

# Integrating Plant Fossil Proxies and Biomarkers to Reconstruct Deep-Time Paleoclimate, Paleoecology, and Evolutionary Dynamics

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## Abstract

Reconstructing Earth's environmental past over geologic timescales is a central challenge in paleoscience. A robust understanding of deep-time paleoclimate, paleoecology, and evolutionary dynamics depends on integrating multiple independent proxies that capture different facets of Earth's complex systems. This paper reviews and synthesizes evidence from plant fossil records—particularly fossil leaves and resins—and their associated biomarkers, along with geological and paleogeographic data, to reconstruct past climates and ecosystems. By bridging fossil morphology with organic geochemical signatures, we provide a comprehensive framework for analyzing climate fluctuations, vegetation dynamics, and biotic responses to major global events across Earth history. We emphasize methodological innovations, discuss case studies across the Phanerozoic, and highlight ongoing challenges and future research avenues in this integrative field.

**Keywords:** plant fossils, biomarkers, paleoclimate reconstruction, paleoecology, evolutionary biology, deep time, fossil resins, paleobotany, leaf physiognomy

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## 1. Introduction

Reconstructing Earth's ancient environments is crucial to understanding the long-term interactions between climate, life, and the Earth system. Over geological time, Earth has experienced dramatic shifts in climate—from greenhouse to icehouse states—and these transitions have profoundly influenced the evolution and distribution of life. Among the various archives of past environmental conditions, the fossil record stands out as one of the most informative, offering direct evidence of biological and ecological responses to climatic fluctuations. Within this record, fossilized plants play a uniquely important role as terrestrial climate proxies due to their widespread distribution, morphological plasticity, and physiological sensitivity to environmental variables such as temperature, precipitation, and atmospheric CO<sub>2</sub> concentrations.

Fossil leaves, in particular, encode valuable climatic information in their morphology. Traits such as leaf size, margin type, and venation patterns have strong empirical relationships with climate and are used to infer paleotemperature and precipitation regimes. Complementing these morphological indicators, fossil resins—often preserved as amber—contain a rich molecular archive of ancient vegetation. These resins encapsulate organic biomarkers, including terpenoids and phenolic compounds, that reflect the chemical ecology of ancient ecosystems and the environmental stresses experienced by resin-producing plants. Together, morphological and molecular plant proxies offer a comprehensive view of past terrestrial climates and ecosystems.

The integration of paleobotanical evidence with sedimentological, stratigraphic, and geochemical data enables a multidimensional reconstruction of deep-time paleoenvironments. Recent advances in climate modeling, paleogeographic reconstructions, and high-resolution analytical techniques have further enhanced our ability to extract meaningful environmental signals from the fossil record. Studies now increasingly combine multiple data sources—leaf physiognomy, biomarker geochemistry, and geochronological constraints—to generate refined reconstructions of temperature trends, vegetation shifts, and ecological responses over hundreds of millions of years.

This paper aims to synthesize these emerging approaches, highlighting the value of integrating plant fossil proxies and biomarkers to reconstruct paleoclimate, paleoecology, and evolutionary dynamics through deep time. By reviewing key methodologies, case studies, and theoretical frameworks, we aim to demonstrate how this interdisciplinary synthesis contributes to our broader understanding of Earth system evolution. Importantly, as anthropogenic climate change accelerates, examining past climate-biota interactions offers crucial insights into the resilience, adaptability, and vulnerability of ecosystems—insights that are deeply rooted in the fossilized remains of ancient plants.

## **2. Background and Theoretical Framework**

Paleoclimate and paleoecological reconstructions often rely on proxies—indirect indicators that record environmental conditions at the time of deposition or growth. Plant fossils offer a unique advantage among terrestrial proxies due to their ubiquity, physiological climate sensitivity, and taxonomic diversity.

One of the most widely used approaches to reconstruct paleoclimate from plant fossils is through leaf physiognomy, which relates leaf morphology to environmental variables. Peppe et al. (2017) provide a detailed methodology for using traits like leaf margin type, size, and vein density to estimate mean annual temperature (MAT) and precipitation. Tools like the Climate Leaf Analysis Multivariate Program (CLAMP) utilize multivariate statistical approaches to predict climatic conditions based on leaf assemblages.

In parallel, fossil resins—organic substances secreted by ancient trees—serve as molecular time capsules, preserving biomarkers that can be analyzed for vegetation type, stress levels, and thermal maturity. Pańczak et al. (2023) showed how terpenoids and other organic compounds in fossil resins reveal ecological and climatic conditions during resin production. These biomarkers complement morphological data by providing chemical fingerprints of ancient biospheres.

Understanding the broader environmental and tectonic context is essential for interpreting these signals. For instance, Marcilly et al. (2021) combined paleogeographic reconstructions with carbon degassing data to improve the accuracy of global climate models. Ruban (2020) demonstrated how stratigraphic events, such as sea-level changes and mass extinctions, leave clear imprints in both marine and terrestrial fossil records.

## **3. Methods for Reconstructing Paleoclimate and Paleoecology**

Accurately reconstructing Earth's ancient climate and ecosystems requires a multi-proxy framework that synthesizes plant fossil morphology, molecular biomarkers, geological context, and climate modeling. Each line of evidence contributes a unique dimension to our understanding of deep-time environmental dynamics. This section outlines the key methodologies used in integrated paleoclimate reconstruction and highlights how recent advances have improved both spatial and temporal resolution.

### **3.1 Leaf Physiognomy and Statistical Modeling**

Fossil leaves are among the most reliable terrestrial proxies for reconstructing paleoclimate, particularly in estimating mean annual temperature (MAT) and precipitation. Leaf traits such as size, shape, and margin type are shaped by climate and can be analyzed statistically to infer environmental conditions at the time of deposition.

One widely used method is Leaf Margin Analysis (LMA), which correlates the proportion of untoothed (entire-margined) leaves in a flora with MAT. Another sophisticated tool, the Climate Leaf Analysis Multivariate Program (CLAMP), employs a suite of leaf traits and a multivariate statistical approach calibrated with modern vegetation datasets to reconstruct past climates with higher accuracy.

Peppe et al. (2017) introduced further refinements to these methods by integrating machine learning algorithms and expanding global calibration datasets. Their work demonstrated that quantitative leaf physiognomic analysis can generate high-resolution climate reconstructions even from diverse and evolutionarily distinct fossil assemblages. Their methods have been successfully applied to both tropical and temperate floras from the Cretaceous and Eocene periods, yielding precise estimates of precipitation seasonality and temperature gradients.

### **3.2 Biomarker Extraction from Fossil Resins**

Fossil resins, particularly those preserved as amber, offer a complementary molecular archive of ancient plant biochemistry and environmental conditions. These resins trap and preserve a suite of organic molecules—biomarkers—that can be traced to specific plant groups and ecological stressors.

Pańczak et al. (2023) employed gas chromatography-mass spectrometry (GC-MS) and nuclear magnetic resonance (NMR) spectroscopy to analyze biomarker profiles from Baltic and Burmese amber deposits. Their results revealed complex assemblages of terpenoids and phenolic compounds, which provide insights into the taxonomic identity of resin-producing plants, the diagenetic alteration of resins over time, and the ecological stresses—such as herbivory or drought—that may have stimulated resin production. These molecular signatures, when integrated with morphological and stratigraphic data, enable a more nuanced reconstruction of past vegetation and climate.

### **3.3 Sedimentological and Stratigraphic Contextualization**

Plant fossils are preserved within specific sedimentary environments, and understanding these depositional contexts is critical for accurate paleoecological interpretation. Sedimentology provides insight into the environmental settings—floodplains, swamps, or deltas—that influenced vegetation structure and preservation.

DiMichele and Gastaldo (2008) emphasized that interpreting paleoecology requires not just fossil identification but an understanding of sedimentary facies and taphonomic processes. Their studies in the Late Paleozoic tropics showed that vegetational assemblages were closely tied to glacial-interglacial cycles, with distinct shifts in floral composition corresponding to changes in sea level, sedimentation rates, and basin hydrology. Such stratigraphic controls must be considered when correlating climate proxies across space and time.

### **3.4 Paleogeographic and Climate Model Integration**

Empirical data from fossil leaves and resins are greatly enhanced when coupled with paleogeographic and Earth system modeling frameworks. Marcilly et al. (2021) updated global paleogeographic reconstructions and degassing rates, which serve as boundary conditions for long-term carbon cycle and climate simulations. Their data help constrain the tectonic and atmospheric dynamics that shaped ancient climates, providing critical validation for proxy-based reconstructions.

### **3.5 Surface Temperature Reconstructions**

The integration of multiple proxy datasets with geochemical and modeling tools culminates in global surface temperature reconstructions. Judd et al. (2024) compiled a 485-million-year surface temperature record by synthesizing marine isotope data, paleobotanical proxies, and climate simulations. This high-resolution temporal framework allows researchers to correlate major biological events—such as mass extinctions or evolutionary radiations—with shifts in climate. It contextualizes terrestrial plant responses within broader Earth system dynamics and underlines the importance of cross-disciplinary integration.

## **4. Evolutionary Insights from Plant Fossils and Biomarkers**

The evolutionary history of land plants is deeply intertwined with climate evolution. Fossil leaves not only reveal environmental preferences but also track key morphological innovations. Hetherington (2024) highlighted how plant development has evolved over geologic time, including transitions in vascular structure, leaf arrangement, and reproductive features.

Plant biomarkers provide an additional evolutionary perspective by capturing biochemical adaptations to stress, defense, and metabolic innovation. Shifts in resin chemistry can reflect evolutionary pressures such as herbivory, fungal pathogens, and climate extremes.

Mass extinctions represent critical junctures in evolutionary history, and plant fossils offer key insights into their ecological aftermath. For instance, Ruban (2020) correlated global eustatic sea-level changes with extinction pulses, observing significant floral turnover in both terrestrial and coastal settings.

To illustrate the effectiveness of a multi-proxy approach in reconstructing paleoclimate and paleoecology, this section presents three well-documented case studies. These examples highlight how integrating leaf physiognomy, biomarkers, and sedimentological data can reveal detailed narratives of ecological transformation in deep time.

### **4.1 Late Paleozoic Rainforest Collapse (LPRC)**

The Late Paleozoic Rainforest Collapse (LPRC), which occurred around 305 million years ago during the Pennsylvanian–Permian transition, represents a major climatic and ecological upheaval. Fossil records from Euramerican basins provide compelling evidence of a dramatic shift from lycopsid-dominated swamp forests to more drought-tolerant, xerophytic plant communities.

DiMichele and Gastaldo (2008) emphasized the significance of repeated glacial-interglacial cycles as the primary driver of this transformation. Fluctuating sea levels and climate oscillations disrupted the waterlogged conditions essential for coal-forming wetlands, leading to habitat fragmentation and a

decline in biodiversity. Leaf physiognomic analyses show changes in size and margin types consistent with increasing aridity, while sedimentological evidence points to a shift from fine-grained, organic-rich deposits to coarser, better-drained substrates. This case demonstrates how the integration of morphological and geological data can trace the ecological consequences of climate variability over geological timescales.

#### **4.2 Paleocene–Eocene Thermal Maximum (PETM)**

The Paleocene–Eocene Thermal Maximum (PETM), approximately 56 million years ago, was a geologically brief but intense interval of global warming associated with massive carbon input into the atmosphere. It profoundly altered both marine and terrestrial ecosystems.

Fossil leaf studies from North America, particularly in the Bighorn and Green River basins, reveal northward shifts in floral distributions and a proliferation of broadleaf angiosperms (Peppe et al., 2017). The leaf margin data indicate an increase in MAT by up to 5–8°C within just a few thousand years. This rapid warming was accompanied by enhanced evapotranspiration and increased precipitation seasonality.

Simultaneously, biomarker analyses of fossil resins from PETM-aged sediments reveal stress-induced resin production and the rise of plant lineages capable of thriving in warmer, wetter environments. The integration of molecular data and leaf morphology paints a comprehensive picture of biotic adaptation and migration under extreme climate forcing.

#### **4.3 Biomarkers in Burmese and Baltic Amber**

Amber deposits offer an exceptional molecular archive of deep-time forests. Pańczak et al. (2023) examined amber from the mid-Cretaceous Burmese deposits and Eocene-aged Baltic sites, focusing on the biomarker composition preserved within the fossilized resins.

GC-MS and NMR analyses revealed complex terpenoid profiles indicative of conifer dominance in high-latitude forests. In both cases, the presence of warm-climate resin-producing taxa supports paleoclimatic interpretations of a greenhouse world. Additionally, differences in biomarker composition between the two amber types reflect not only phylogenetic shifts but also changing environmental stresses and resin chemistries over time. This case highlights how molecular fossils contribute to resolving vegetation structure and climate conditions across disparate temporal and geographic contexts.

### **5. Challenges and Future Directions**

Despite methodological advancements, several challenges hinder fully integrated paleoclimate reconstructions:

- **Preservation Biases:** Plant fossils are more likely to be preserved in specific depositional environments, skewing the fossil record.
- **Taxonomic Uncertainty:** Fossil leaves are often difficult to assign to modern lineages, complicating physiological interpretations.
- **Diagenesis:** Biomarker preservation varies depending on burial conditions and thermal history.

- Model Uncertainties: Paleogeographic reconstructions and climate simulations contain inherent assumptions that influence interpretations.

Future work should emphasize:

- Cross-validation of proxies using modern calibration studies.
- Expanded sampling of tropical fossil sites.
- Integration of isotopic and biomolecular data.
- Development of open-access databases linking plant traits, biomarker profiles, and geospatial metadata.

## 6. Conclusion

The integration of plant fossil proxies and biomarkers provides a multidimensional view of Earth's deep-time environments. From morphological traits in fossil leaves to molecular signatures in ancient resins, these indicators reveal how terrestrial ecosystems have responded to climatic shifts, tectonic events, and evolutionary pressures. Coupling these biological signals with paleogeographic and modeling frameworks enhances our ability to reconstruct past climates with unprecedented resolution. As climate change accelerates in the modern era, these historical insights become ever more vital for predicting future ecological responses.

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