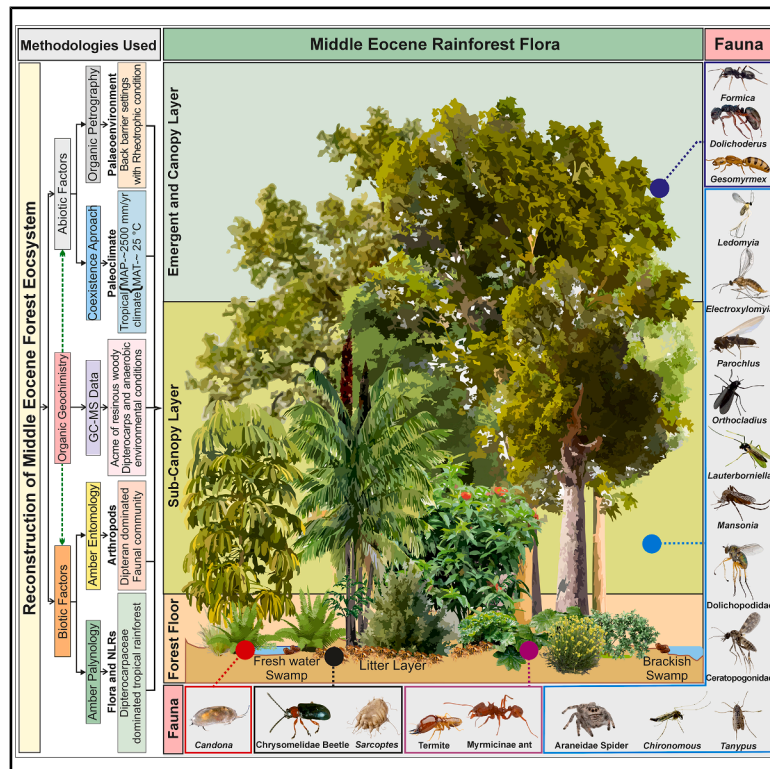


# Eocene amber fossils reveal how complex trophic interactions shaped tropical rainforest biodiversity

## Graphical abstract



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## In brief

Paleontology; Interaction of plants with organisms; Paleobiology; Interaction of plants with arthropods

## Highlights

- Reconstructs Eocene tropical rainforest ecosystems using fossilized amber biota
- Emphasizes climate stability, area, and time in diversity—supports ESAT theory
- Demonstrates ancient origins of modern tropical lineages in India
- Shows biodiversity resilience to past climate shifts—vital for future predictions



## Article

# Eocene amber fossils reveal how complex trophic interactions shaped tropical rainforest biodiversity

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## SUMMARY

The Eocene Epoch represented a pinnacle in Indian paleobiodiversity, explained by the ESAT (energy-stability-area-time) theory, which links climatic stability and geological time in fostering immense biodiversity. We provide a reconstruction of a middle Eocene tropical ecosystem from an amber biota recovered from the Harudi Formation ( $\sim 41.6 \pm 0.5$  to  $\sim 40.8 \pm 0.5$  Ma), Umarsar Lignite Mine (ULM), western India. It reveals a highly diverse ecosystem ( $>800$  arthropods of various taxonomic ranks along with 78 genera and 118 species of palynomorphs) thriving in warm and humid conditions (mean temperature  $\sim 25^\circ\text{C}$ ; rainfall  $\sim 2,450$  mm/year), analogous to modern tropical climates. The findings show that favorable climate, ecological complexity, and India's northward drift facilitated tropical lineage diversification, reinforcing ESAT as a robust explanatory model for deep-time biodiversity patterns. These findings also offer valuable analogs for predicting how biodiversity and functional networks in current tropical forests might respond to ongoing climate change, emphasizing the need to conserve both species and their ecological interactions.

## INTRODUCTION

Tropical rainforests exemplify Earth's most intricate and biologically diverse terrestrial ecosystems, hosting a disproportionate share of global biodiversity despite covering just  $\sim 7\%$  of the planet's land surface.<sup>1</sup> These ecosystems largely found in the equatorial Americas, Africa, and Indo-Pacific support nearly 50% of all known species.<sup>2</sup> Their exceptionally high primary productivity coupled with intense interspecies interaction, establishes them as the “cradle” and “museum” of biodiversity.<sup>3,4</sup> The exceptional diversity and ecological interactions have long fascinated evolutionary biologists, including Darwin, Bates, and Wallace, who regarded these ecosystems as ancient evolutionary crucibles, and are central to theories explaining the origins and persistence of biodiversity.

One such framework, the ESAT (energy-stability-area-time) theory, attributes high tropical diversity to elevated solar energy input, ecological stability over geological timescales, expansive historical distribution, and evolutionary time.<sup>5,6</sup> Warmer, equable temperatures result in more species generations each year, with concomitantly higher rates of genetic variation and opportunities for both adaptive and phyletic evolution.<sup>5</sup> The ecological stability of broad-leaved tropical forests particularly in terms of their taxonomic composition over geological timescales has likely played

a key role in reducing extinction rates. These ecosystems have generally remained buffered from severe seasonality, glaciation, extreme droughts, tectonic upheaval, and other large-scale geophysical stresses.<sup>7,8</sup> However, direct evidence of biodiversity in early tropical forests remains limited, particularly from low-latitude regions. The “area” variable within the ESAT model may seem counterintuitive, given the present-day restricted distribution of tropical forests. However, it is inextricably linked to the other variables, including *Time*. Angiosperm-dominated tropical rainforests commonly referred to as “megathermal” forests,<sup>9</sup> appear to have existed since at the least early Paleocene ( $\sim 65$  Ma),<sup>10–12</sup> based on fossil records from the Western Hemisphere and the Maastrichtian-early Paleocene (late Cretaceous-early Paleocene) of the Southern Hemisphere.<sup>8,13,14</sup>

The Paleotropics, comprising about 50% of the world's tropical rainforests coverage, host several biodiversity hotspots across Africa and Asia.<sup>9,15</sup> India offers a compelling case study due to its dynamic geological history and rich fossil record.<sup>16</sup> Currently, approximately 33% of all angiosperm species and 28% of all plant species in India are endemic.<sup>17</sup> Interestingly, during the late Maastrichtian, India supported a highly endemic flora, with around 40% of its fossil floral assemblage being regionally unique.<sup>8</sup> These assemblages are strikingly modern in composition and more taxonomically diverse than

