

Continental-scale reorganization of North American pollen assemblages since the Last Glacial Maximum

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ABSTRACT

Climate change may cause ecological communities to reorganize into novel combinations of species and environmental conditions. The fossil pollen record offers long-term context for understanding such biodiversity responses. Here, we present a continental-scale analysis of North American pollen assemblages since the Last Glacial Maximum, using more than 50,000 fossil pollen records from 1384 sites from the Neotoma Paleoecology Database. Our objectives were to identify major pollen assemblage types within a common continental-scale framework, track their geographic distributions through time, and compare their associated climate space. Pollen records were grouped with a constrained clustering approach that accounts for both pollen composition and associated climatic conditions. The resulting groups correspond closely to modern vegetation zones but also include transient assemblages that were widespread during deglaciation and have no direct equivalent in the 4–0 ka reference interval, including a Birch Parkland pollen assemblage, a Montane Steppe in western North America, and a Spruce Woodland with unusually high representation of broadleaf taxa. Ordination in multivariate climate space showed that Birch Parkland and Montane Steppe occupied climates distinct from modern analogues, whereas Spruce Woodland was compositionally distinct but not separated in climate space, suggesting a stronger role for deglacial landscape history. This contrast suggests that transient assemblages can arise either from novel climate conditions or from novel combinations of familiar climates with edaphic and biotic factors. Similar disequilibrium states may be an early and widespread response to rapid future climate change.

1. Introduction

The composition and geographic distribution of species and ecological communities are strongly influenced by climate. Major climatic transitions have been shown to alter species distributions, disrupt existing species associations, and create new combinations of taxa and environments (Williams et al., 2001, 2004). Understanding how biodiversity responded to environmental change in the past can provide context for anticipating ecological responses to future climate change as well (Reu et al., 2014; Mottl et al., 2021). The transition from the Last Glacial Maximum to the present represents the largest natural climate transition of the late Quaternary, involving substantial warming, retreat of continental ice sheets, and widespread changes in temperature and moisture regimes across North America. These environmental changes were accompanied by major shifts in vegetation composition and biome distributions, recorded in extensive fossil pollen archives throughout the continent (Williams et al., 2004, 2018).

One notable outcome of the postglacial transition period was the emergence of plant communities with no direct modern equivalent. In eastern North America, late-glacial no-analogue communities were characterized by unusual combinations of boreal and temperate species, including spruce-dominated forest types with a high representation of temperate hardwoods (Overpeck et al., 1992; Williams et al., 2001). In Beringia, fossil pollen records suggest unique communities that were distinct from modern tundra and boreal forest ecosystems (Edwards et al., 2005). More broadly, pollen records show that locally novel plant communities have emerged regularly during periods of major climatic transitions (Williams and Jackson, 2007; Williams et al., 2013; Staples et al., 2022). Their causes are not necessarily climatic alone. Novel plant communities in North America have also been linked to broader late-Pleistocene megafaunal decline and altered fire regimes (Gill et al., 2009). Together, this work shows that vegetation responses to environmental change are not usually simple shifts in the locations of modern biomes. Instead, species may respond individualistically to

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changing temperature, moisture, seasonality, disturbance, and dispersal conditions, producing community states that are transient, spatially restricted, or absent from the modern landscape (Williams et al., 2004; Williams and Jackson, 2007).

Although the existence of no-analogue plant communities is well documented, their detection and definition can be difficult due to the taxonomic resolution of pollen data and the spatial scale of the study (Williams and Jackson, 2007; Staples et al., 2022). A community that appears unique within a regional comparison may have closer analogues when the comparison is expanded across a continent. Continental-scale analyses can also reveal shifts of ecological communities and broad patterns of turnover that are difficult to detect from individual records or regional studies. Continental pollen databases therefore provide an opportunity to examine whether postglacial vegetation change mainly involved redistribution of recognizable biome types, or whether, and how regularly, major climatic transitions also produced plant communities with no direct modern counterpart.

However, continental-scale synthesis of fossil pollen records is especially affected by the limited taxonomic resolution of many pollen types and by often multiple species that are represented by those types. Fossil pollen is commonly identified to genus or family rather than species, so pollen assemblages that appear compositionally similar may nevertheless represent different ecological communities in different regions (Nieto-Lugilde et al., 2015). For example, pollen assemblages containing similar proportions of *Picea*, *Tsuga*, *Acer*, and *Thuja* may correspond to different species assemblages on the east and west coast of the North American continent. In addition, pollen taxa differ in production, dispersal, preservation, and diagnostic value, making pollen assemblages an imperfect proxy for past vegetation. These challenges do not preclude broad-scale synthesis, but they require approaches that emphasize robust, interpretable patterns rather than exact reconstruction of local species composition (Gavin et al., 2003; Nieto-Lugilde et al., 2015).

Here, we use a continental-scale fossil pollen dataset from the Neotoma Paleocology Database to analyze broad patterns of North American vegetation reorganization since the Last Glacial Maximum. Our goal is to place postglacial pollen assemblage change into a common continental framework that allows assemblage composition, geographic distribution, temporal occurrence, and climatic context to be compared directly. We classify pollen assemblages with climatic constraints so that groups reflect both pollen composition and associated climatic conditions. This approach is intended as a synthesis tool to track climatically and compositionally similar pollen assemblages through time across the continent, rather than as a reconstruction of local species composition or a replacement for established no-analogue dissimilarity analyses. Our specific objectives were (1) to identify major pollen assemblage types within a common continental-scale classification; (2) to determine whether any assemblage types lacked direct counterparts in the 4–0 ka reference interval; and (3) to compare their composition, geographic distributions, temporal occurrence, and associated climate space through time.

2. Materials and methods

2.1. Pollen and paleoclimate data

We used fossil pollen records from the Neotoma Paleocology Database for North America from the Last Glacial Maximum to the present (Williams et al., 2018). Fossil pollen records were obtained through the *neotoma* package for the R programming environment (Goring et al., 2015; R Core Team, 2025). Sites with radiocarbon-dated pollen records were converted to calendar years using the *IntCal13* calibration curve (Reimer et al., 2013). Differences between *IntCal13* and the updated *IntCal20* calibration (Reimer et al., 2020) are small relative to the multi-millennial analytical intervals used here.

Paleoclimate estimates were used to provide environmental context

for pollen assemblages and to support the climate-informed classification described below. We used paleoclimate reconstructions centered on 21, 16, 14, 11, and 6 ka from the Community Climate Model version 1 (CCM1, Kutzbach et al., 1998). Although newer paleoclimate products are available, CCM1 was selected because it provides gridded climate change factors for several intermediate time steps spanning the rapid warming of the last deglaciation between approximately 18 and 11 ka (Fig. 1).

Available pollen records are generally sparse for describing continent-wide vegetation assemblages, especially farther back in time (Fig. 1). We therefore aggregated pollen assemblages into six broad intervals corresponding to the paleoclimate reconstructions: 23–18, 18–15, 15–12, 12–10, 10–4, and 4–0 ka. These intervals either represent periods of relatively stable climate or approximate temperature mid-points of intervals with rapid climatic transitions (Fig. 1).

For this continental-scale synthesis, the chosen paleoclimate change factors from the CCM1 dataset were sufficient to represent broad departures from modern climate, rather than precise local paleoclimate conditions. The coarse resolution gridded change factors were bilinearly interpolated and superimposed on 1961–1990 climate normals with the ClimateNA software version 5.21 (Wang et al., 2016), preserving modern topographic climate gradients at high resolution, while adjusting regional climate means for each paleoclimate period.

We characterized the climate associated with each pollen assemblage using 12 biologically relevant variables representing temperature, precipitation, seasonality, and moisture balance. Nine variables were selected from the *biovars* function in the R package *dismo*: mean annual temperature, temperature seasonality, temperature annual range, mean temperature of the wettest, driest, warmest, and coldest quarters, mean annual precipitation, and precipitation seasonality (Hijmans et al., 2025). An additional three variables were estimated with the ClimateNA software (Wang et al., 2016): growing season precipitation, annual heat-moisture index as a temperature-to-precipitation dryness index, and climate moisture index as a water-balance index. Together, these variables represent major thermal, moisture, and seasonal gradients relevant to vegetation composition across North America.

2.2. Climate-informed classification of pollen assemblages

We used 18 pollen taxa selected to provide broad diagnostic information for continental-scale vegetation classification, guided by the taxonomic framework of Gavin et al. (2003): *Abies*, *Acer*, *Alnus*, *Betula*, *Carya*, Cyperaceae, *Fagus*, *Fraxinus*, *Juglans*, *Ostrya/Carpinus*, *Picea*, Poaceae, *Quercus*, *Tilia*, *Tsuga*, *Ulmus*, *Liquidambar*, and *Prairie* Forbs. Taxa were retained when they were sufficiently frequent across the dataset and useful for distinguishing broad North American vegetation gradients, including boreal, temperate hardwood, maritime, montane, grassland, tundra, wetland, and steppe assemblages. Taxa were excluded when they were generally very rare or provided limited diagnostic value at the continental scale.

Two taxa illustrate this rationale. *Liquidambar* was retained despite its restricted geographic distribution because that restriction makes it diagnostically useful for identifying southeastern temperate hardwood assemblages and distinguishing them from other eastern forest groups. By contrast, *Pinus* was excluded from the MRT classification because its high pollen production, good preservation, and long-distance transport result in broad representation across many assemblage types, including grasslands and deserts where most other tree taxa are low. In this analysis, *Pinus* therefore compromised the geographic and ecological coherence of broad assemblage boundaries. Other conifers, including *Picea* and *Abies*, were retained because they had greater diagnostic value for distinguishing boreal, montane, maritime, and late-glacial spruce-rich assemblages.

Multiple pollen samples from the same site within a given time interval were combined into a single site × time-interval observation. For each taxon, the percentage was calculated as the summed pollen count

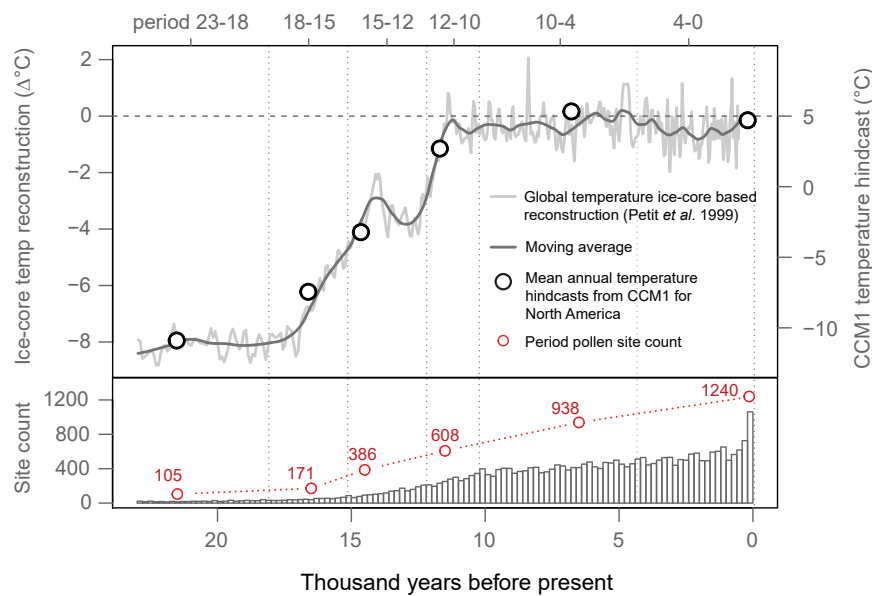


Fig. 1. Reconstructed temperature and available pollen sites for six periods from the Last Glacial Maximum to the present. The upper panel shows an ice-core based temperature reconstruction from Petit et al. (1999), included as broad context for glacial-interglacial temperature change, together with CCM1 mean annual temperature hindcasts for North America. The lower panel shows the availability of pollen records through time. Red circles indicate the cumulative number of pollen sites available for each of the six analytical periods, and bars show the number of pollen sites in 200-year intervals.

of that taxon across all samples within the site $\times$ time interval, divided by the summed total pollen count across the combined samples. This standardization was necessary because Neotoma records differ in total pollen counts, taxonomic resolution, preservation, and sampling density, making absolute counts difficult to compare across records and time intervals. Non-diagnostic taxa, including *Pinus*, were then excluded from the pollen assemblage classification without recalculating the retained taxa to sum to 100%. Thus, removing *Pinus* did not inflate the proportion of remaining taxa used for classification. The final dataset for classification comprised 1384 sites, 3847 site $\times$ time-interval observations, and 51,427 site $\times$ time-interval $\times$ pollen-taxon records.

We used multivariate regression tree analysis to classify pollen assemblages into broad pollen assemblage groups, implemented with the *mvpart* package for the R programming environment (DeAth, 2002). This approach partitions pollen assemblages using climatic variables as explanatory constraints, producing groups that are similar in pollen composition and associated with distinct regions of climate space. The purpose of this classification was to summarize broad continent-scale assemblage patterns while reducing ambiguity caused by genus-level pollen types that may represent different species in different regions.

The initial classification on the full dataset resulted in 22 terminal groups. We did not interpret all terminal groups separately because some represented fine-scale regional variants, especially in densely sampled regions such as the Great Lakes and eastern North America. Sample density can influence where recursive partitioning places fine-scale splits, even though the MRT is used here as a descriptive classification tool. We therefore aggregated the 22 terminal groups into 11 broader assemblage categories based on taxonomic composition, geographic coherence and ecological interpretability. This aggregation retained all groups interpreted as having no direct modern counterpart, while combining local or regional variants that were more appropriately treated as part of broader continental-scale assemblage types. The full set of 22 terminal groups, their dominant pollen taxa, and final 11-group assignment are provided in Appendix 1.

We assigned descriptive names to the final eleven multivariate clusters, based on their dominant pollen taxa and geographic distribution. These clusters and their names are not intended to imply precise reconstructions of local species communities. Instead, they are meant to visualize and describe vegetation reorganization at broad continental

scales through time.

2.3. Climate space occupied by pollen assemblages

To visualize how these pollen assemblages were associated with climatic conditions, we used canonical discriminant analysis based on the 12 climate variables described above. The analysis was applied to all pollen groups across all periods so that shifts of groups in climate space among periods would be apparent. Because several climate variables were skewed, mean annual precipitation and precipitation seasonality were log-transformed, and growing season precipitation was square-root transformed for this analysis. Because several climate variables were correlated, we interpret the CDA as an ordination of assemblage positions in multivariate climate space rather than as a predictive discriminant model or as evidence for independent effects of individual climate variables. Climate vectors are therefore used only as visual guides to broad temperature, moisture, and seasonality gradients.

The MRT and CDA are not independent analyses, but are complementary by design: the MRT selects climatic variables as grouping criteria to partition similar pollen assemblages, while the CDA summarizes and visualizes the climatic dimensions along which the resulting assemblage groups differ. The ordination was then used to compare the climatic separation among assemblage groups, including transient assemblages without a direct modern analogue (15–12 ka) with groups represented in the most recent interval (4–0 ka). In addition, Walter & Lieth climatic diagrams were generated with the *climatol* R package (Guijarro, 2025) to support interpretation of seasonal temperature and precipitation differences among modern and transient assemblages.

We interpreted assemblages as having no direct modern counterpart when they were absent from the 4–0 ka reference interval but had substantial representation in earlier intervals. This inference is made at the level of broad pollen assemblage types, which is the appropriate scale for continental fossil pollen synthesis. Although pollen data cannot reconstruct complete species-level communities, the absence of the assemblage types identified here from the late-Holocene reference interval supports their interpretation as no-analogue paleoecological communities within the taxonomic and spatial resolution of the dataset.

3. Results

3.1. Reference-period pollen assemblages correspond to broad modern vegetation zones

The classification of pollen records from the 4–0 ka reference interval produced pollen groups that broadly corresponded to major modern vegetation zones of North America (Fig. 2). The first split separated northern and southern assemblages along a major temperature gradient, with subsequent splits distinguishing boreal, tundra, temperate forest, grassland, montane, and maritime assemblage types. Individual split variables should be interpreted as representing multivariate climatic gradients rather than as unique causal drivers, with alternate variables resulting in identical or near identical splits (Fig. 2C). The resulting groups were interpretable as major modern ecosystem classes or biomes. This correspondence provided a 4–0 ka reference for interpreting assemblage turnover and transient pollen assemblage groups in earlier time intervals.

3.2. Continental turnover of pollen assemblages since the Last Glacial Maximum

The full classification across all time intervals revealed substantial shifts of pollen assemblages during the last deglaciation (Fig. 3). The eleven assemblage groups differed in taxonomic composition (Table 1), providing the basis for their descriptive names. *Pinus*, although excluded from the MRT classification, is reported in Table 1 and shows broad representation across forested and open assemblages, illustrating its limited diagnostic value for distinguishing continental-scale assemblage types. Most assemblage types corresponded to modern vegetation zones that shifted in geographic extent through time, but several compositionally distinctive pollen clusters were restricted to earlier time intervals and were absent from the most recent period. The relative frequency of about half the assemblage groups changed markedly across intervals, and some transient assemblages occurred only during deglaciation and were largely absent during the glacial maximum and the most recent time interval (Fig. 4).

Three assemblage groups were interpreted as having no direct counterpart in the 4–0 ka reference interval: Birch Parkland, Spruce Woodland, and Montane Steppe. Birch Parkland, with a distinctly high birch frequency of 47.2% (Table 1), was the most spatially extensive of

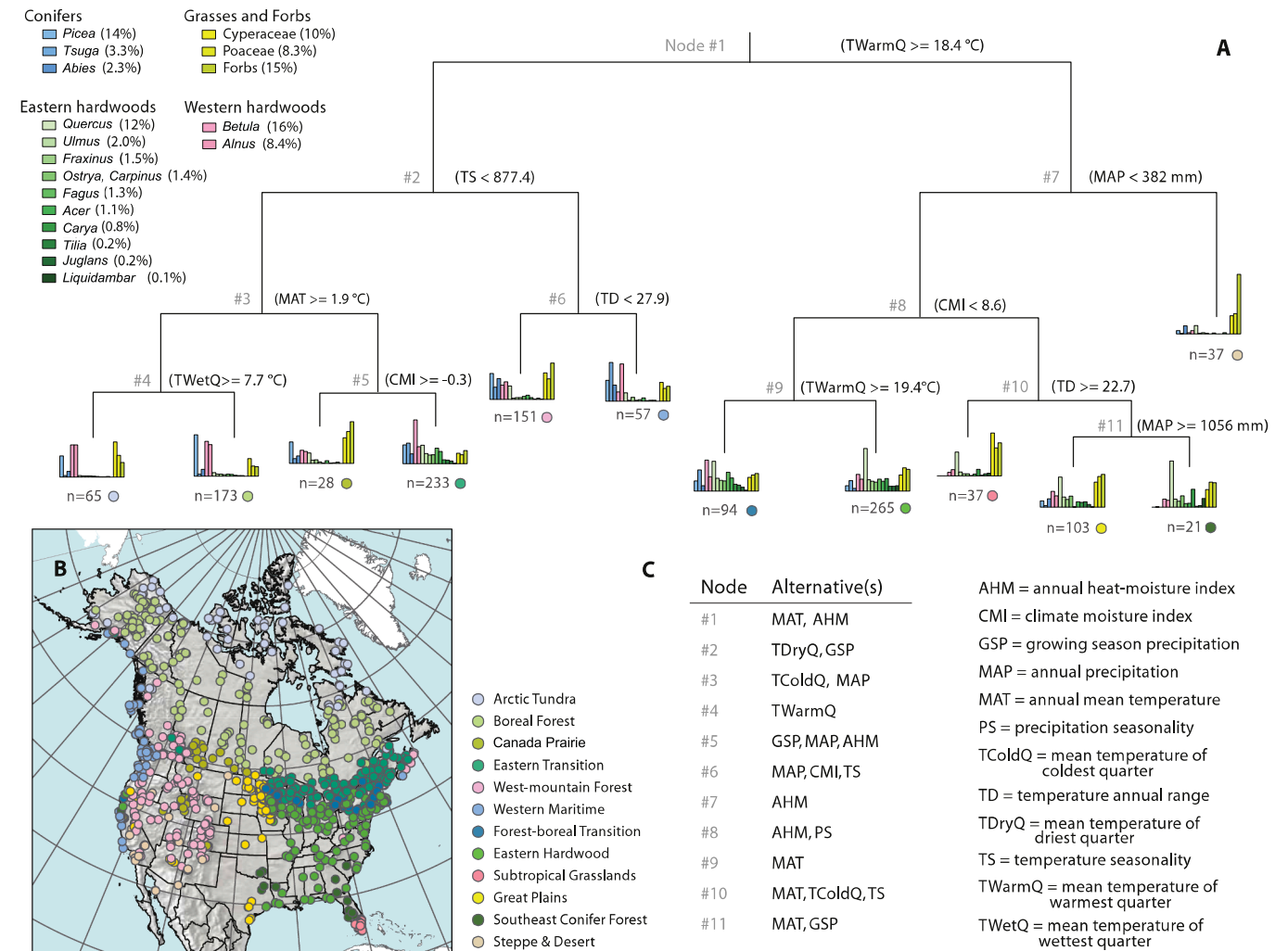


Fig. 2. Classification of pollen data for the 4–0 ka reference interval with multivariate regression tree (MRT) analysis. The regression tree for modern pollen data (A) reports the primary climate variable and threshold value for each split, the number of pollen assemblages in each terminal group, and the square-root-transformed frequencies of pollen taxa as bar charts. The overall frequency of each pollen taxa across all sites is reported in parentheses in the legend. Colors and legend order in the map of pollen sites (B) correspond to the MRT groups shown above. Correlated climate variables that could have provided alternative criteria for each split are reported in panel (C).

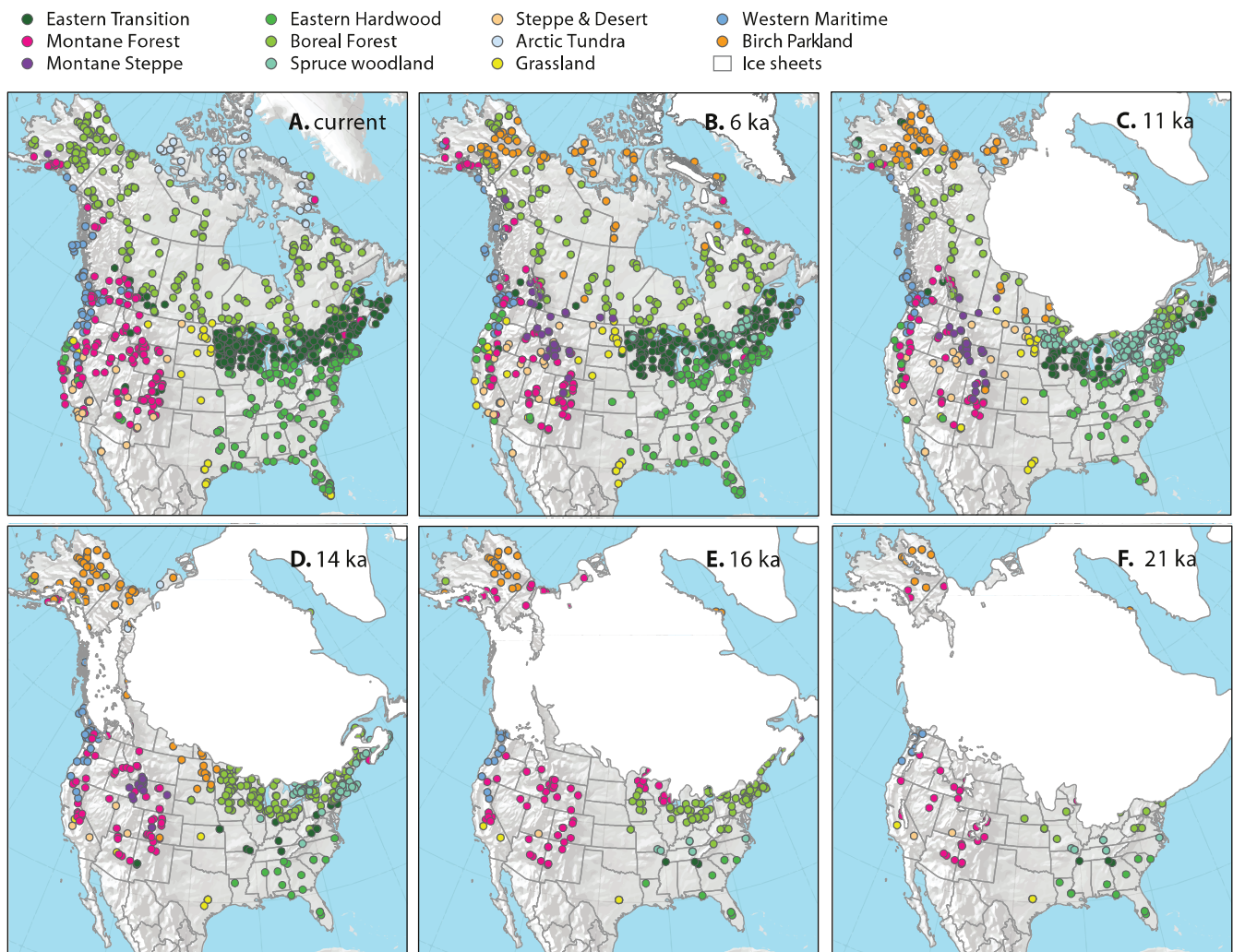


Fig. 3. Geographic distribution of eleven pollen assemblage groups for six periods since the Last Glacial Maximum. The eleven groups are based on an initial set of 22 terminal groups generated by regression tree analysis across all time periods. These groups were subsequently summarized into 11 assemblage categories for concise reporting and mapping, while retaining transient assemblages with no direct counterpart in the 4–0 ka reference interval: Montane Steppe, Birch Parkland, and Spruce Woodland.

these groups, occurring both in Beringia and south of the continental ice sheets during late-glacial time intervals. Spruce Woodland was most prominent in eastern North America during deglaciation and was characterized by substantial *Picea* representation (14.8%) which distinguishes it from Eastern Transition (3.2%), together with elevated representation of more southern broadleaf pollen taxa relative to Boreal Forest, including *Quercus* (6.1% vs. 2.0%), *Ulmus* (1.8% vs. 0.7%) and *Ostrya/Carpinus* (1.3% vs. 0.7%). The Montane Steppe cluster occurred primarily in western montane regions during the late-glacial and early Holocene time intervals and was distinguished by higher representation of herbaceous taxa and lower representation of mesic forest tree species relative to montane forest communities in the 4–0 ka reference interval (Table 1).

3.3. Climatic context of transient assemblages

Ordination of pollen assemblages in multivariate climate space showed that Birch Parkland and Montane Steppe occupied climatic regions that differed from comparable reference-period assemblages, whereas Spruce Woodland was not clearly separated in climate space (Fig. 5). The first canonical axis primarily separated assemblages along gradients of temperature seasonality and moisture availability (Fig. 5A, G), while the second axis represented broad temperature gradients.

Additional axes captured variation in precipitation seasonality and growing-season climate (Fig. 5B, H).

The transient Birch Parkland assemblage (orange symbols in Fig. 5) overlapped partly with cold-climate assemblages along higher dimensions (Fig. 5H), but differed from tundra and boreal assemblages in dimensions associated with temperature seasonality and moisture availability. The climate diagram for the late-glacial Birch Parkland groups (Fig. 5I, K) with distributions north and south of the ice sheets (compare with Fig. 3), indicated cool annual conditions, very high temperature seasonality in the northern group, and comparatively moist growing-season environments.

The second transient pollen assemblage without a direct analogue in the 4–0 ka reference interval, Montane Steppe occupied warmer and drier growing-season conditions than montane forest assemblages (purple symbols in Fig. 5G, H, and climate diagrams in Fig. 5D vs. 5J). The third transient Spruce Woodland group (turquoise symbols in Fig. 5G, H) was not clearly separated from the Boreal Forest and Eastern Transition assemblages in climate space (also compare Fig. 5L with Fig. 5E, F).

4. Discussion

The continental-scale analysis presented here recovered assemblage

Table 1

Mean pollen taxon frequencies for the eleven assemblage groups shown in Fig. 3. Values are mean percentages of each pollen taxon within each assemblage group, calculated across site $\times$ time-interval observations assigned to that group. Frequencies are rounded to one decimal place; non-zero values below 0.1% are reported as < 0.1 . *Pinus* is reported here for completeness, although it was not used as a diagnostic variable in partitioning. A breakdown of pollen assemblage groups into 22 groups from recursive partitioning is provided as [Supplementary Appendix Table S1](#).

Taxon	Arctic Tundra	Birch Parkland	Western Maritime	Boreal Forest	Spruce Woodland	Eastern Transition	Eastern Hardwood	Grassland	Montane Forest	Montane Steppe	Steppe & Desert
<i>Picea</i> (spruce)	7.1	0.9	6.5	21.7	14.8	3.2	1.4	1.2	6.3	5.7	0.4
<i>Tsuga</i> (hemlock)	< 0.1	0	13.4	0.2	1.6	3.7	1.6	< 0.1	0.7	0	0
<i>Abies</i> (fir)	< 0.1	0	4.1	0.8	1.1	0.7	0.4	0.2	1.4	1.6	0.5
<i>Betula</i> (birch)	29.0	47.2	1.0	15.9	9.7	13.2	2.6	0.9	3.5	1.9	0.2
<i>Alnus</i> (alder)	4.8	2.4	19.5	8.8	2.3	2.3	2.0	5.2	3.8	1.6	0.1
<i>Quercus</i> (oak)	0.1	0	0.3	2.0	6.1	11.1	25.1	5.5	0.8	0.2	0.9
<i>Ulmus</i> (elm)	0.1	0	< 0.1	0.7	1.8	2.8	1.6	1.0	0.1	0	0.1
<i>Fraxinus</i> (ash)	0.1	0	< 0.1	1.1	1.4	1.5	1.1	0.6	0.3	0	< 0.1
<i>Ostrya</i> /Carp. (hornbeam)	0	0	< 0.1	0.7	1.3	1.8	1.1	0.2	0.1	0	0.1
<i>Fagus</i> (beech)	< 0.1	0	< 0.1	0.2	0.4	2.5	1.7	< 0.1	0.1	0	0
<i>Acer</i> (maple)	< 0.1	0	< 0.1	0.2	0.6	1.7	0.9	0.1	0.1	0	< 0.1
<i>Carya</i> (hickory)	< 0.1	0	0	0.1	0.2	0.5	2.4	0.4	< 0.1	0	0
<i>Tilia</i> (linden)	< 0.1	0	< 0.1	< 0.1	0.1	0.4	0.1	< 0.1	0	0	0
<i>Juglans</i> (walnut)	< 0.1	0	< 0.1	0	0.1	0.2	0.3	< 0.1	0	0	0
<i>Liquidambar</i> (sweetgum)	0	0	0	0	0	< 0.1	0.3	0	0	0	0
Cyperaceae (sedge)	14.8	6.5	2.9	7.5	6.1	3.4	3.2	8.4	6.2	4.8	5.6
Poaceae (grasses)	7.5	5.1	1.8	3.1	2.1	4.8	4.9	12.4	4.7	4.5	4.5
Prairie Forbs	5.3	2.5	2.1	3.8	3.0	5.7	4.3	14.6	15.7	18.4	33.8
<i>Pinus</i> (pines)	2.1	0	20.1	13.6	30.5	26.0	20.2	14.7	29.3	37.9	11.7

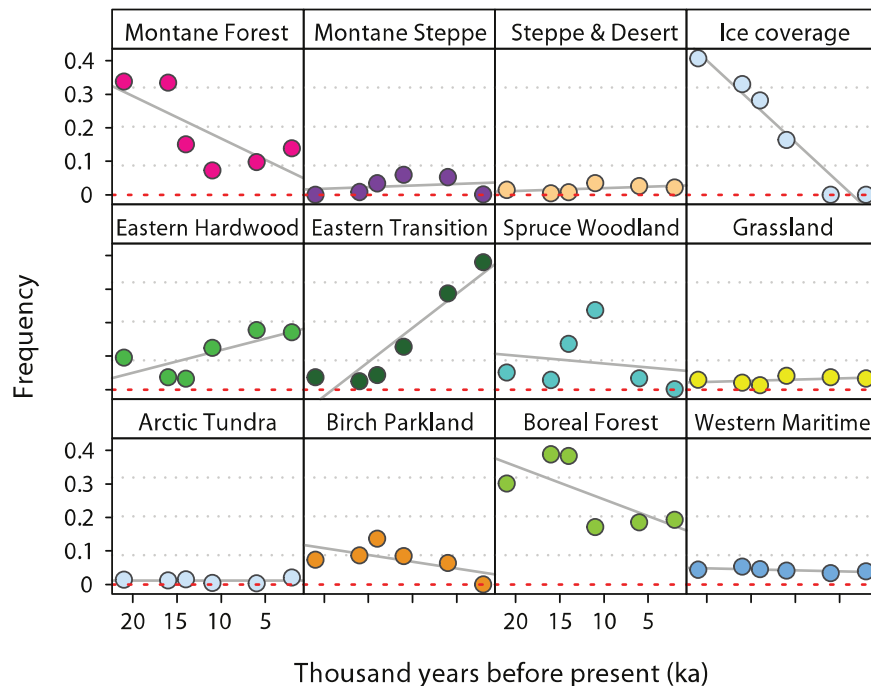


Fig. 4. Relative frequencies of pollen assemblage groups from the Last Glacial Maximum to the present. For each of the six time intervals, frequencies are expressed as the percentage of all site $\times$ time-interval observations assigned to each assemblage group. Ice coverage, expressed as percentage of total land area, is included for reference in the upper-right panel. Major frequency changes between the LGM and present are highlighted with trend lines.

groups that broadly correspond to recognizable modern vegetation types, but also identified three transient assemblages that were widespread during deglaciation and absent from the most recent time interval. These results are consistent with previous work showing that late-Quaternary environmental change produced no-analogue or locally novel plant communities in North America and elsewhere (Overpeck et al., 1992; Williams et al., 2001, 2013; Edwards et al., 2005;

Williams and Jackson, 2007; Staples et al., 2022). The contribution of the present analysis is to place these patterns into a broad continental perspective that compares pollen assemblage composition, geographic distribution, temporal occurrence, and climatic context across the same classification system. Our paleoecological interpretation of the assemblage groups draws on this combined evidence, together with prior regional studies, rather than on the statistical classification alone.

Current climate (A–F)

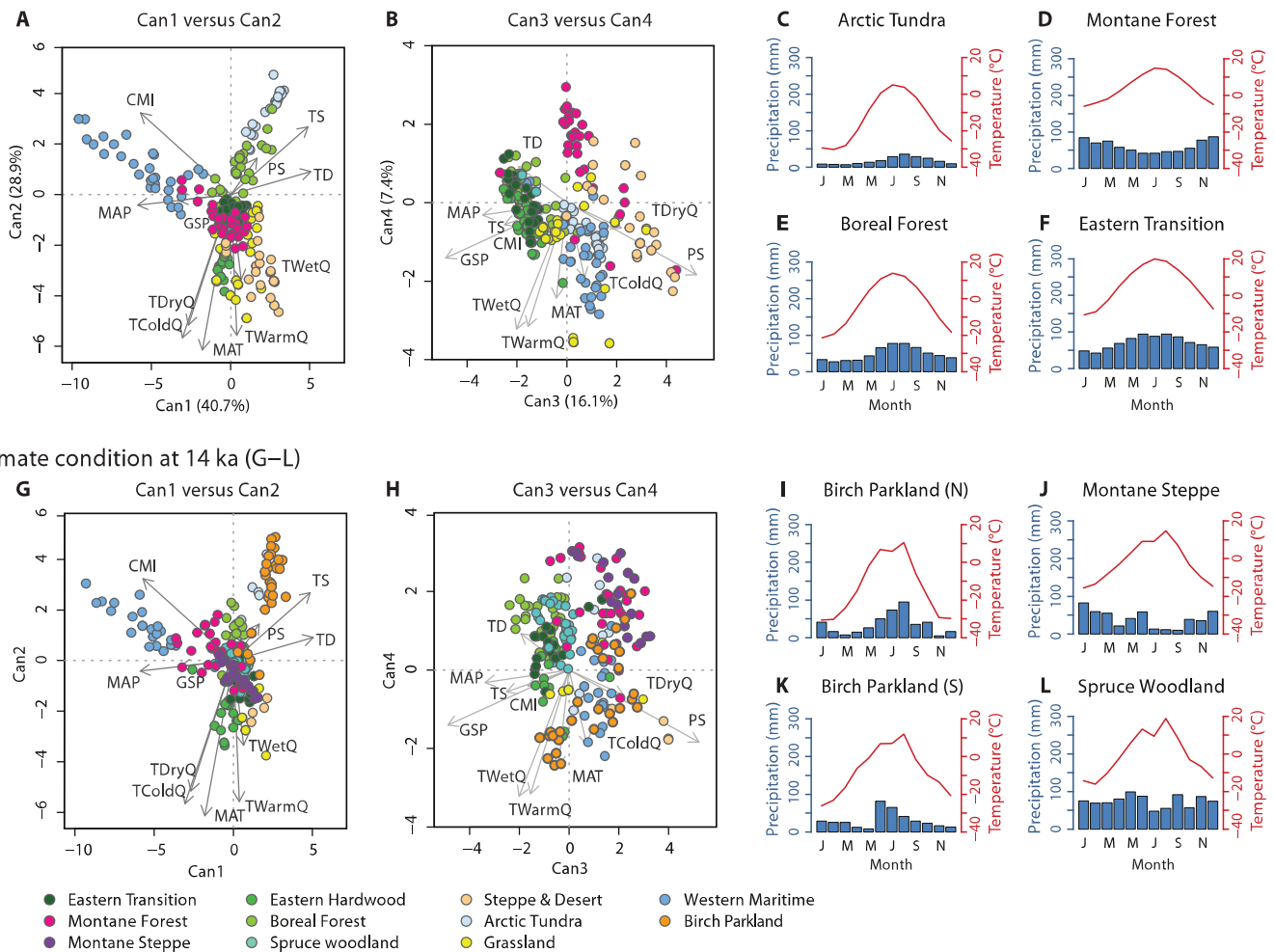


Fig. 5. Multivariate climate conditions of pollen assemblage groups and climate diagrams for selected groups. Canonical discriminant analysis shows the position of pollen assemblage groups in multivariate climate space for modern climate and for the 14 ka climate period. Vectors in the CDA panels represent the direction and relative strength of the climatic gradients associated with separation among pollen assemblage groups. Climate variable abbreviations are provided in Fig. 2. Standard monthly climate diagrams are shown for transient assemblages without analogue in the 4–0 ka reference interval (I–L), and for comparable assemblage groups corresponding to modern forest types (C–F). Separate diagrams are shown for Birch Parkland climate conditions in Beringia (I) and south of the ice sheet (K).

The no-analogue interpretation should be understood at the scale of this synthesis. Fossil pollen data do not resolve complete species-level communities, and our broad analytical time intervals may average over shorter-lived assemblages that emerged and disappeared within individual intervals. These limitations mean that some finer-scale species-level analogues, or additional short-lived no-analogue communities, may not be detected. However, they do not weaken the inference that the recurring pollen assemblage types identified here were absent from the late-Holocene reference interval at the taxonomic, spatial, and temporal resolution of the analysis. Our analysis therefore identifies major no-analogue assemblage types that were widespread enough to be resolved at the continental scale, rather than providing a complete inventory of no-analogue community formation during postglacial reorganization.

The Birch Parkland assemblage is the clearest example of a distinct pollen assemblage without an analogue in the 4–0 ka reference interval. Previous work has described structurally novel Beringian biomes during past warming (Edwards et al., 2005), but our classification describes a broader birch-dominated parkland assemblage that occurred both in Beringia and south of the continental ice sheets. Its climate space was characterized by cool annual conditions, strong seasonality, and comparatively moist growing-season environments. Although absent from modern North America in the form identified here, this assemblage

may be comparable to modern western Fennoscandian forest-tundra ecosystems, where mountain birch forms open forests or parklands adjacent to tundra heath (Ecoregion PA1110, Olson and Dinerstein, 2002).

The Montane Steppe assemblage provides a second example of a transient community associated with a distinctive climate space. It occupied warmer and drier growing-season conditions than modern montane forest communities. This result is consistent with long-term records from western North America showing repeated shifts between forested and more open steppe-like vegetation under changing moisture regimes (Whitlock and Bartlein, 1997). Together with Birch Parkland, this suggests that some transient assemblages were closely associated with climatic conditions that differ from those occupied by comparable modern North American vegetation types.

The Spruce Woodland assemblage appears to represent a different form of transient community. It was compositionally distinct, with high representation of *Picea* together with elevated representation of temperate broadleaf taxa, but it was not separated from comparable modern forest assemblages in the climate ordination. This finding is consistent with the well-known late-glacial spruce-hardwood assemblages of eastern and mid-continental North America, where pollen and macrofossil records indicate combinations of boreal conifers and temperate hardwoods that lack close modern analogues (Overpeck et al.,

1992; Williams et al., 2001; Gill et al., 2009). The lack of strong climatic separation in our ordination suggests that the distinctiveness of this assemblage may not be well explained by climate. Newly exposed substrates after deglaciation, migration disequilibrium, and changed disturbance regimes may all have contributed to this late-glacial community configuration (Gill et al., 2009).

5. Conclusions

This study provides a common continental-scale framework for identifying, mapping, and comparing major North American pollen assemblage types since the Last Glacial Maximum. Within this framework, Birch Parkland, Montane Steppe, and Spruce Woodland were identified as spatially extensive and temporally sustained transient assemblages without direct counterparts in the 4–0 ka reference interval. Their contrasting positions in climate space suggest that transient pollen assemblages can arise through different pathways.

Some assemblages, such as Birch Parkland and Montane Steppe, were associated with climatic conditions that differed from those occupied by comparable modern vegetation types. Although they occurred during deglaciation, these assemblages persisted across multiple millennia and broad geographic regions, suggesting that they were not short-lived local anomalies. Others, such as Spruce Woodland, were compositionally distinctive without being clearly separated in climate space, suggesting that transient assemblages can also reflect new combinations among climate and non-climatic factors, such as soils, landscape history, and disturbance regimes.

Because contemporary climate change is occurring rapidly relative to many ecological processes, the contrast among transient assemblages suggests a possible sequence of vegetation responses to climate change. Near-term responses may resemble the Spruce Woodland case, in which assemblages become compositionally novel before strong climatic differentiation is apparent. More climate-defined assemblages analogous to Birch Parkland or Montane Steppe could emerge later as species distributions, soils, disturbance regimes, and competitive interactions adjust to new environmental conditions. In this sense, the most immediate ecological signature of rapid warming may not be the formation of stable new biomes, but a prolonged period of transient assemblage composition.

CRedit authorship contribution statement

Zihaohan Sang: Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Andreas Hamann:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.hisbio.2026.100049](https://doi.org/10.1016/j.hisbio.2026.100049).

Data availability

Pollen records and climate data are publicly available as cited in this article

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