored by log-transformed values, with labels indicating values back-transformed to original units) are shown for (a) Specific leaf area, (b) plant height, (c) seed mass, (d) stem specific density, and (e) leaf nitrogen per unit mass. (f) First principal component of FMs. (g) Functional diversity (FD; convex hull volume of  $\log_e$ -transformed values); (h)  $FD_{res}$ , the residual of FD regressed on species richness, and (i) Species richness. The black polygon indicates the maximum ice sheet extent during the Last Glacial Maximum

functional composition was predicted in North America by paleo MAT mean values, paleo MAT temporal standard deviations, and paleo MAP temporal standard deviation, and in South America by paleo MAP mean values and paleo MAP mean values. Paleo MAT and MAP mean values had similar effects over time, while in North America MAT temporal standard deviation at the Last Glacial Maximum and Last Interglacial had strongest effects, and in South America MAP temporal standard deviation at the Younger Dryas and the

17 ka Heinrich event had strongest effects. Thus climate immediately after the Last Glacial Maximum appears to have left a strong legacy on contemporary functional composition. We also found that paleoclimate was a useful predictor of contemporary functional composition, supporting Hypothesis 0. Predictive errors for predicting FMs, FD, and  $FD_{res}$  were lower when paleoclimate variables were incorporated into regression models than when only including contemporary climate variables.



**FIGURE 4** Predictive uncertainty in models for FD for (a) North America and (b) South America as measured by the cross-validated root mean squared error of prediction (RMSEP) for increasing numbers of PLS components. Y-axis units correspond to units of functional diversity (compare to Figure 3g). Results are for PLS regression models generated using trait data for all species and climate data from HadCM3. Light orange lines indicate models using only contemporary climate predictors; dark blue lines, models using contemporary and paleoclimate predictors [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

The PLS models support several of the hypotheses. Hypothesis 1 (a relationship between contemporary FMs and contemporary climate mean values, with fast immigration and fast exclusion) was supported in South America for MAP. Hypothesis 2 (a positive relationship between contemporary FD and paleoclimate temporal standard deviation, with fast immigration slow exclusion) was supported for MAP in North America and in South America. Hypothesis 3 (a negative relationship between contemporary FD and paleoclimate temporal standard deviation, with slow immigration and fast exclusion) was supported for MAT in North America. Hypothesis 4 (a relationship between contemporary FMs and paleoclimate mean values, with slow immigration and slow exclusion) was supported for MAP in North and South America. Thus, all of the scenarios of Figure 1 received some support in either North or South America. The general implication is that processes of species immigration or exclusion can sometimes be slow, leading to spatial variation in colonization and extinction debts across these continents.

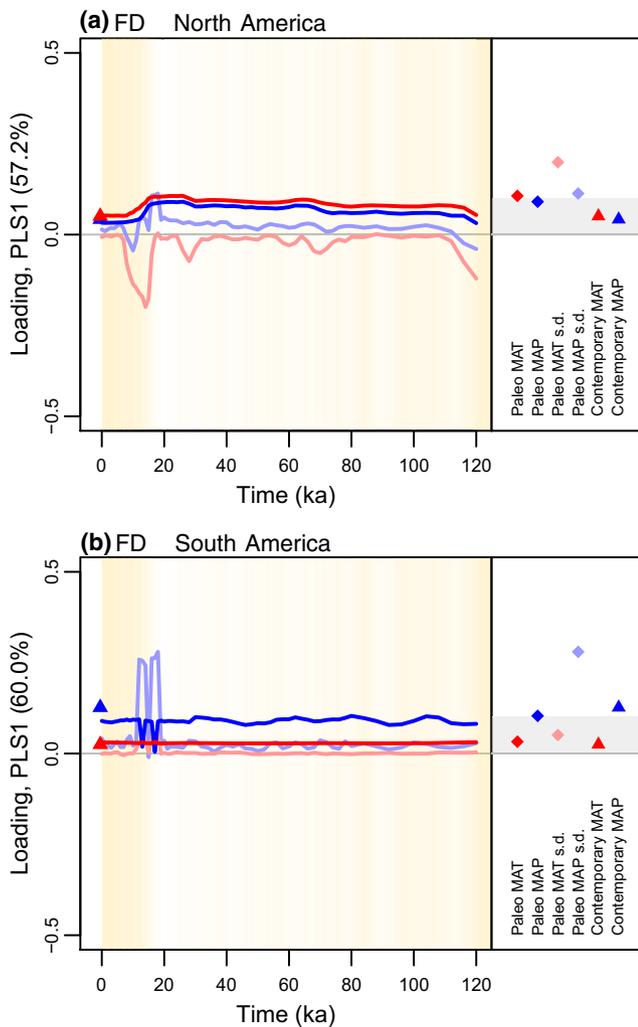
The results therefore do not map cleanly onto any one class of dynamics dominating at continental scales. Elucidating the details of these sometimes slow immigration and exclusion dynamics more precisely would require comparing time series of functional composition to time series of paleoclimate (Blonder et al., 2017). That approach contrasts with the approach taken in the present study, which compared time series of paleoclimate to a single time-point estimate of functional composition, and tested hypotheses most relevant for single linear climate changes. Time series data for functional composition are highly challenging to obtain from available paleoproxies. However, such data would enable direct measurement of the rates and lags in temporal response of functional composition to climate variation.

Results in North America are consistent with limited dispersal after ice sheet retreat (Davis & Shaw, 2001; Morueta-Holme et al.,

2013; Svenning et al., 2015), and on thermal tolerances that constrain species distributions in high-latitude environments (Hawkins, Rueda, Rangel, Field, & Diniz-Filho, 2013; Körner, 2003; Morin & Lechowicz, 2011; Sakai & Weiser, 1973). The paleoclimate MAT signal seen in these data may be driven by cooling in temperate and boreal portions of the continent during the last glacial period that have caused regional extinctions and slow recolonization dynamics (Davis, 1984). These findings extend the spatial and temporal extent of analyses exploring glacial effects on biodiversity (Ordóñez & Svenning, 2017), providing additional confidence that this period had a key role in shaping contemporary biodiversity patterns.

Results in South America supported the importance of paleoprecipitation variation in shaping contemporary biodiversity patterns in tropical areas (Blach-Overgaard et al., 2013; Gödel, Kissling, & Svenning, 2015; Rakotoarinivo et al., 2013), possibly by survival and recolonization from refugia along hydrological gradients. Lower precipitation values and higher precipitation temporal variation in the Late Pleistocene in certain coastal regions of this continent have led to contemporary FD being lower than expected based on contemporary climate. The strong precipitation effects in South America caused by Northern hemisphere ice melting during the 17 ka Heinrich event and the Younger Dryas are consistent with strong cross-hemisphere telecoupling of climate during these intervals, in which ice sheets and ice melting in the Northern hemisphere caused atmospheric and ocean circulation changes, leading to changes in Southern hemisphere climate regimes (Clement & Peterson, 2008; Jones et al., 2018). This result suggests that other climate telecoupling may also drive initially unintuitive relationships between climate change and functional composition change.

The spatial uncertainties in our results are possibly large. Biases in trait data coverage could spatially bias our maps of FMs and FD if botanical collecting effort in certain areas were focused on certain



**FIGURE 5** Contemporary climate and paleoclimate effects on functional diversity (FD), for the first PLS component, for (a) North America, and (b) South America. Results are for models generated using trait data for all species and using climate data from HadCM3. Left subpanels indicate effect sizes (loading coefficients) for each model component at different times. Contemporary climate data are shown in triangles; paleoclimate values as dark lines and temporal standard deviations as lighter lines. Red indicates MAT, blue MAP. Right subpanel symbols indicate the maximum absolute effect for each variable class over time. Points above the gray background exceed our significance threshold. Orange shading behind each panel indicates global atmospheric temperatures reconstructed by Bintanja, Wal, and Oerlemans (2011), with deeper shading indicating warmer conditions. Results for FM and  $FD_{res}$  are shown in Supporting Information Figure S8

taxonomic or functional groups (Borgy, Violle, Choler, Garnier, et al., 2017). Because our maps of functional composition are broadly consistent with other estimates (Butler et al., 2017; Šimová et al., 2018; van Bodegom, Douma, & Verheijen, 2014), this is unlikely to be a major concern. Nevertheless, trait data and species occurrence are poor in some regions (e.g. the central Amazon, as well as southern South America). Thus, this approach is unlikely to be able to parse

out sub-regional biodiversity patterns because of limitations in available data. The spatial resolution of paleoclimate simulations ( $>2^\circ$  per grid cell) also limits parsing of sub-regional spatial patterns due to within-pixel climate heterogeneity (Stein, Gerstner, & Kreft, 2014). Nevertheless, the broad consistency of our findings across methodological choices gives some confidence in the generality of our conclusions.

The temporal uncertainties in our results are probably smaller than the spatial uncertainties. The HadCM3 simulations included multimillennial drivers of climate change (orbit, greenhouse gases, ice sheets), as well as the Heinrich event at 17 ka (Hemming, 2004) and the Younger Dryas event at 13 ka (Alley, 2000). Detailed simulations of similar events in deeper time were not available (e.g. the Heinrich event at  $\sim 45$  ka (Hemming, 2004), or Dansgaard-Oeschger millennial events that may increase the variability of temperature and precipitation, especially between 30 and 60 ka), but it is possible that these events also have large and persistent effects on contemporary functional composition. Regardless, these models provide some of the best available estimates of past climates, though independent paleo-proxy validation of predictions remain sparse, especially in South America (Harrison et al., 2014).

Non-climate factors may also be important drivers of functional composition over multiple timescales. For example, past human impacts on landscapes via active propagation, land clearance, or fire regimes (Bond & Keeley, 2005; Keeley, Pausas, Rundel, Bond, & Bradstock, 2011) are widely acknowledged throughout tropical (Levis et al., 2017; Malhi, 2018; Ross, 2011) and temperate (Abrams & Nowacki, 2008; Borgy, Violle, Choler, Denelle, et al., 2017; Feng, Mao, Benito, Swenson, & Svenning, 2017; Nowacki & Abrams, 2008) regions. Soil and surficial geology may also be important in determining plant species distributions (Ordoñez et al., 2009). However, the mechanisms linking specific traits to different non-climate abiotic variables are not yet completely clear. Moreover, all of these variables remain difficult and controversial to estimate over time and space. While we were unable to include them in our analysis, there is likely scope to extend our approach as datasets improve.

Climate may also indirectly drive changes in functional composition through changes in species interactions. Megafauna had large impacts on plant assemblages; these impacts would have shifted after the extinction of many megafauna in North and South America during the late Pleistocene (Gill, Williams, Jackson, Lininger, & Robinson, 2009; Johnson, 2009). While humans are acknowledged to be a major driver of these extinctions (Lorenzen et al., 2011), many also were strongly linked to climate change during this period on these continents (Bartlett et al., 2016). Indeed, some of the changes in immigration and exclusion rates could have been driven indirectly by these organisms, e.g. reduction in seed dispersal services leading to slow immigration (Pires, Guimarães, Galetti, & Jordano, 2018) (but see (van Zonneveld et al., 2018)), or reduced trampling leading to slow exclusion (Bakker et al., 2016). The temporal and spatial dynamics of megafaunal distributions remains poorly constrained by data, but such information may ultimately provide additional insight into climate-linked drivers of plant functional composition.

Our findings suggest that when predicting the future response of biodiversity to climate change, disequilibrium effects due to slow immigration or exclusion may be important. Statistical models based on the assumption that trait-environment relationships calibrated from contemporary climate data are at equilibrium (Laughlin, Joshi, Bodegom, Bastow, & Fulé, 2012; Shipley, Vile, & Garnier, 2006) could potentially be improved by incorporating paleoclimate predictors. Alternatively, it could be useful to include more mechanistically model processes of slow immigration and/or exclusion dynamics (Blonder et al., 2017; Fukami, 2015; Svenning et al., 2015). Such models, e.g. demography-constrained species distribution models (Zurell et al., 2016) or dynamic global vegetation models (van Bodegom et al., 2014), can represent disequilibrium dynamics that may result in nonlinear relationships between climate, paleoclimate, and functional traits.

The overall conclusion of our study is that functional trait patterns are predicted better when including paleoclimate as well as contemporary climate predictors. There is a Pleistocene temperature legacy in North America and a precipitation legacy in South America. While current functional composition may be well-adapted to contemporary environments, the high importance of paleoclimate suggests that the equilibrium assumption of functional ecology may be inappropriate for plant functional traits over  $10^3$ – $10^5$  years time-scales and continental spatial scales. The interplay between contemporary climate and paleoclimate drivers of biodiversity patterns will need to be better understood in order to accurately predict assemblage responses to future climate change.

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## AUTHOR CONTRIBUTION

BB conceived the project and carried out analyses. JK provided trait data. JS, PV, and AO provided paleoclimate data. BJE and JCS provided species occurrence data. NMH contributed to species distribution modeling. All authors contributed to writing the manuscript. Authors were ordered alphabetically by last name after the first author.

## DATA ACCESSIBILITY

All georeferenced data products underlying this analysis are available in Supporting Information File S1.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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