Amber and the Cretaceous Resinous Interval

Xavier Delclòs [a,b,*,1], Enrique Peñalver [c,**,1], Eduardo Barrón [c], David Peris [d], David A. Grimaldi [e], Michael Holz [f], Conrad C. Labandeira [g,h,i], Erin E. Saupe [j], Christopher R. Scotese [k], Mónica M. Solórzano-Kraemer [l], Sergio Álvarez-Parra [a,b], Antonio Arillo [m], Dany Azar [n,o], Edwin A. Cadena [p], Jacopo Dal Corso [q], Jiří Kvaček [r], Antonio Monleón-Getino [s], André Nel [t], Daniel Peyrot [u], Carlos A. Bueno-Cebollada [c], Alejandro Gallardo [a], Beatriz González-Fernández [v], Marta Goula [b,w], Carlos Jaramillo [x], Iwona Kania-Kłosok [y], Rafael López-Del Valle [z], Rafael P. Lozano [c], Nieves Meléndez [aa], César Menor-Salván [ab], Constanza Peña-Kairath [a,b], Vincent Perrichot [ac], Ana Rodrigo [c], Alba Sánchez-García [c], Maxime Santer [a,b], Víctor Sarto i Monteys [ad], Dieter Uhl [l], José Luis Viejo [ae], Ricardo Pérez-de la Fuente [af]

[a] Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona, Spain
[b] Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona, Spain
[c] CN Instituto Geológico y Minero de España (IGME)-Consejo Superior de Investigaciones Científicas (CSIC), Madrid, Spain
[d] Institut Botànic de Barcelona, CSIC-Ajuntament de Barcelona, Barcelona, Spain
[e] Division of Invertebrate Zoology, American Museum of Natural History, New York, USA
[f] Instituto de Geociências, Universidade Federal da Bahia, Salvador da Bahia, Brazil
[g] National Museum of Natural History, Smithsonian Institution, Washington, D.C, USA
[h] Department of Entomology, University of Maryland, MD, USA
[i] College of Life Sciences & Academy for Multidisciplinary Studies, Capital Normal University, Beijing, China
[j] Department of Earth Sciences, University of Oxford, Oxford, UK
[k] Department of Earth & Planetary Sciences, Northwestern University, Evanston, IL, USA
[l] Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Frankfurt am Main, Germany
[m] Departamento de Biodiversidad, Ecología y Evolución, Facultad de Biología, Universidad Complutense, Madrid, Spain
[n] Natural Sciences Department, Faculty of Science II, Lebanese University, Fanar-El-Matn, Lebanon
[o] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China
[p] Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia
[q] State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences, Wuhan, China
[r] National Museum, Prague, Czech Republic
[s] Department de Genètica, Microbiologia i Estadística, Facultat de Biologia, Universitat de Barcelona, Spain
[t] Institut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP50 Paris, France
[u] School of Earth Sciences, University of Western Australia, Crawley, Australia
[v] Departamento de Explotación y Prospección de Minas, Universidad de Oviedo, Oviedo, Spain
[w] Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Spain
[x] Smithsonian Tropical Research Institute, Panama
[y] Department of Biology, Institute of Biology and Biotechnology, University of Rzeszów, Poland
[z] Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, and Cueva El Soplao, Celis, Santander, Cantabria, Spain
[aa] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Spain
[ab] Departamento de Biología de Sistemas, Universidad de Alcalá, Alcalá de Henares, Spain
[ac] Géosciences Rennes - UMR 6118, University of Rennes, CNRS, Rennes, France
[ad] Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, Spain
[ae] Departamento de Biología, Facultad de Ciencias, Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Cantoblanco, Madrid, Spain
[af] Oxford University Museum of Natural History, Oxford, UK

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* Corresponding author at: Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, Universitat de Barcelona, Spain.
** Corresponding author.
    E-mail addresses: xdelclos@ub.edu (X. Delclòs), e.penalver@igme.es (E. Peñalver).
[1] (X. Delclòs), (E. Peñalver). These contributed equally to this work.

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ABSTRACT

Amber is fossilized resin that preserves biological remains in exceptional detail, study of which has revolutionized understanding of past terrestrial organisms and habitats from the Early Cretaceous to the present day. Cretaceous amber outcrops are more abundant in the Northern Hemisphere and during an interval of about 54 million years, from the Barremian to the Campanian. The extensive resin production that generated this remarkable amber record may be attributed to the biology of coniferous resin producers, the growth of resiniferous forests in proximity to transitional sedimentary environments, and the dynamics of climate during the Cretaceous. Here we discuss the set of interrelated abiotic and biotic factors potentially involved in resin production during that time. We name this period of mass resin production by conifers during the late Mesozoic, fundamental as an archive of terrestrial life, the 'Cretaceous Resinous Interval' (CREI).

1. Introduction

Resins are secondary metabolites synthesized by specialized cells of "gymnosperm" and angiosperm plants, whose composition consists of amorphous mixtures of carboxylic acids, essential oils and isoprene-based hydrocarbons (Langenheim, 2003). Resin production is conditioned by temperature, solar radiation, evapotranspiration, and soil water deficit (Allen et al., 2010; Rodríguez-García et al., 2015). The primary functions of resins relate to defense against herbivores and pathogens, and as a healing mechanism, sealing wounds and vulnerable parts after damage caused by physical or biological agents (Langenheim, 2003; Seyfullah et al., 2018).

Resins can remain sticky from just hours to several months after being secreted, which can ensnare organisms or parts of them —known as bioinclusions— found mostly in the same ecosystem as the resin-producing plant (Solórzano Kraemer et al., 2018). The crosslinking of resin takes place over millions of years, resulting in gradual hardening, decrease in thermal denaturation, and loss of free methyl groups, all of which lead to a relatively inert, hardened form called amber (Langenheim, 1990; Anderson et al., 1992; McCoy et al., 2017; Solórzano-Kraemer et al., 2020). Only a few types of resins can fossilize based on their chemical composition (Anderson and Crelling, 1995; Langenheim, 2003).

Most amber deposits have yielded few or no bioinclusions. The reasons for this scarcity of bioinclusions are variable, but usually relate to the paucity of resin production during some periods of time (this paper), where the resin was produced (under aerial or underground conditions; Álvarez-Parra et al., 2021), and/or how long the resin retained its stickiness (Solórzano Kraemer et al., 2018). Amber-bearing outcrops that preserve bioinclusions are a type of Konservat-Lagerstätte. Indeed, the preservation of organisms in amber is exceptional and differs from other organic or inorganic mechanisms that retain organismic detail for millions of years (Martínez-Delclòs et al., 2004; Ross, 2009; Grimaldi and Ross, 2017). Despite taphonomic biases inherent in resin entrapment (Solórzano Kraemer et al., 2018), amber can provide exceptional external and internal anatomical detail of the bioinclusions and evidence of past animal behaviors (Labandeira, 2014a; Grimaldi, 2019). Amber deposits are typically parautochthonous-allochthonous, in which resin was dislodged by gravity, transported and concentrated by water, and accumulated in a primary or secondary location (Martínez-Delclòs et al., 2004). However, a few autochthonous-parautochthonous deposits are known, in which resin experienced minimal to virtually no transport (Schmidt et al., 2012; Seyfullah et al., 2018; Álvarez-Parra et al., 2021).

Resin crosslinking, which begins once the resin is exuded by the plant, continues after burial in sealed, anoxic sediments (e.g., within or under layers of clay) that have little interaction with meteoric water (Martínez-Delclòs et al., 2004). Resin has almost the same density as freshwater but is buoyant in sea water or in freshwater with sediments in suspension and is therefore easily transported by flotation and concentrated by currents. For these reasons, transitional settings with large accumulations of continental organic matter, such as deltas, estuaries, swamps or oxbow lakes, are the most favorable sedimentary environments for resin fossilization (Grimaldi et al., 2000b; Martínez-Delclòs et al., 2004; Iturralde-Vinent and MacPhee, 2019). Resiniferous trees are often located on emergent topography within these transitional environments (Álvarez-Parra et al., 2021) or close to areas where resin primarily accumulated by low-energy transport, indicated by the preservation of fragile resin structures (Grimaldi et al., 2000b; Perrichot, 2005; Rust et al., 2010; Veltz et al., 2013). The association of amber-bearing deposits with coal (lignite) or other rocks rich in organic matter suggests episodes of inland environments flooded by marine transgression (Najarro et al., 2009; Rodríguez-López et al., 2020).

Although resin is exuded by different tissues and organs of plants, amber deposits —at least those from the Cretaceous and whose taphonomy has been addressed— were formed primarily by resin produced by root tissues that generally lack bioinclusions (root resin) and, more minorly, by the trunk, branches, or above-soil plant parts (aerial resin) (Langenheim, 1995; Álvarez-Parra et al., 2021), the latter of which has the potential to contain abundant bioinclusions. Although the oldest fossil resin dates from the late Carboniferous (Bray and Anderson, 2009), oldest amber with bioinclusions dates from the Late Triassic, which preserves a few minute arthropods (Schmidt et al., 2012; Sidorchuk et al., 2015). Jurassic amber is scarce and may be associated with the tropical-equatorial zone, since it has been found primarily in Thailand, Italy, and Lebanon; no macroscopic bioinclusions have been hitherto reported from this amber (Nohra et al., 2013; Neri et al., 2016). The oldest amber deposits rich in bioinclusions are Barremian in age (Early Cretaceous) (Maksoud et al., 2017).

The Cretaceous (~145.0–66.0 Ma) represents a time of rapid evolutionary turnover and diversification of organisms. From a macroecological perspective, it was a key period in Earth history in which the Angiosperm Terrestrial Revolution (ca. 100 to 50 Ma), inclusive of the formerly defined Cretaceous Terrestrial Revolution (Lloyd et al., 2008; Benton et al., 2022), occurred. During this time, the Mesophytic paleobiome dominated by "gymnosperms" was replaced by a Cenophytic paleobiome dominated by angiosperms (Labandeira, 2014b; McElwain, 2018; Birks, 2020; Condamine et al., 2020). This turnover altered the base of trophic networks within continental ecosystems (Labandeira, 2014b), substantially modifying communities of herbivores (Labandeira, 2007; Kergoat et al., 2014) and, therefore, affecting the composition and evolution of continental biotas (Meredith et al., 2011; McKenna et al., 2015; Peris et al., 2017; Benson et al., 2021; Peris and Condamine, 2023).

The climate of the Cretaceous was warmer and more humid than that of today, probably due to very active, sustained volcanism associated with unusually extensive seafloor spreading that elevated atmospheric CO_2 and O_2 values (Royer et al., 2004; Poulsen and Zhou, 2013). During most of the Cretaceous, polar regions were virtually devoid of ice (Scotese, 2021) and continental land masses were largely occupied by forests dominated by conifers (Hay and Floegel, 2012; Peralta-Medina and Falcon-Lang, 2012), thereby significantly reducing albedo. The

decrease in latitudinal desert belts during the Early Cretaceous and long-lasting humid conditions during the Late Cretaceous were driven by the breakup of Pangea (Chaboureau et al., 2014; Landwehrs et al., 2021).

Cretaceous amber-bearing deposits, at least those currently documented, have a limited temporal and geographical distribution (Martínez-Delclòs et al., 2004; Labandeira, 2014a). They are known from the Valanginian to the Maastrichtian, but they are particularly abundant and significant from the Barremian to the Campanian (these ages ranging from 125.77 to ~72.1 Ma at present), and, although numerous and widely distributed, occur predominately in the Northern Hemisphere, which may reflect present-day sampling biases (Fig. 1A). Several Cretaceous amber-bearing deposits yield abundant amber and bioinclusions (Martínez-Delclòs et al., 2004; Penney, 2010; Seyfullah et al., 2018). The most studied fossiliferous amber-bearing outcrops from the Cretaceous are found in Lebanon (Barremian), Congo (Aptian), Spain (Albian), France (Cenomanian), Myanmar (Cenomanian), New Jersey in the USA (Turonian), Taimyr in Russia (Santonian) and western Canada (Campanian). In addition to these localities, amber (with or without bioinclusions) has been reported from Cretaceous deposits in many other regions worldwide (Fig. 2; Supplementary data A).

Molecularly analyzed amber, Pleistocene and Holocene copals, and Defaunation resin (produced after the beginning of the Industrial Revolution, see Solórzano-Kraemer et al., 2020) are valuable tools for interpreting the botanical origin of amber (McCoy et al., 2017, 2021).

However, the identity of Cretaceous resin-producing plants remains unknown in most cases. The taxonomic affinities of Cretaceous trees that produced abundant resin remain elusive for a variety of reasons, which include extensive chemical variation observed in the composition of Cretaceous amber samples (Menor-Salván et al., 2016; McCoy et al., 2021), molecular convergence (Bray and Anderson, 2009), and the usually scarce record of plant remains in amber as bioinclusions (Kvaček et al., 2018; Moreau et al., 2020). Nevertheless, geochemical studies have ruled out angiosperms as resin-producing plants during the Cretaceous (Anderson et al., 1992; Lambert et al., 1996; Menor-Salván et al., 2016), with a few minor exceptions (Grimaldi et al., 2000a). Most likely, angiosperms did not acquire the ability to produce resin in sufficient quantities to form amber-bearing deposits until the Early Eocene (Jossang et al., 2008). As for "gymnosperms", the coniferous tree families of Araucariaceae, Cheirolepidiaceae†, Cupressaceae s.l., Podocarpaceae, and Pinaceae were widely distributed during the Cretaceous (Peralta-Medina and Falcon-Lang, 2012) (Fig. 2) and have been identified as likely resin sources of Cretaceous amber deposits (Azar et al., 2010; Peñalver and Delclòs, 2010; Perrichot et al., 2010; Nohra et al., 2014; Menor-Salván et al., 2016; McCoy et al., 2021) (Supplementary data B). The Erdtmanithecales†, a group of non-coniferous "gymnosperms" related to the Gnetales or the Bennettitales†, and namely known for their pollen, have been suggested as possible producers of resin that generated amber deposits in the Aptian of Brazil (Seyfullah et al., 2020).
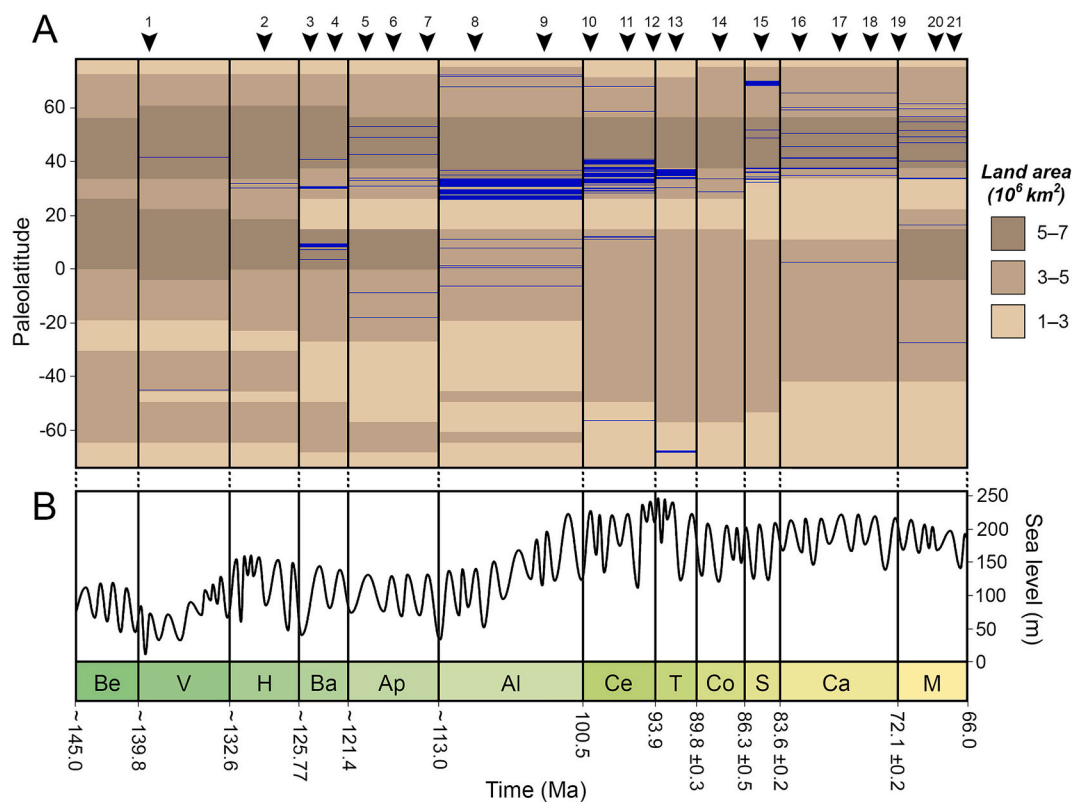

Fig. 1. Paleolatitudinal distribution of 239 Cretaceous amber-bearing deposits, grouped by geological age (A) and sea level changes (B) throughout the Cretaceous. Amber-bearing deposit data are provided in Supplementary data A. Amber deposits represented by thin blue stripes of the same thickness; deposits within the same age box and close in paleolatitude appear as stripes of greater thickness due to superposition. Proportion of area occupied by land indicated in shades of brown (modified from Landwehrs et al., 2021: Fig. 3). Representative amber deposits: 1- Hastings (UK); 2- Golling (Austria); 3- Isle of Wight (UK); 4- Twenty-nine localities in Lebanon, Zarzar Lake (Syria); 5- Chōshi (Japan); 6- Doumanga (Congo); 7- Araripe (Brazil); 8- Ariño (Spain), Hkamti (Myanmar), Estoril (Portugal), Archidona (Ecuador); 9- Eleven localities in Spain, Salignac-Eyvigues (France), Wadi Zerqa (Jordan); 10- Six localities in France, Kachin (Myanmar); 11- Nizhnyaya Agapa (Russia), Agdzhakend (Azerbaijan); 12- Chatham Island (New Zealand); 13- Sayreville in New Jersey (USA), La Garnache (France); 14- Shavarshavan (Armenia); 15- Five localities in Taymyr (Russia), Kuji (Japan), Piolenc (France); 16-Ajka (Hungary), Eutaw Fm. in Alabama (USA), Tuna-1 (Australia); 17- Cedar Lake, Grassy Lake (and other localities, Canada); 18- Tilin amber (Myanmar); 19- Arctic Coastal Plain in Alaska (USA); 20- Hanna Basin in Wyoming (USA); 21- Hell Creek Fm. in South Dakota (USA). Eustatic sea-level changes modified from Ray et al. (2019) and after Haq (2014). Geological Timetable based in the International Commission on Stratigraphy (v 2023/06), https://stratigraphy.org/chart. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
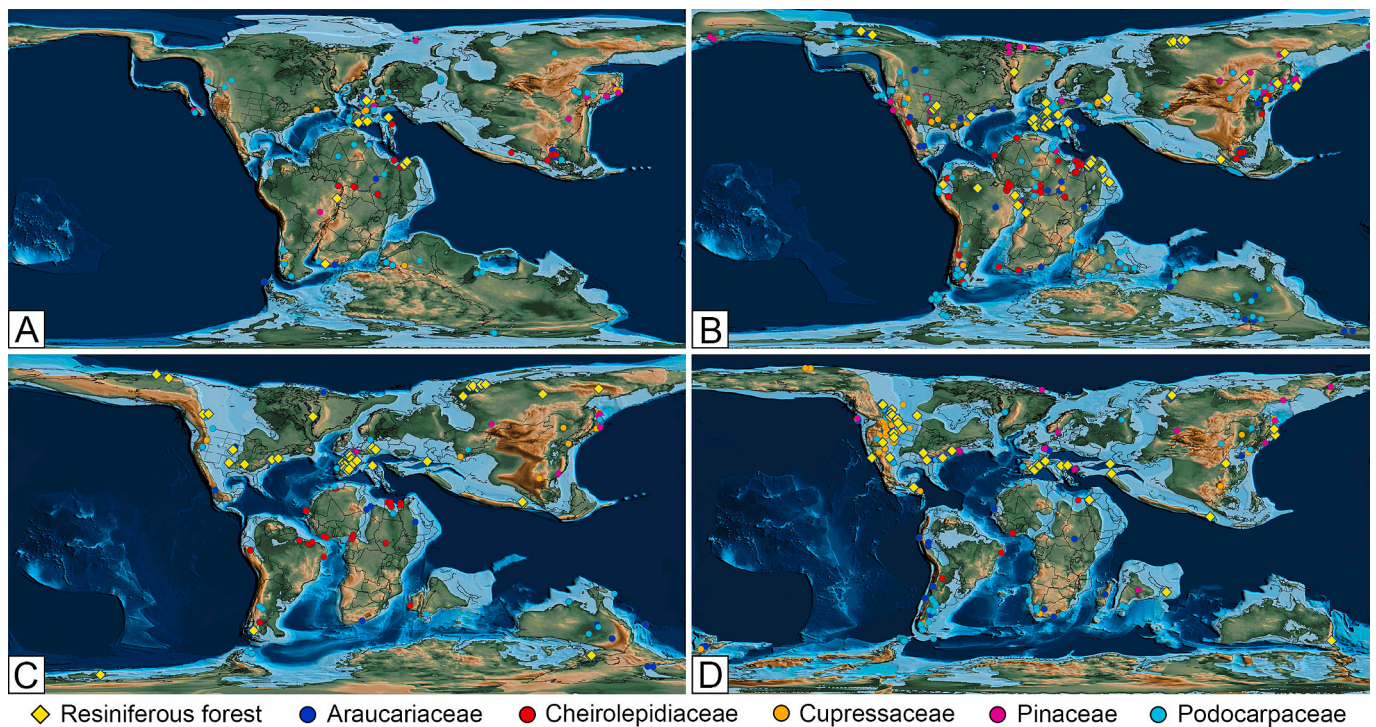
Fig. 2. Distribution of resiniferous forests based on known amber-bearing localities and known occurrences of potential coniferous resin-producing tree families throughout the Cretaceous: Araucariaceae, Cheirolepidiaceae†, Cupressaceae, Pinaceae, and Podocarpaceae. The dataset/sources related to the paleobotanical groups used to construct this figure is formed by Supplementary data B (data from Peralta-Medina and Falcon-Lang (2012) and our own bibliographic search) and data downloaded from Paleobiology Database (https://paleobiodb.org). A) Berriasian–Hauterivian; B) Barremian–Albian; C) Cenomanian–Turonian; D) Coniacian–Maastrichtian. Paleogeographic maps obtained from Scotese et al. (2021). The present-day spatial coordinates and ages from a total of 299 Cretaceous amber outcrops and 1252 paleobotanical records were obtained from a bibliographic survey (Supplementary data A and B, respectively). Present coordinates of amber outcrops and paleobotanic occurrences were rotated to paleocoordinates using R v.4.0.4 and GPlates v.2.2.0. Map visualization and imaging was made using QGIS v.3.22.3 software. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Actuotaphonomic studies (Peñalver et al., 2018), plant bioinclusions (Kvaček et al., 2018; Moreau et al., 2020) (Fig. 3A−B), and examination of wood logs and cone scales with embedded amber in amber-rich levels (Perrichot, 2005; Mays et al., 2019) provide important evidence for determining specific conifer taxa involved in resin mass production during the Cretaceous. Although modern Pinaceae resin is poorly crosslinked due to its molecular composition, a few moderate-size amber deposits resulting from this resin have been found (Bray and Anderson, 2008; Menor-Salván et al., 2016). Cretaceous Cupressaceae produced resin but generally in small amounts (e.g. Otto et al., 2000). Cheirolepidiaceae† conifers lack resiniferous structures, except for some taxa presenting traumatic resin canals (Bodnar et al., 2013; Rombola et al., 2022).

In this contribution, we define and outline the Cretaceous Resinous Interval (CREI) by integrating diverse lines of evidence and analyzing the set of interrelated abiotic and biotic factors that characterized this interval. The data presented herein was compiled from the literature and our own fieldwork in Cretaceous amber localities from Lebanon, Jordan, Congo, Ecuador, Spain, France, Myanmar, USA, and New Zealand; Cenozoic amber localities from France, Mexico, Dominican Republic, New Zealand, India, China, and Ethiopia; and copal and Defaunation resin deposits from Colombia, Dominican Republic, New Caledonia, New Zealand, and Madagascar. In the latter three regions, our fieldwork focused on actuotaphonomic processes aimed at understanding the conditions of production and conservation of Defaunation resin and the formation of copal deposits.

The materials figured in this work are housed at the El Soplao Cave amber collection, Spain (Figs. 3A, E, 5C), the University of Barcelona, Spain (Figs. 3B, 5D), the Nanjing Institute of Geology and Palaeontology, China (Fig. 5A), and the Museu de Ciències Naturals de Barcelona, Spain

(Fig. 5B). Photographs and data used in the figures are our own when not specified in the captions.

2. Definition of the Cretaceous Resinous Interval

We define the Cretaceous Resinous Interval (CREI) as *global mass resin production and burial interval that occurred from the Barremian to the Campanian stages of the Cretaceous Period.* We posit that, during a relatively continuous time interval of about 54 million years, a suite of factors led to the formation of rich amber deposits with similar characteristics and of wide geographic distribution (Figs. 1, 2). This time-delimited interval is based on the known geological record, which provides evidence of numerous amber-bearing deposits (Supplementary data A) from the Barremian (Early Cretaceous), namely those from Lebanon (Maksoud et al., 2022), to the Campanian (Late Cretaceous), particularly Canadian (McKellar et al., 2008) and Tilin in Myanmar (Zheng et al., 2018) ambers. Most of these amber deposits occur in the Northern Hemisphere, between 5° and 75° N paleolatitude, and are especially abundant in low to mid latitudes from the Barremian to Coniacian and in mid to high latitudes from the Santonian to the Campanian (Fig. 1A). Some Cretaceous amber-bearing deposits are found in the Southern Hemisphere between the Aptian–Turonian, but they are scarce (Fig. 1A). Cenozoic amber deposits first appear during the Mid Paleocene of Wyoming, USA (~61 Ma) and Late Paleocene of Alaska, USA (~57 Ma) (Grimaldi et al., 2000a, 2018), and the Eocene of Oise, France (~53 Ma), Fushun, China (53–50 Ma) and Cambay, India (~52–50 Ma) (Jossang et al., 2008; Rust et al., 2010; Wang et al., 2014a).

There are five primary shared characteristics among amber deposits formed during the CREI. First, resin production was restricted to conifers
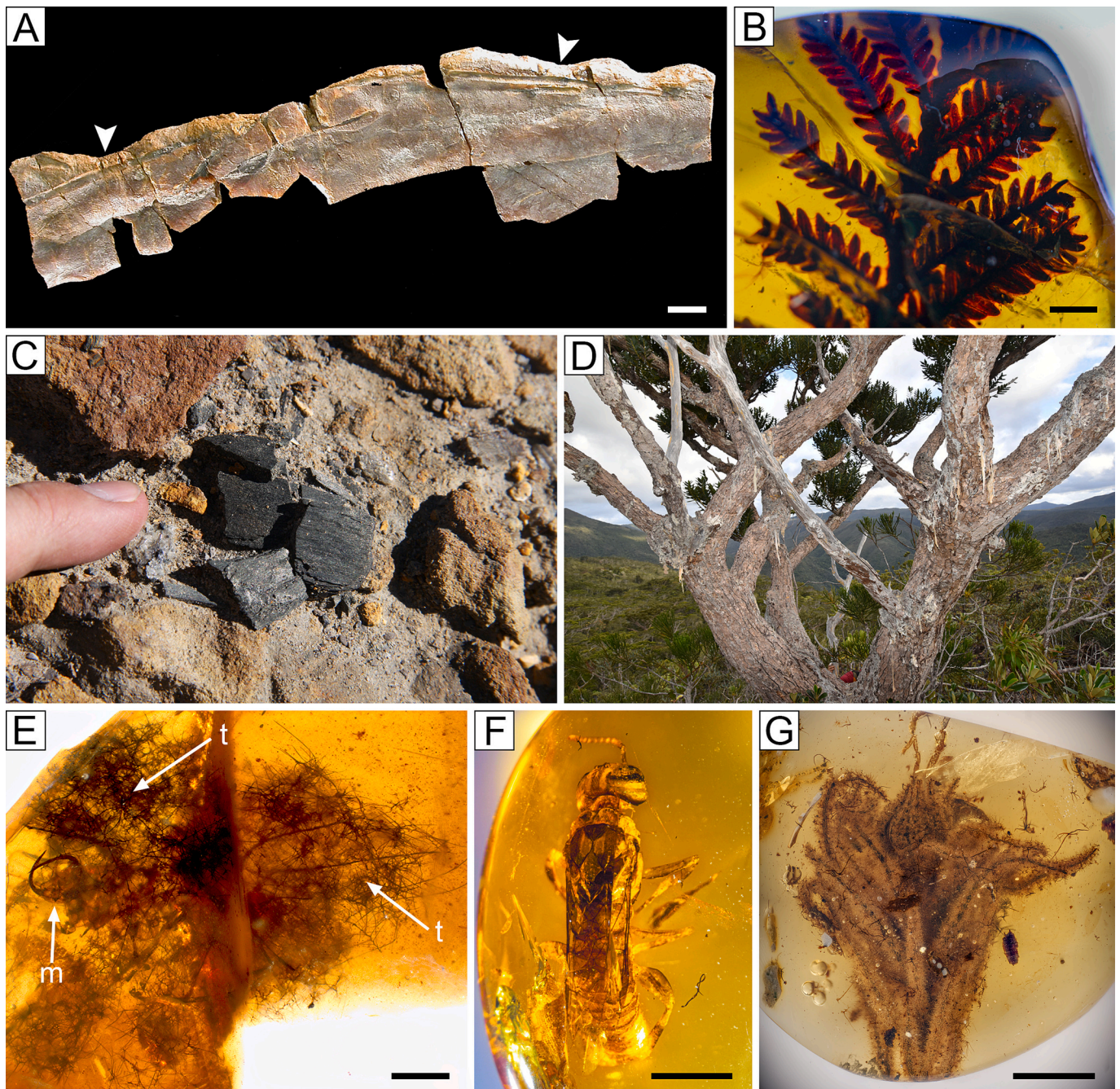
Fig. 3. Mass resin tree producers and development of fires during the Cretaceous. A) Aerial amber piece with surface imprints and bioinclusions of *Frenelopsis* (Cheirolepidiaceae†) axes, from the Albian of El Soplao (Spain); based on taphonomic studies, the largest number of plant bioinclusions corresponds to this resin-producing tree (Peñalver et al., 2018); B) One of the most abundant plant remains in the Cenomanian amber of Kachin (Myanmar) are axes with leaves of araucariaceans (Poinar et al., 2007) (University of Barcelona); C) Charcoal from the Albian amber-bearing outcrop of San Just, level SJ2 (Spain), commonly found in amber-bearing levels (Peñalver and Delclòs, 2010); D) *Agathis ovata* from Col de Yaté, New Caledonia, producing copious quantities of resin in an area burned several years ago; E) The immature insect related to green lacewings, *Hallucinochrysa diogenesi* (Neuroptera: Chrysopoidea), from the Albian amber of El Soplao (Spain), preserved with a debris-carrying packet of trichomes with gleicheniaceous affinity; today, gleicheniacean ferns opportunistically colonize burned areas (Pérez-de la Fuente et al., 2012); F) *Orthosyntexys elegans*, a wasp from the relict family Anaxyelidae (Hymenoptera: Symphyta) from the Cenomanian amber of Kachin, Myanmar; the living representatives of this family lay eggs in the sapwood of conifers, preferring recently burned wood (Gao et al., 2021), photograph courtesy of T. Gao; G) *Eophylica priscastellata*, an angiosperm flower of the family Rhamnaceae from the Cenomanian amber of Kachin (Myanmar) showing morphological specializations identical to those of modern relatives adapted to recurrent wildfires (Shi et al., 2022); photograph courtesy of C. Shi and R. Spicer. Abbreviations: m = mandibulo-maxillary stylets (feeding structures), t = trichomes. Scale bars = 2 mm (B, F), 1 mm (E, G), 0.5 mm (A). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Araucariaceae, Cheirolepidiaceae†, Cupressaceae s.l., Podocarpaceae, and Pinaceae) (Langenheim, 2003; Menor-Salván et al., 2010; Seyfullah et al., 2018). Second, charcoal, resulting from plant material charred by wildfires, is commonly found in the same stratigraphic level as amber,

particularly in the Northern Hemisphere (Brown et al., 2012; Tappert et al., 2013; Supplementary data C) (Fig. 3C). Third, when bioinclusions are preserved, they correspond to similar fauna and flora under comparable biases (Penney, 2010; Solórzano Kraemer et al., 2018), although
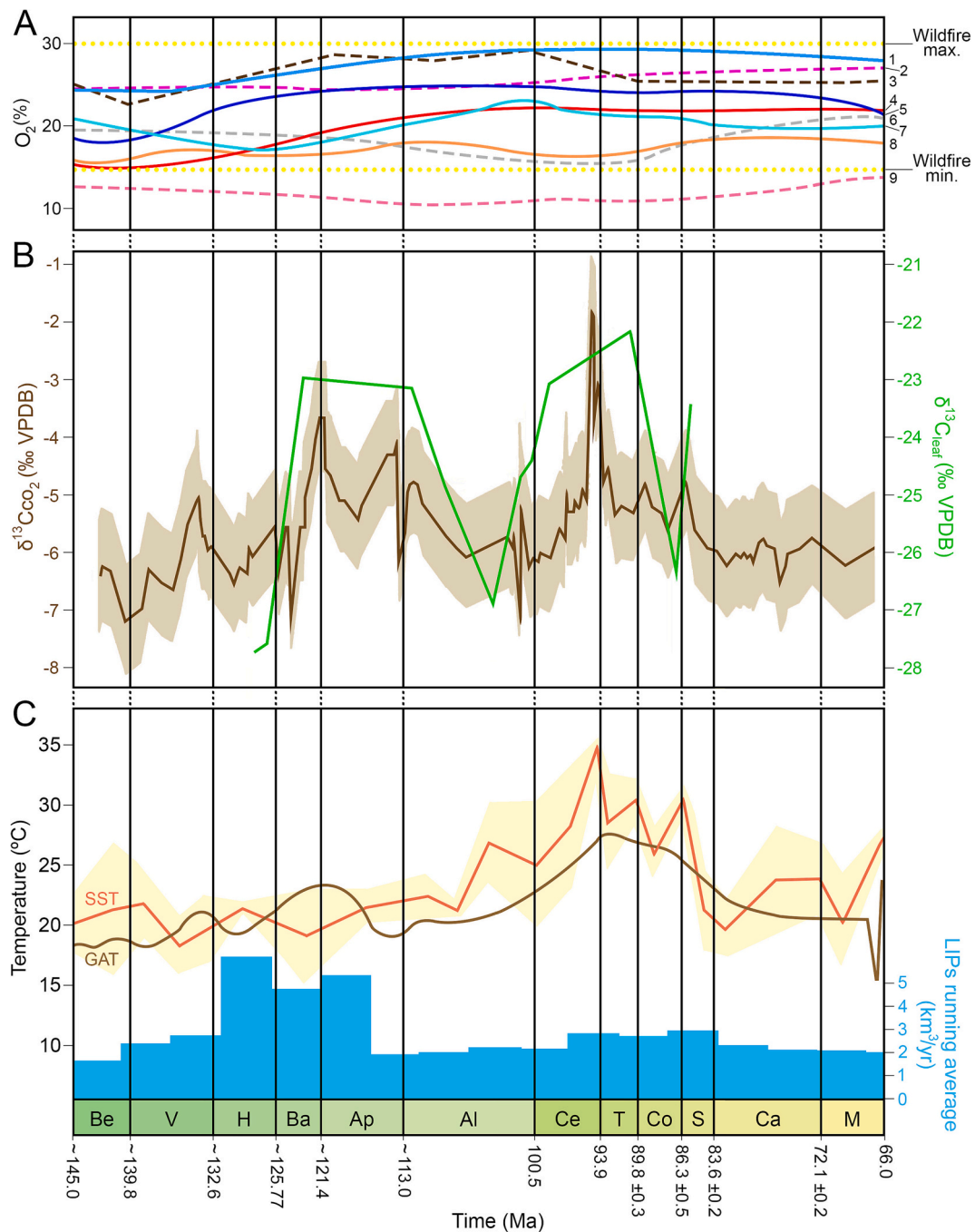

Fig. 4. Oxygen (O_2) and carbon dioxide (CO_2) atmospheric composition, temperature, and Large Igneous Province (LIP) activity throughout the Cretaceous. A) Reconstruction for Cretaceous O_2 mixing ratio (from Mills et al., 2016). Forward models of O_2 based on nutrient/weathering (1, 5, 7), including isotope mass balance models (4, 8) and "proxy inversion" methods that estimate atmospheric oxygen by reference to geochemical data, assuming relationships between O_2 concentration and either fossil charcoal abundance (3), carbon-to-phosphorus ratios in sediments (6), carbon isotope composition of plant resins (9), or combined estimates for sedimentation rate and abundance of organic carbon and pyrite in rock samples (2). Also represented: wildfire minimum (for ignition) and maximum (in the Phanerozoic, Carboniferous–Permian). References used: 1- Bergman et al. (2004), 2- Berner and Canfield (1989), 3- Glasspool and Scott (2010), 4- Berner (2009), 5- Arvidson et al. (2013), 6- Algeo and Ingall (2007), 7- Hansen and Wallman (2003), 8- Falkowski et al. (2005), 9- Tappert et al. (2013); B) Comparison of the carbon isotope composition of leaves of the Cheirolepidiaceae† conifer *Frenelopsis* ($\delta^{13}C_{leaf}$, in green) with the evolution of the carbon isotope composition of atmospheric CO_2 ($\delta^{13}C_{CO_2}$, in brown), from Barral et al. (2017). The *Frenelopsis* samples from the upper Barremian–lower Santonian interval come from amber outcrops; C) Reconstructed Cretaceous Sea Surface Temperature (SST) (from Martin et al., 2014 in Barral et al., 2017), Global Average Temperature (GAT) (from Scotese et al., 2021) and LIP running average every 5 Ma (from Eldholm and Coffin, 2000). Geological Timetable based in the International Commission on Stratigraphy (v 2023/06), https://stratigraphy.org/chart. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

often bioinclusions are absent likely due to taphonomic reasons. Fourth, resin accumulation occurred in transitional sedimentary environments under subtropical and temperate paleoclimates. And fifth, resin accumulation coincides with the maximum regressive surface (or transgressive surface) (Bowen and Jux, 1987; Villagómez et al., 1996; Najarro et al., 2009) (Fig. 1B). Spatially, the CREI appears to be global in nature, since amber-bearing outcrops are distributed worldwide throughout the Cretaceous, although they are particularly concentrated in Laurasia and the northern margin of Gondwana (Figs. 1, 2). In any case, we use the term 'global' in its broader sense as we posit that the CREI did not necessarily take place in both hemispheres simultaneously throughout the entire interval.

3. Conditional factors on resin production and preservation

Two basic conditions need to co-occur in time and space to generate an accumulation of resin with the potential to become an amber-bearing deposit. First, there needs to exist resin-producing plants with the capacity to secrete large amounts of resin. Second, there needs to be a suitable sedimentary setting, namely a transitional environment that buries resin under anoxic conditions. Known Cretaceous amber-bearing deposits are restricted geographically despite the worldwide distribution of resin-producing conifers during various Cretaceous stages (Fig. 2). Consequently, potential lack of suitable depositional environments for the accumulation and preservation of resin may have limited the distribution of amber-bearing deposits. However, transitional sedimentary environments during major marine transgressions were equally probable anywhere on Earth's surface, and have occurred cyclically throughout time (Haq, 2014). Thus, the two conditions noted above may not fully explain the observed distribution of Cretaceous amber-bearing deposits, such that other abiotic or biotic factors, and the confluence of several factors, likely promoted the production of resin by trees and/or its subsequent accumulation and preservation. These factors could be global or more localized in spatial scale and are not necessarily mutually exclusive.

3.1. Abiotic factors

Multiple abiotic factors were potentially related to the mass production and/or accumulation of resin during the CREI. Although these factors are interrelated and feedback on each other, we group them here to facilitate discussion: (1) atmospheric gas composition, temperature, and wildfires; (2) volcanism and changes in sea level; and (3) oceanic physicochemical properties and hurricanes. An overview of the global climate throughout the CREI is provided at the end of this section.

3.1.1. Atmospheric gas composition, temperature, and wildfires

Atmospheric gas composition (Fig. 4A–B) has a major effect on climate. Atmospheric greenhouse gases such as carbon dioxide (CO_2) and methane (CH_4), as well as oxygen (O_2) may have directly or indirectly impacted global resin production. Estimates of atmospheric CO_2 concentration during the Cretaceous vary according to the authors and proxies used (Tappert et al., 2013; Landwehrs et al., 2021) but generally is considered to have been more than twice that of preindustrial values, between 560 and 1680 ppm (Barral et al., 2017).

High CO_2 levels are due to extensive volcanic emissions during the Cretaceous from Large Igneous Provinces (LIPs, Fig. 4C) and seafloor formation (Condie et al., 2021). Wildfires, changes in ocean chemistry, biotic respiration, and organic matter decomposition also released significant amounts of CO_2 to the atmosphere during the Cretaceous (Hu et al., 2012; Wang et al., 2014b; Scott, 2018). Methane has a greater greenhouse potential than CO_2, and is likely to have notably increased during the Cretaceous (Jahren et al., 2001; Chang et al., 2022). Higher CH_4 levels were related to the liberation of methane hydrate from the seafloor by rising water temperatures (Wagner et al., 2007) and from seafloor spreading. Global temperatures fluctuated during the

Cretaceous (Holz, 2015; Landwehrs et al., 2021) (Fig. 4C), with generally elevated temperatures and reduced latitudinal temperature gradients between the equator and the poles of ≤35 °C mean annual temperature (MAT) in both hemispheres (O'Brien et al., 2017; Huber et al., 2018) compared with current values. The Northern Hemisphere thermal gradient showed a ca. 5 °C decrease from the Late Jurassic into the Late Cretaceous due to increased CO_2 and associated warming, while in the Southern Hemisphere the temperature gradient increased during this time due to the migration of Antarctica towards the South Pole (Landwehrs et al., 2021). Higher temperatures also brought more extreme atmospheric precipitation regimes and the establishment of more extensive regions under arid or monsoonal climates (Hasegawa et al., 2012), although the latter would have been influenced more by palaeogeography than by atmospheric gas concentration (Farnsworth et al., 2019).

Continental precipitation during the mid-Cretaceous was roughly mirrored between the Northern and Southern Hemispheres according to coupled ocean-atmosphere general circulation simulations, with maximum precipitation at the equator that decreased steeply to a minimum around 30° paleolatitude, which then increased again to a peak at around 50° paleolatitude (Zhou et al., 2012). This pattern situates the bulk of Cretaceous amber deposits with bioinclusions (particularly during the mid-Cretaceous) (Fig. 1A) in areas of moderate to relatively low average rainfall. Remarkably, the occurrence of the first significant Triassic amber deposits with inclusions in northern Italy coincides with the Carnian Pluvial Episode, associated with an important evolutionary radiation of "gymnosperms" (Roghi et al., 2022).

The increase in atmospheric CO_2 below the RuBisCo (the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase, involved in the first major step of carbon fixation) saturation limit accelerates plant photosynthesis and growth under present conditions (Dalling et al., 2016; Olivoto et al., 2017). In principle, such acceleration would suggest that increasing atmospheric CO_2 could result in higher metabolic rates and thus increased production of secondary metabolites, such as resin (Trapp and Croteau, 2001; Novick et al., 2012). However, related plant species may show opposite responses to CO_2 changes due to differences in physiological plasticity (Berini et al., 2018; Kurepin et al., 2018), thereby limiting the ability to infer resin production by fossil plant species based on CO_2 concentration alone. Even so, CO_2 and O_2 values might be indirectly linked with resin production, as elevated levels would be expected to impact the physiological features of plants that, in turn, could increase the herbivorous, wood-boring or pathogenic activity of other organisms such as arthropods or fungi (Lake and Wade, 2009; Labandeira, 2013; Couture et al., 2015; see section 3.2 below).

Numerous proxies suggest that atmospheric O_2 increased continuously from the Barremian to the late Cenomanian (Fig. 4A) to about 29%–31% (Berner, 2006; Glasspool and Scott, 2010; Brown et al., 2012), but decreased from the Turonian to the end of the Paleocene to the current value of 21% (Wade et al., 2019). The high O_2 content in the atmosphere during the Cretaceous favored recurrent wildfires in coniferous forests (Belcher and McElwain, 2008), which were also promoted by increased electrical storms and intensive volcanism (Scott, 2018). Charcoal is indicative of paleowildfires (Brown et al., 2012; Scott, 2018) and is abundant in most Cretaceous amber-bearing deposits (Peñalver and Delclòs, 2010; Shi et al., 2012; De Lima et al., 2019) (Fig. 3C), but mainly in the Northern Hemisphere deposits (Supplementary data C), including the presence of charcoalified remains within amber (Grimaldi et al., 2000b; Najarro et al., 2010). Partially burned amber pieces have been found occasionally together with charcoalified plant material (Grimaldi et al., 2000b).

Extant trees increase resin exudation if injured by fire (Fig. 3D) as a physiological response that prevents pathogenic activity or arthropod invasion (Langenheim, 2003; Della Prasetya et al., 2017). Fire has played a key role in reshaping ecosystems, particularly after the accumulation of flammable biomass arising from increased productivity of terrestrial ecosystems linked to the predominance of angiosperms (Bond

and Scott, 2010) and from the altered ignitability and flammability of angiospermous plant matter (Belcher and Hudspith, 2017). Different groups of Cretaceous conifers exhibit pyrophilous modifications linked to recurrent wildfires (He et al., 2016), in lifestyles such as serotiny that has endured into the present (Pausas, 2018). Moreover, there are diverse instances of organisms associated with fire that are preserved in Cretaceous ambers (Ortega-Blanco et al., 2008; Pérez-de la Fuente et al., 2012; Shi et al., 2022) (Fig. 3E−G).

The above lines of evidence suggest wildfires played a role in the genesis of resin deposits during the CREI, at least in some deposits, by favoring resin exudation but also subsequent accumulation, since deforested soils experienced increased erosion. However, based on the global occurrence of wildfires (Brown et al., 2012; Scott, 2018; Supplementary data C) and the broad distribution of potential resiniferous plants during the CREI (Fig. 2; Supplementary data B), a global distribution of Cretaceous amber deposits would be expected, for which there is currently no evidence (Fig. 2). Wildfires were globally distributed but seems only involved in local and regional resin production and accumulation during the CREI (e.g., the Raritan Fm. amber in New Jersey, USA or Spanish and French ambers), but appear not to be a definitive cause of resin production on a global scale.

3.1.2. Volcanism and changes in sea level

The abundant record of volcanic rocks associated directly or laterally with Cretaceous amber-bearing deposits such as those in Lebanon (Veltz et al., 2013), Myanmar (Shi et al., 2012), Ecuador (Balseca et al., 1993), and Canada (Eberth, 2005) is evidence that resin mass production took place in environments amid local volcanic influence, with this factor intimately related to wildfires (see above). Aside from increasing atmospheric O_2 concentrations that promoted wildfires, large amounts of volcanic emissions over a long period of time in LIPs could have affected global climate in other ways (Johansson et al., 2018; Macdonald et al., 2018). The maximum development of LIPs during the last 2500 million years occurred during the Cretaceous (Eldholm and Coffin, 2000; Condie et al., 2021). This peak of LIP development (Fig. 4C) altered atmospheric composition and circulation patterns and changed the geometry of sedimentary basins and sea level. The formation of LIPs and seafloor spreading, in combination with increased global MATs, led to the melting of polar ice caps (Zhou et al., 2008; Hay, 2017) and to significant reductions in the Earth's albedo (Kent and Muttoni, 2022) during the Cretaceous. These changes produced a global marine transgression trend (Fig. 1C) from the Valanginian to the Turonian (Wagreich et al., 2020). This global transgression was only interrupted by a regression at the Aptian−Albian boundary, after global MATs (Haq, 2014) fell to 12 °C (Hay, 2017). Maximum transgression was reached in the Turonian and sea level remained at high stands into the Campanian (Olde et al., 2015). All resin-bearing deposits were developed in periods of maximum regression, onlapped by the second-order marine transgressive strata (Grimaldi et al., 2000b; Perrichot, 2005; Najarro et al., 2009) (Fig. 1C).

The globally-high sea level during the CREI increased insularization, changing the extent and distribution of land masses and epicontinental seas such as the Late Cretaceous European archipelago, and the Mid-continental Seaway of North America. Extensive regions were flooded, which produced the remobilization of abundant resin stored in the soils due to erosion resulting from the transgressions, establishing new areas of shallow deposition, reducing terrestrial biotopes, and increasing flooding stress (Erwin, 2009). Marine transgressions have been associated with higher global temperature and paleogeographic changes, both of which caused more emergent land masses at mid to high latitudes in the Northern Hemisphere (Landwehrs et al., 2021), which potentially allowed for more colonization by plants and distribution of coniferous forest (Klages et al., 2020). This pattern contrasts with what occurred in the Southern Hemisphere during the Cretaceous, wherein the proportion of emerged land masses at mid to high latitudes remained low, similar in extent to that of the present day (Figs. 1, 2).

3.1.3. Oceanic physicochemical properties and hurricanes

Amber-bearing deposits are frequently associated with transitional sea-to-land environments. Thus, the properties of ocean waters, namely salinity and sea surface temperature (SST), and paleocirculation patterns may have affected the formation of resin deposit. Salinity may have controlled the formation of resin deposits because resin has a lower density than seawater, rendering it buoyant and making its burial and preservation in environments with high salinity difficult. High salinity conditions did occur in regions where amber-bearing deposits are found in the Northern Hemisphere, such as Myanmar and New Jersey of the USA (Poulsen et al., 1998; Ladant et al., 2020; Topper et al., 2011), and Brazil and the Congo in the Southern Hemisphere (Pérez-Diaz and Eagles, 2017). However, the formation of resin deposits in high salinity zones suggest only temporary marine influence. The record of frequent, yet rarely diverse, marine protists and invertebrates, such as oysters or crinoids, and plant macroremains in amber deposits (Néraudeau et al., 2008; Barrón et al., 2015; Peyrot et al., 2019) supports a transitional depositional setting with occasional marine influence.

Global average SST during the mid-Cretaceous was >6 °C higher than that of today (Hay, 2009; Torsvik and Cocks, 2016), but disparate data exist regarding SSTs throughout the entire Cretaceous (Hay and Floegel, 2012) (Fig. 4C). Global ocean circulation changed significantly during the Cretaceous due to progressive opening of the South Atlantic Ocean and the Tethyan Circumglobal Current, providing east to west flow around the globe at low latitudes of the Northern Hemisphere. In addition, the transfer of heat from the hydrosphere to the atmosphere from water vapor played an important role in cooling the tropics and in warming at high latitudes, establishing the diminished latitudinal gradient of temperature noted earlier. These factors conditioned global temperature and climate during the CREI (Hay, 2009; Wohlwend et al., 2015), and thus may have indirectly impacted resin formation and/or accumulation.

Linked to high average SST during the Cretaceous (O'Brien et al., 2017), heavy rainfall and winds, such as those during hurricanes, have been proposed as an abiotic cause of resin production. High winds can cause severe damage to trees, which is sealed by resin to minimize opportunistic insect attacks or pathogenic infections (Langenheim, 1994; Seyfullah et al., 2018). Climate models based on marine and continental distribution and topography suggest winds were generally weaker during the Cretaceous than at present (Cousin-Rittemard et al., 2002; Hay, 2009), but the consistently high annual SST could have promoted the development of hurricanes in low to mid latitudes. The absence of high topographic relief (Hay et al., 2019) would have allowed the wind to circulate without diverting its zonal flow (Scotese et al., 2021).

3.1.4. Climatic overview throughout the CREI

Based on paleoclimate data and maps (Chumakov et al., 1995), most Cretaceous amber-bearing deposits originated in the northern mid-latitude warm humid belt. Nevertheless, during the Albian and Santonian, some amber-bearing localities were present well within the northern high-latitude temperate humid belt, and during the Albian and Cenomanian other amber-bearing localities were present within the equatorial humid belt and northern hot arid belt, respectively. Based on global circulation models, the depositional environments that gave rise to amber-bearing deposits in Lebanon (Barremian) were located within the tropical climate belt (Sewall et al., 2007; Ohba and Ueda, 2010). During the lower to middle Aptian, the climate cooled globally (Mutterlose et al., 2010), which coincides with a reduction in currently known amber deposits, although this cold interval was recently questioned (Huber and O'Brien, 2020).

At the Aptian–Albian boundary, warm greenhouse conditions were re-established due to intense volcanism, coinciding with amber deposits in Brazil, Ecuador, and the Congo at low latitudes in the Southern Hemisphere (Pereira et al., 2009; Cadena et al., 2018; Bouju and Perrichot, 2020). During the Albian, an extensive subtropical arid belt

developed in the equatorial zone, which subsequently migrated poleward (Scotese, 2021). Abundant resin accumulations were common in tropical mid latitude areas, such as Iberia, leading to the present-day Spanish amber deposits (Peñalver and Delclòs, 2010).

During the Cenomanian–Turonian, climate zones began to organize latitudinally (Sewall et al., 2007), although still under hothouse conditions (Kidder and Worsley, 2010; Mills et al., 2017), enabling the tropical biota to migrate poleward of 40°N latitude. Although currently there are important forests of conifers in very high latitudes (Fig. 2), resin deposits were formed at that time mostly between 30° and 40°N latitude, with some exceptions at higher latitudes (Fig. 1), corresponding to a MAT of around 30 °C (Hay and Floegel, 2012); these conditions may have produced the resin corresponding to amber-bearing deposits from the lower Cenomanian of France (Perrichot et al., 2010), Myanmar (Ross et al., 2010), and from the Turonian of New Jersey in the USA (Grimaldi and Nascimbene, 2010).

During the upper Turonian–Maastrichtian, climate changed considerably (Tabor et al., 2016). Simulated global mean surface air temperatures (GMST) show temperatures of 21.2 °C–19.5 °C during the Campanian. These cooling trends are associated with changes in the fraction of Earth's surface occupied by land (Fig. 1B), which has a higher average albedo than that of the ocean, caused by lower sea levels that resulted in greater exposure of continental areas (Landwehrs et al., 2021). Although average global temperatures decreased during the Turonian–Maastrichtian, most resin deposits formed at high latitudes, namely of the Northern Hemisphere, and were rare at mid to low latitudes (Fig. 1B). From this interval are known the amber deposits of the Santonian from the Taymyr region in Russia (Perkovsky and Vasilenko, 2019), from the Campanian of Cedar Lake and Grassy Lake in Canada (McKellar et al., 2008), and from the Campanian–Maastrichtian of the Arctic Coastal Plain in Alaska (Langenheim et al., 1960).

3.2. Biotic factors

The mass production of resin during the CREI may have been promoted by biotic factors acting at a regional scale (Martínez-Delclòs et al., 2004; Seyfullah et al., 2018). These factors include arthropod damage, pathogenic activity, and the emission of volatile compounds by the resins to attract pollinators and other insects (Langenheim, 1994; Pichersky and Gershenzon, 2020; Peris et al., 2021).

Terrestrial arthropods (insects, mites) can cause severe damage to plants through feeding- or development-related activity. Different wood-boring insects, namely beetles (Coleoptera), but also some wasps such as wood wasps (Hymenoptera: Siricidae) and moths such as cossid millers or clearwing moths (Lepidoptera: Cossidae and Sesiidae), bore into wood for nest building and offspring development, at times cultivating fungi as a food source in galleries within woody tissues (Hulcr and Stelinski, 2017; Peris et al., 2021). The diseased tree reacts against invasive agents by developing secondary defensive compounds such as terpene-rich oleoresins in conifers, which flood the area to physically repel the invasion, while different toxins and volatiles act as a chemical defense (Raffa, 2014; Krokene, 2015). The influence of massive attacks of wood-boring beetles on resiniferous ancient forests has been widely cited in the literature based on their abundance in Cenozoic ambers, Pleistocene and Holocene copals, and Defaunation resins (Martínez-Delclòs et al., 2004; Labandeira, 2014a; Seyfullah et al., 2018; Peris, 2020). However, there is no significant direct evidence of beetle infestations in Cretaceous ambers yet found, although scarce wood boring beetles such as auger beetles (Bostrichidae), spider beetles (Ptinidae), ship timber beetles (Lymexylidae) and weevils (Curculionidae) are found occasionally (Chen and Zhang, 2020; Peris, 2020; Peris and Rust, 2020) (Fig. 5A–B). Herbivorous insect groups such as true bugs (Hemiptera), thrips (Thysanoptera) (Fig. 5D), grasshoppers and crickets (Orthoptera), and termites (Isoptera) have been found in major Cretaceous amber deposits, including taxa that currently cause significant damage to plants. However little evidence exists of intense arthropod

herbivory during the CREI in rock deposits (Labandeira, 1998, 2014b; Xiao et al., 2022a, 2022b), and there has been no assessment of the herbivory in amber due to the scarcity of damaged leaves and other photosynthetic structures (such as cheirolepidiacean axes) as bioinclusions.

Pathogenic organisms can invade plant tissues directly or through a vector. Aside from their ability to cause direct harm, some extant species from insect groups transmit pathogens to their plant hosts, including viruses, bacteria, fungi, oomycetes, and nematodes (Labandeira and Prevec, 2014).

The development of insect-borne pathogens depends on population dynamics, dispersal ability, host selection behavior, and the feeding behavior of the insect vectors (Labandeira and Prevec, 2014; Eigenbrode et al., 2018). Bacteria and fungi are chiefly spread by adhering to the insect's body, so their vector relationship is not as specific as that which occurs in the transmission of viral diseases (Jones, 2005). Oomycetes are remarkable plant pathogens, because infection by these fungus-like microorganisms can induce copious resin exudation, as observed in the genus *Agathis* in New Zealand (Fig. 5E–G), which produces a particular variation in the color of large resin exudates (Weir et al., 2015). Unfortunately, this type of resin would be difficult to recognize once transformed into amber; future studies may be able to distinguish this resin isotopically or by the presence of oomycete spores as bioinclusions.

Plants are known to emit volatile compounds to attract or repel insects (Raffa, 2014; Pichersky and Gershenzon, 2020). However, many insect species are attracted to volatile plant mixtures that indicate stress, as this signaling can allow insects to enter tissues free of defense and, potentially, competition (Hulcr and Dunn, 2011). Angiosperm resin terpenoids attract insect pollinators (Armbruster, 1984; Boncan et al., 2020). Highly specialized pollination relationships between some groups of insects and "gymnosperms" have been discovered in amber since the Albian (Fig. 5C), in some instances lacking extant representatives of such pollination interactions (Peñalver et al., 2012, 2015; Peris et al., 2017, 2020; Peña-Kairath et al., 2023). Resin exudation by conifers during the CREI could be related to the attraction of certain groups of insects to assist in pollination. This idea was proposed for Cenozoic ambers produced by angiosperms (Armbruster, 1993). The hypothesis is challenging to test at present, and the absence of Cretaceous insects with attached coniferous pollen (Peris et al., 2020) renders it unlikely. Nevertheless, cheirolepidiaceous pollen has been found on the mouthparts of insects in compression–impression deposits from non-amber producing environments of the Middle Jurassic to the Early Cretaceous (Labandeira et al., 2016), indicating insect pollination of at least one reproductively specialized cheirolepidiaceous conifer was an exception (Labandeira et al., 2007).

4. Present limitations and future directions

We propose that the CREI represented a distinct mass resin production that occurred over a continuous time interval from the Barremian to the Campanian, despite differences in the known record of amber-bearing deposits between Cretaceous geochronologic stages (Fig. 1A). The causal mechanisms underlying such fluctuations are not well understood, although they may relate to circumstances that are best studied on a case-by-case basis by integrating multiple approaches.

Although we hypothesize that the same set of general processes that promoted resin mass production and accumulation acted for the entirety of the CREI, we posit that these were under the influence of possible local or regional controls that determined the intensity of the effect. The relative importance of the abiotic and biotic factors influencing resin production and accumulation during the CREI at regional geographical scales, among other variables, will need to be rigorously tested in future studies.

We established the CREI with a stage/age hierarchy (apud IUGS Chronochart - Gradstein et al., 2021). Finer temporal resolution would
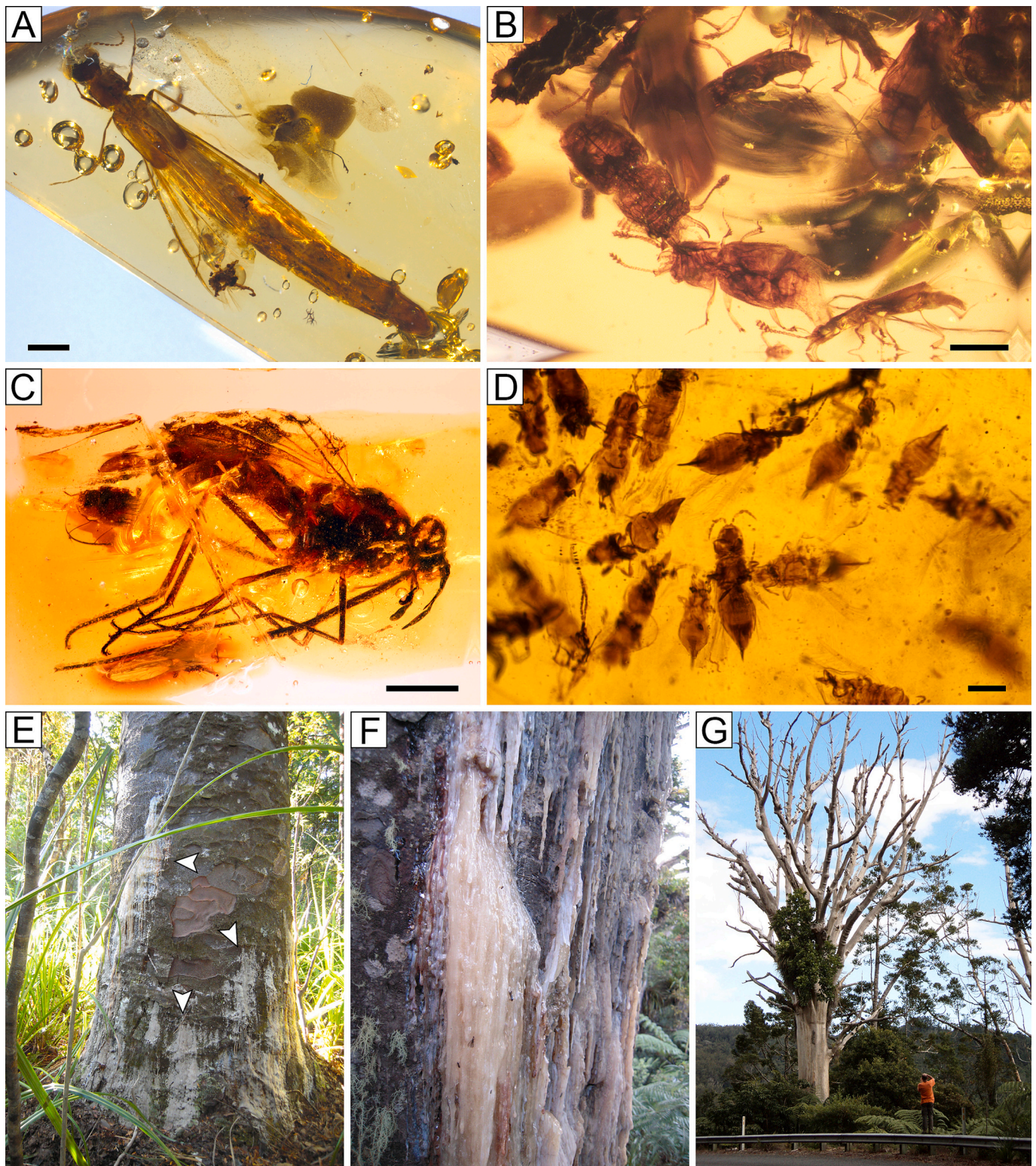
Fig. 5. Biotic factors that could have promoted resin mass production during the Cretaceous: wood-boring insects, pollination, and pathogens. A) A lymexylid beetle; larvae of this group of beetles today penetrate living and decaying wood, consuming fungus in a symbiotic association; unpublished specimen from the Nanjing Institute of Geology and Palaeontology, China Academy of Sciences; B) Bostrichid beetles *Cretaretes minimus*, from Kachin amber (Peris and Jelínek, 2020); these beetles could have been among the first wood-boring beetles and transmitters of pathogens; C) The zhangsolvid fly *Buccinatormyia magnifica*, from El Soplao amber (Peñalver et al., 2015); the oldest instances of "gymnosperm" pollinators in amber are found in the Albian of Spain; D) Thrips (Thysanoptera) swarm from Kachin amber with attached pollen grains (unstudied, UB); thrips were "gymnosperm" pollinators, but this group could have also been the cause of massive attacks on resinous trees; E–G) *Agathis australis* (Araucariaceae) attacked by the oomycete *Phytophthora agathidicida* (Oomycota) in Waipoua Forest, New Zealand, causing copious resin production (E, F) and the eventual death of the tree (G). Scale bars = 1 mm (A), 0.5 mm (B), 2 mm (C), 0.2 mm (D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reduce considerable noise to the analyses at present, as many amber deposits and conventional paleobotanical deposits are characterized by significant temporal uncertainty.

Further work to improve temporal resolution will involve more accurate dating of the deposits, more detailed identification of changes in atmospheric gas composition, more precise evaluations of meso- and macroplant remains from amber deposits, and other studies within each Cretaceous stage. These studies may provide further insight into the causal mechanisms for enhanced resin production and accumulation during the CREI. A higher-resolution temporal framework might also allow identification of distinct subintervals or even events within the Cretaceous Resinous Interval.

Although sampling bias may be an explanation for the apparently skewed presence of amber deposits towards the Northern Hemisphere during CREI (Figs. 1, 2), paleogeographical circumstances may contribute to explain the pattern. First, a greater proportion of land had emerged in the Northern Hemisphere (Landwehrs et al., 2021) during the Cretaceous, and was thus sustaining potentially greater extensions of resin-producing forests. Second, different resiniferous species distributed among both hemispheres could have had different capacities to produce resin even under comparable environmental conditions and, thus, a different potential to produce amber deposits; this has been observed at present even between closely related species (Langenheim, 1995; Seyfullah et al., 2018). It will be necessary to substantially increase reconnaissance efforts in the Southern Hemisphere to shed light on this matter.

Taphonomic knowledge on the known Cretaceous amber deposits is scarce, fundamentally limiting understanding of the CREI. It is imperative to improve efforts studying amber deposits (both the amber itself and the associated stratal context) from a detailed taphonomic standpoint. Such studies would aim to elucidate the paleoenvironmental, paleoecological, and geological circumstances surrounding the production and accumulation of resin and the formation of amber. A particular emphasis should be on improving paleobotanical analyses of meso- and macro-remains, including fossilized wood. A focus on actuotaphonomic experiments, both in the field and the laboratory, will further complement our view on the subject.

5. Conclusions

The Cretaceous distribution of amber-bearing deposits is clustered around an interval of roughly 54 Ma, from the Barremian to the Campanian, and reflects global, massive resin production during the late Mesozoic. Prior to this interval, amber is remarkably scarce, appears in small quantities and, save from some Triassic amber, has not hitherto yielded macroscopic bioinclusions. We place the end of the interval in the Campanian, provided that during the Maastrichtian amber is latitudinally well distributed but appears in small quantities and is scarcely fossiliferous. Shortly before the K-Pg boundary lignite deposits exist but with the absence of amber that extends into the Paleocene, establishing a gap of several million years without amber and obviously bioinclusions.

In the Cenozoic the resin producers were no longer exclusively conifers, but rather the first deposits of angiosperm resins appeared. Shared characteristics of Cretaceous amber deposits are herein used to formally establish the Cretaceous Resinous Interval, or CREI, and are distinct from those shown by Cenozoic amber deposits. The resin that generated the amber during the CREI was produced by conifers and accumulated in transitional sedimentary environments from subtropical and temperate regions, commonly associated with charcoal and coinciding with the maximum regressive surface. Moreover, the fauna and flora preserved within the CREI share comparable group compositional characteristics, possibly due to similar original paleoenvironment, and suffered comparable taphonomic biases (Martínez-Delclòs et al., 2004; Solórzano Kraemer et al., 2018; Seyfullah et al., 2018).

The potential causal factors for the CREI are complex and interrelated. Abiotic conditions potentially related to massive resin production and accumulation during the CREI include: (1) increased global average temperatures, including SST, with the consequent reduction in albedo due to the absence of icy poles, (2) reduced latitudinal temperature gradients, which allowed the development of forests at high latitudes, (3) higher levels of greenhouse atmospheric gases (carbon dioxide, methane) and oxygen, which promoted changes in the growth and development of the biota, (4) increased volcanic activity, which promoted an increase in temperature and changes in the composition of atmospheric gases, (5) moderate or relatively high average rainfall that could favor the development of large forests and the production of resin, (6) enhanced wildfire activity due to volcanism and high O_2 levels, (7) transgressive sea level periods and overall trend, which reduced terrestrial land area but led to the filling of large areas of lowlands and formation of resin deposits, and (8) increased storm and hurricane activity that could have promoted wildfires and/or destruction of large areas of forest, and consequently resin production. Biotic factors partially explaining the CREI at a more localized scale could include arthropod damage, pathogenic activity due to high temperatures and humidity, and the emission of insect-attracting compounds by resins. Future studies on the CREI will need to focus on elucidating the relative importance of each of these abiotic and biotic factors, enhancing the spatial and temporal resolution of the succession of paleoevents, increasing prospective efforts −particularly in the Southern Hemisphere−, and improving taphonomic understanding of Cretaceous amber deposits.

Our multidisciplinary approach will hopefully stimulate future research efforts aimed at elucidating past dynamics between the geosphere and the biosphere. Increased knowledge of when, how and why the CREI occurred will shed light on its global impact for Cretaceous terrestrial ecology and the establishment of modern terrestrial ecosystems. The exceptionally preserved record trapped in resin during the Cretaceous Resinous Interval is crucial to unravel the evolutionary history of many key terrestrial lineages, including plants, arthropods, and vertebrates, and for understanding life in a moment of critical change for terrestrial ecosystems at the transition from the Mesozoic to the Cenozoic.

Author contributions

Study conception and design, contributed equally: X.D. and E.P.
Data collection: X.D., E.P., D.P., D.G., M.H., C.L., Ch.S., M.M.S-K and

R.P.-d.l.F.

Conducted the fieldwork and the preparation, identification, and analysis of the field samples: X.D., E.P., E.B., D.P., D.G., C.L., M.M.S-K., S.Á.-P., D.A., E.C., R.L-D., A.N. and V.P.

Analysis and interpretation of results: X.D., E.P., D.P., D.G., M.H., C. L., Ch.S., M.M.S-K, S.Á.-P. and R.P.-d.l.F.

Database creation: X.D., S.Á.-P. and A.M.-G.

Manuscript preparation. Wrote the manuscript: X.D., E.P., D.P. and R.P.-d.l.F. All authors contributed to the discussion, reviewed the results, and approved the final version of the manuscript.

Imaging and figure preparation: X.D., D.P., S.Á.-P., C.P.-K.

Funding acquisition and project administration: X.D., E.B., M.M.S.-K

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.

Data availability

All data is available as supplementary files. Part of the dataset of plants plotted in the paleomaps in Fig. 2 was downloaded from Paleobiology Database (https://paleobiodb.org) on 17 September 2022.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2023.104486.

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