Plant-insect interactions in the mid-Cretaceous paleotropical El Chango Lagerstätte (Cintalapa Fm., Mexico)—patterns of herbivory during the Angiosperm Terrestrial Revolution

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Plants and insects are two of the more diverse and abundant organisms in terrestrial ecosystems. The fossil record of plant-insect interactions offers crucial insights into the coevolutionary dynamics between these groups, shedding light on the intricate relationships that have shaped terrestrial ecosystems. The study of fossil interactions is especially relevant in mid-Cretaceous ecosystems, a time of dramatic changes in the composition of floras and, consequently, in plant-insect relationships. Here, we describe the first suite of plant-insect interactions from the mid-Cretaceous of Mexico. We studied 554 plant fossils from the El Chango Lagerstätte (Cintalapa Formation, Chiapas, Mexico), including vegetative (leaves) and reproductive structures (fruits and seeds). The flora was dominated by gymnosperms (89.3%) followed by angiosperms (10.7%); other groups, such as pteridophytes and bryophytes, were absent. In total, 5.4% of the plant specimens hosted some damage. Angiosperms (all broad-leafed forms), despite being much less common than gymnosperms, expressed more evidence of damage by herbivores (35.6% of specimens damaged). In contrast, the narrow-leafed gymnosperms, the dominant group in the flora, hosted a much lower proportion of herbivory damage (1.8% of specimens damaged). The diversity of damage types (DTs) was relatively low: 14 DTs were identified, corresponding to seven FFGs, including margin feeding, hole feeding, surface feeding, piercing and sucking, oviposition, galling, and mining. Comparison with the other mid-Cretaceous plant-insect assemblages reveals a similar richness of DTs for angiosperms but a lower richness and diversity of DTs on gymnosperms from El Chango. These results indicate preferential herbivory on angiosperms (rather than on the available gymnosperms in the assemblage) by terrestrial arthropods during a period of major changes in the structure of terrestrial ecosystems.

However, it is challenging to resolve whether this apparent preference is because insects particularly targeted angiosperms or if the herbivores simply targeted broad leaves in general, since most of the available gymnosperms from El Chango are scale-leafed forms.

1 Introduction

Plants and arthropods represent the two dominant groups with respect to biodiversity and biomass in terrestrial ecosystems (Bar-On et al., 2018). Their importance extends back to the earliest terrestrial biotas, where fossil interactions provide evidence of the structure of the first land-based ecosystems (Labandeira and Wappler, 2023). Fossil evidence of plant-insect interactions provides one of the few windows into the past relationships between these two groups, offering tangible records of coevolutionary processes and provides valuable data on the evolutionary history of both plants and insects. These data enhance our understanding of the structure and development of ancient ecosystems, biodiversity patterns, and the intricate web of biotic relationships that have shaped the natural world over geological time scales (e.g., Mcloughlin et al., 2015, Santos et al., 2021, Santos et al., 2022a, Santos et al., 2022b, Santos et al., 2022c, Santos et al., 2023; Labandeira and Wappler, 2023).

Plant-arthropod interactions have been recorded in the fossil record since the Silurian-Devonian (Scott et al., 1992; Hagström and Mehlqvist, 2012), during the early colonization of terrestrial environments by plants. Since then, the interactions between these two groups have become more complex and abundant in the fossil record and have experienced successive phases of development. During the mid-Cretaceous, the Cretaceous Terrestrial Revolution (KTR), and the closely related Angiosperm Terrestrial Revolution (ATR), occurred. This interval encompassed significant changes in the composition, structure and complexity of terrestrial ecosystems, especially marked by the diversification and expansion of angiosperms, which came to dominate plant communities worldwide (McLoughlin et al., 1995, 2010; Villanueva-Amadoz et al., 2010; Coiffard et al., 2012; Condamine et al., 2020; Santos et al., 2022a; Xiao et al., 2022a; 2023). These changes at the base of the food chain led to significant shifts in the representation, morphology, and behaviour of numerous groups of terrestrial parasites, saprotrophs, and consumers, among which insects were key (Peris and Condamine, 2024). Some previous works (see Table 1 for details) suggested that, in Europe, insect herbivores adapted rapidly to angiosperms, targeting them as their preferred food source in some areas (Santos et al., 2022a). However, little is known about how these floristic changes affected the dynamics of herbivory in other regions of the world.

Evidence of fossil plant-insect interactions from Mexico is scarce, thus far being confined to studies of just a few specimens. The oldest fossil evidence of interactions from that country is from the Permian Matzitzi Formation (Flores-Barragán et al., 2023). There has been a single study of Jurassic interactions from the Otlaltepec Formation from which 22 bennettitalean and fern remains were reported with some evidence of herbivory damage (Velasco de León et al., 2015). There are a few reports of fungal-insect interactions in Miocene amber samples from Chiapas (Arroyo-Sánchez et al., 2023). Thus far, no formal studies have been published on plant-insect interactions from the Cretaceous of Mexico. Our study provides the first evidence of plant-insect interactions from the mid-Cretaceous of Mexico and southern portion of North America. This offers the opportunity to explore how insects reacted to the profound changes in terrestrial ecosystems in the region that would become the precursor to the modern Neotropical biogeographic realm (Carvalho et al., 2021). The main objectives of this work are to: 1, document the first occurrences of plant-insect interactions from the El Chango Lagerstätte; 2, identify and discuss the diversity and intensity of interactions expressed by Damage Types (DTs) and Functional Feeding Groups (FFGs) in this paleoforest; and 3, statistically appraise the palaeoecology of this fossil site.

2 Geological context

The El Chango outcrop hosts a fossil Lagerstätte and is located 30 km southeast of the Guadalupe Victoria locality, Chiapas, southeastern Mexico (coordinates: N 16°34'14", W 93°16'11": Figures 1A, B). Strata exposed at this site belong to the Cintalapa Formation within the Sierra Madre Group. This group consists of a 700–1600-m-thick succession of marine laminated dolomites with sporadic flint levels (Moreno-Bedmar et al., 2014).

The sedimentary succession at El Chango (Figure 1C) was deposited in a brackish estuary or salty lagoon with episodic influx of freshwater (Vega et al., 2006; Moreno-Bedmar et al., 2014). The remains of several marine/coastal organisms have been found in the Cintalapa Formation. The fossil assemblages are recognized globally for their exceptional marine fish diversity and preservation, as documented by, e.g., Alvarado-Ortega et al.

TABLE 1 Selection of Cretaceous plant-insect interactions. Modified from Santos et al. (2022a).

Age	Geographic area	Formation/Basin	Damage/Interaction	References
Late Cretaceous (Maastrichtian)	Patagonia (Argentina)	Lefipán Fm.	Hole feeding, margin feeding, skeletonization, surface feeding, piercing and sucking, mining, and galling on angiosperms. More than 50 DTs	Donovan, et al. (2014, 2016, 2018, 2020)
Late Cretaceous (Campanian)	Southern Utah (USA)	Kaiparowits Fm.	Leaf mine of *Leucopteropsa spiralae* in an angiosperm leaf and Acarodomatia interactions on angiosperm leaves	Maccracken et al. (2019, 2021)
Late Cretaceous (Coniacian)	Vancouver Island (Canada)	Comox Fm.	Feeding galleries and damage (putative lepidoptera) on cones of *Acanthostrobus edenensis* (Cupressaceae)	Klymiuk et al. (2015)
Late Cretaceous (Turonian)	Negev (Israel)	Ora Fm.	Hole feeding, margin feeding, mining, galling, oviposition, Skeletonization. Mainly on angiosperms	Krassilov (2007, 2008a, 2008b); Krassilov et al. (2007, 2008); Krassilov and Rasnitsyn (2008); Krassilov and Shuklina (2008)
Late Cretaceous (?Campanian)	Nelson Island (Antarctic Peninsula)	Fildes Fm.	Hole feeding, margin feeding, skeletonization, and galls on angiosperms	Santos-Filho et al. (2023)
Late Cretaceous	Gobi (Mongolia)	?	Gallery system of a bark beetle in Araucariaceae wood	Petrov (2013)
Late Cretaceous	Patagonia (Argentina)	Unnamed Fm.	Six ichnospecies in wood remains (*Cycalichnus garciorum*; *Stipitichnus koppae*; *Xylonichnus, Carporichnus maximus*; *C. bertheorum*, and *C. minimus*)	Genise (1995)
Mid-Cretaceous (Cenomanian)	Tonnay-Charente (France)	Puy-Puy quarry (Aquitaine Basin)	Quantitative/semiquantitative study of plant-insect interactions on 1605 plant remains. 71 distinct DTs	Santos et al. (2022a)
Mid-Cretaceous (early Cenomanian)	Chiapas (Mexico)	El Chango Site (Cintalapa Fm.)	Quantitative/semiquantitative study of plant-insect interactions on 554 plant remains. 13 distinct DTs	This study
Mid-Cretaceous (Albian)	Teruel (Spain)	Escucha Fm.	23 DTs from eight FFGs (hole feeding, margin feeding, skeletonization, surface feeding, piercing and sucking, mining, oviposition and galling) in aquatic and terrestrial basal angiosperms	Santos et al. (2023)
Mid-Cretaceous (Albian)	Teruel (Spain)	Escucha Fm.	Margin feeding, hole feeding, and mining on 75 specimens of *Sagenopteris* sp. (Caytoniales)	Sender et al. (2022)
Mid-Cretaceous (Albian)	Teruel (Spain)	Utrillas Fm.	Margin and hole feeding on Nymphaeaceae leaves	Estevez-Gallardo et al. (2018)
Mid-Cretaceous (Albian)	Patagonia (Argentina)	Piedra Clavada Fm.	A new petalurid ichnospecies: *Maichnus wetkaroae*	Genise et al. (2020)
Mid-Cretaceous (Aptian-Albian)	Gansu (China)	Zhonggou Fm.	Hole feeding, margin feeding, skeletonization, and galling	Zhang et al. (2023)
Early Cretaceous (Aptian)	Nebraska (USA)	Dakota Fm.	Margin feeding, surface feeding, skeletonization, hole feeding, oviposition, piercing and sucking, leaf-mining, galling, seed predation, borings; and pathogens (114 DTs)	Xiao et al. (2022b)
Early Cretaceous (Aptian)	Liaoning (China)	Yixian Fm.	Margin feeding, surface feeding, hole feeding, oviposition, piercing and sucking, leaf-mining, galling, borings; and pathogens	Ding et al. (2015); Xiao et al. (2022a)
Early Cretaceous (Berriasian)	Araripe Basin (Brasil)	Missão Velha Fm.	Isoptera galleries in wood of conifers	Pires and Sommer (2009)

(Continued)

TABLE 1 Continued

Age	Geographic area	Formation/ Basin	Damage/Interaction	References
Early Cretaceous	Araripe Basin (northeast Brazil)	Crato Fm.	Margin feeding, galling, oviposition and piercing and sucking on ferns; margin feeding, skeletonization and galling on angiosperms	Santos-Filho et al. (2019)
Early Cretaceous	Rajmahal Hills (India)	Rajmahal Fm.	Margin feeding in *Ptilophyllum* sp., oviposition on *Phyllopteroides*; galling on *Nipaniophyllum*	Banerji (2004)
Early Cretaceous (Berriasian)	Bornholm (Denmark)	Rabekke Fm.	Insect boring (putative fungus-farming beetle) on wood	Mikuláš et al. (2020)

(2009), Alvarado-Ortega and Than-Marchese (2012, 2013), Díaz-Cruz et al. (2019, 2020), Than-Marchese et al. (2020) and Cantalice et al. (2021). Additionally, deposits from this formation contain significant fossils of decapods (e.g., Vega et al., 2006; 2022; Bruce et al., 2021), plants (González-Ramírez et al., 2013; Guerrero-Márquez et al., 2013; this study), and even insects, including remains of Odonata and Hemiptera (Vega et al., 2006).

According to Vega et al. (2006), the El Chango deposits are late Albian in age. However, Moreno-Bedmar et al. (2014) suggested an earliest Cenomanian age for the upper part of the stratigraphic section at El Chango based on the presence of diagnostic ammonoids (*Graysonites*: Acanthoceratidae). The lower part of the section has not been calibrated with ammonoids, and consequently, a late Albian age for this interval cannot be excluded. Mexico was located in low northern latitudes (<15°N) during the mid-Cretaceous (McLoughlin, 2001).

3 Material and methods

We noted 858 plant remains from the El Chango site. Only well-preserved terrestrial plant remains with dimensions of at least 2 × 2 cm were selected for this study. This left an inventory of 554 plant fossils (See details in the Supplementary Data), including vegetative remains (536 leaves, 97%; Figures 2–6) and reproductive structures (18 fruits and seeds, 3%; Figures 3, 5). The plant fossils are preserved as carbonaceous films or impressions that were analyzed for evidence of interactions. The relatively good preservation of the leaves suggests that transport distances were short, indicating a parautochthonous origin of the plant fossils and, consequently, of the interactions.

The fossils were prepared following standard techniques in the Department of Palaeontology in the IGL-UNAM, using a micropneumatic hammer and needles. Selected fossils were photographed using a Canon EOSM50, and detailed photos were taken with a micro-camera Axiocam 503 Color attached to a Zeiss Axio Zoom V.16 microscope. Some samples were photographed submerged in distilled H_2O to improve image contrast and quality. The fossils will be stored in the Laboratory of Palaeobotany of Dr. Sergio RS Cevallos-Ferriz in the IGL-UNAM, Ciudad de México.

We have followed the classification system proposed by Labandeira et al. (2007) to identify plant-arthropod interactions. In this system, the interactions observed on the leaves are classified into different morphotypes, named Damage Types (hereafter DTs), followed by an identifying number, where most of the DTs belong to specific Functional Feeding Groups (hereafter FFGs). Additionally, each DT is connected to a certain degree of specialization, based on the occurrence on different host plants (Labandeira et al., 2007).

The statistical analyses were undertaken using R i386 3.6.0 (R Development Core Team) and R Commander. We have used codes based on Gunkel and Wappler (2015) to calculate the richness and rarefaction of DTs and FFGs (Figures 7, 8); to obtain standard deviations, we employed the procedures of Heck Jr et al. (1975). Rarefaction was calculated using both damaged and undamaged plant remains. Statistically analyzed plant-insect associations from Cretaceous deposits are scarce, which limits the options for comparisons with other floras. To make comparisons between the interactions of El Chango and other assemblages of mid-Cretaceous (especially Cenomanian) plant-insect interactions, we re-processed the data of Santos et al. (2022a) from the early Cenomanian plant assemblage from Puy-Puy (France), which was the only available relevant dataset from this time interval (Figure 8). We analyzed the rarefaction of DTs and FFGs of the Puy-Puy dataset following the same methodology applied to our Mexican data.

4 Results

4.1 Plant assemblage

The fossil assemblage at El Chango is dominated by gymnosperms (495 specimens; 89.3%; Figure 7A). Angiosperm remains are remarkably scarce in the assemblage (59 specimens; 10.7%; Figure 7A). The most abundant remains were attributed to the conifer *Geinitzia* sp. (62.3% relative abundance), followed by Podocarpaceae indet. (13.9%) and by the cupressacean *Brachyphyllum* sp. (10.1%). Other taxa or morphotypes represent less than 10% of the assemblage. Angiosperms, such as *Sapindopsis* sp. (Platanaceae; Figures 1C, 2) and *Eucalyptolaurus* sp. (Lauraceae; Figure 1C), were also present in the assemblage. Poor preservation of some angiosperm leaves did not permit identification to genus or species level. Consequently, some were classified into various "angiosperm morphotypes".

The taxon that dominates the plant fossil assemblage, *Geinitzia* sp., has xerophytic adaptations (Moreau et al., 2021). The third-
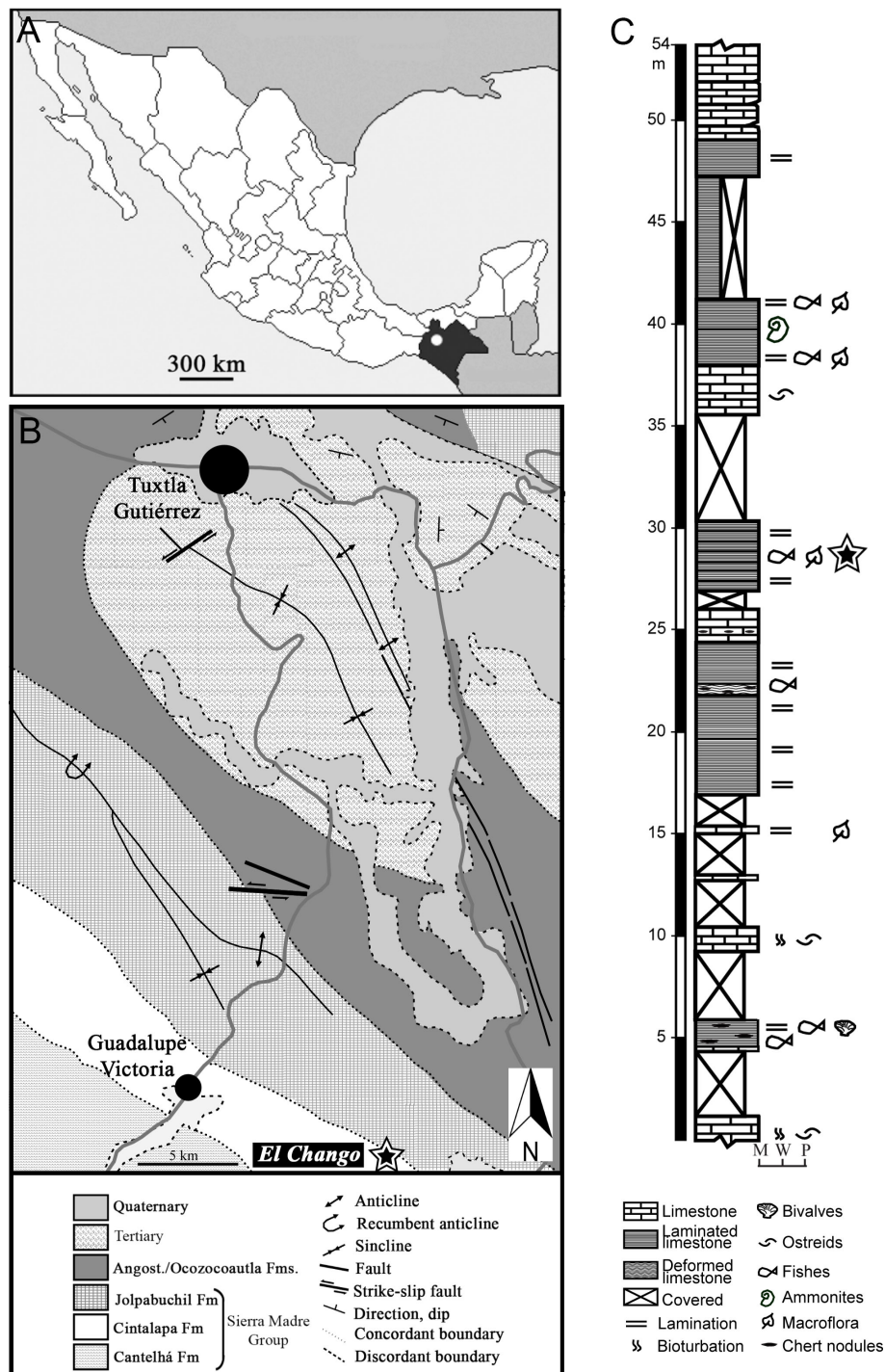
FIGURE 1
(A, B) Geographical and geological map showing (white dot in A and star in B) the position of El Chango Lagerstätte locality (Chiapas, Mexico).
(C) Stratigraphic section of the studied interval of the Cintalapa Formation indicating the plant-bearing levels (star) and the lithological characters.
M: Mudstone; W: Wackestone; P: Packstone. (Modified from Moreno-Bedmar et al., 2014).

most abundant genus (*Brachyphyllum*: 9.1%) also has xerophytic characters, e.g., small appressed leaves, thick cuticle, and sunken stomata to limit water loss (Moreau et al., 2022). There is also a remarkable dearth of hygrophilous plants, such as ferns and bryophytes, in this mid-Cretaceous assemblage. These groups, especially ferns, are common in other Cretaceous floras (being represented in both macrofloras and palynofloras) from the Northern Hemisphere (e.g., Vajda et al., 2013; Villanueva-Amadoz et al., 2014; Santos et al., 2018, 2022a; Estrada-Ruiz et al., 2018; Rodríguez-Barreiro et al., 2022; 2024; Cevallos-Ferriz et al., 2022; Herman and Domogatskaya, 2023; Martínez de Espronceda et al., 2024). Cycadales and Bennettitales were not
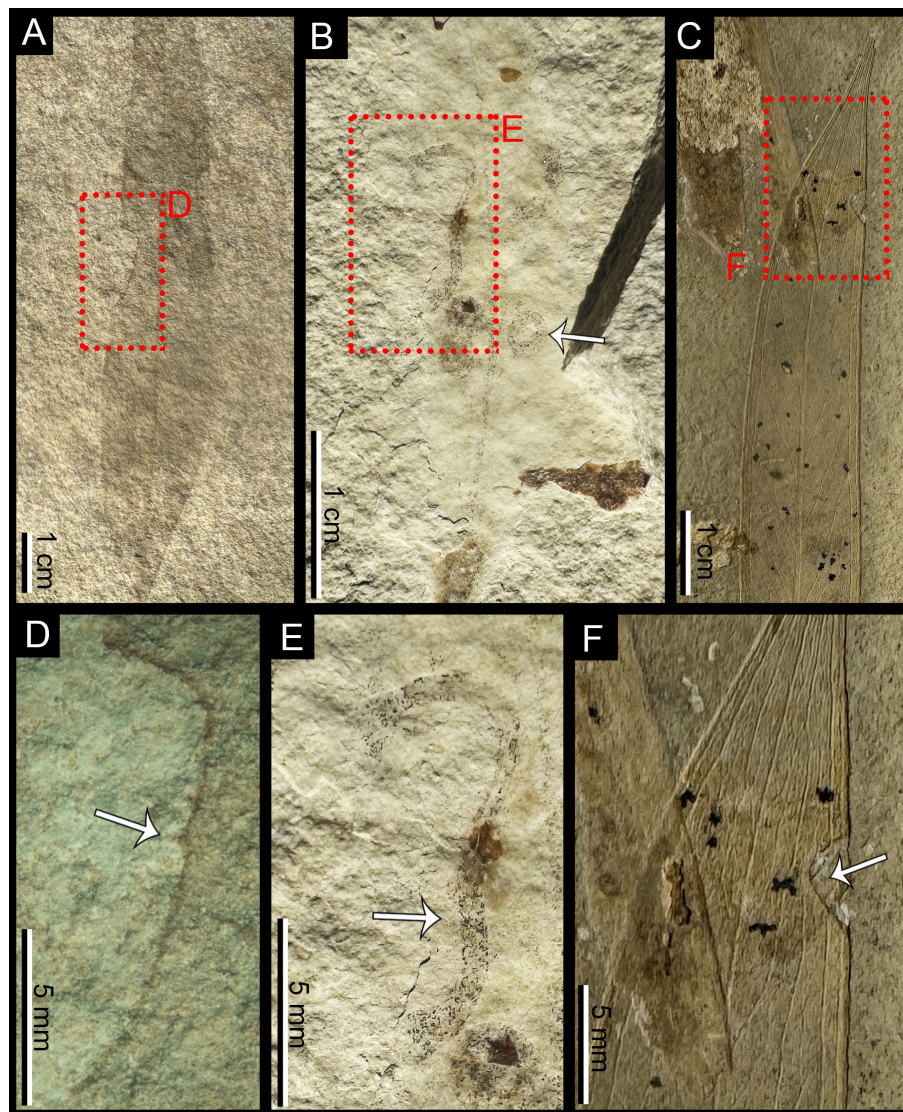
FIGURE 2
Various DTs of margin feeding on basal angiosperms at El Chango. **(A)** Two occurrences of DT012 on *Eucalyptolaurus* sp. Scale Bar = 1 cm (10 mm); **(B)** Margin feeding with developed reaction rim (DT200) and hole feeding on the left side of the leaf (DT113) in Angiosperm MF16. Scale Bar = 10 mm; **(C)** Evidence of DT012 on aff. *Sapindopsis* sp. Scale Bar = 10 mm; **(D)** Detail of A showing the dark reaction rim of one DT012 (see white arrow) on *Eucalyptolaurus* sp. Scale Bar = 5 mm; **(E)** Detail of B, white arrow shows the slightly cuspate margin and thickened reaction rim of a DT200. Scale Bar = 5 mm; **(F)** Detail of C, showing the DT012 on aff. *Sapindopsis* sp.; Scale Bar = 5 mm.

recorded in the fossil flora. The absence of these taxa in the assemblage does not necessarily mean their absence in the biocenosis since taphonomic processes may have excluded them. On the other hand, the flora also contained seeds and fruits, some of which bore potential anti-herbivore defences, e.g., the spinescence expressed in the Papaveraceae-like fruit (Figures 3C, G).

4.2 Plant-arthropod interactions

Fourteen DTs were identified in the plant assemblage (Figures 7C, D) corresponding to seven FFGs, including two DTs of margin feeding (DT012, DT200), four DTs of hole feeding (DT001, DT005, DT008, DT113), one DT of surface feeding

(DT030), three DTs of piercing and sucking (DT046, DT047, DT053), one example of oviposition (DT076), two putative DTs of galling (DT080, and a galling structure that shares some affinities with DT336), and one DT corresponding to mining (DT129).

Of the 554 plant remains included in the study, only 5.4% show evidence of herbivory or oviposition scars (Figure 7B). Nevertheless, when this richness of damage is analyzed by botanical groups, the results show high disparity. Only 1.8% of gymnosperm specimens were damaged, whereas 35.6% of angiosperms bore damage features (Figure 7B). The frequency of arthropod damage varied among each FFG. Hole feeding was the most common functional feeding group (2.5%), followed by margin feeding (present in 1.1% of specimens), piercing and sucking (1.1% of affected plants), galling (0.9%), mining (0.2%), and surface feeding (0.2%). No clear evidence of
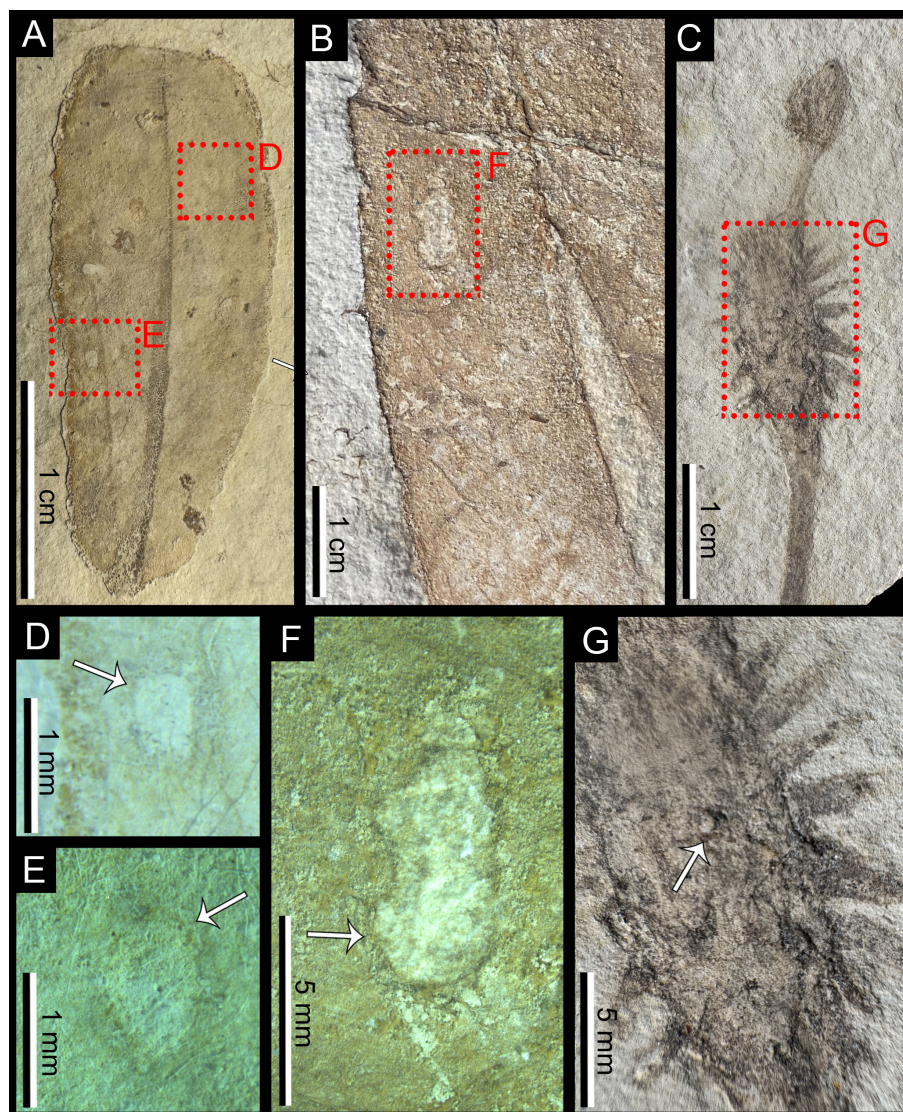
FIGURE 3
Various DTs of hole feeding on early angiosperms from the studied site. **(A)** Leaf of Angiosperm MF7 with some hole-feeding interactions (DT001). Scale Bar = 10 mm; **(B)** Polylobate hole feeding (DT005) on Angiosperm MF3. Scale Bar = 10 mm; **(C)** Angiosperm fruit (Papaveraceae-like fruit) bearing some herbivory-defense structures (spines) and with a possible hole-feeding scar (DT001). Scale Bar = 10 mm; **(D)** Detail of A, white arrow shows the reaction rim around the small hole (DT001) in the angiosperm leaf. Scale Bar = 1 mm; **(E)** Detail of A, white arrow shows the plant reaction to the hole-feeding damage (DT001). Scale Bar = 1 mm; **(F)** Detail of the irregular (polylobate) hole feeding (DT005) illustrated in **(B)**. Scale Bar = 5 mm; **(G)** Detailed photo of C, showing more detail on the spines of the Papaveraceous-like fruit and the putative DT001 (see white arrow).

skeletonization, seed predation, or pathogen attack was found in the El Chango flora.

4.3 Filamentous drapes on plants

Two specimens of cf. *Geinitzia* sp. host intriguing plant-algae interactions (Figure 6). Delicate filamentous structures coat the branch axis and its helically arranged leaves, forming dense threads around these gymnosperms. The distinct arrangement of these filaments, exclusive to the gymnosperms and absent in the adjacent rock matrix, strongly suggests a preferential association with the plant. Detailed discussion of this specimen is included in the end of the following section.

5 Discussion

5.1 Herbivory and plant palatability at the El Chango paleoforest: palaeoecological and paleoenvironmental insights

We identified seven FFGs and 14 DTs in the El Chango Lagerstätte, representing a generally low diversity of interactions. Herbivory is represented predominantly by relatively simple hole feeding (2.5% incidence in the flora), piercing and sucking (1.1% of affected plants), and margin feeding (1.1% of the flora). Most identified DTs were found on broad-leafed angiosperm remains (12 DTs), whereas only two DTs were identified in gymnosperms (Figure 7D). The absence of other FFGs, such as skeletonization or
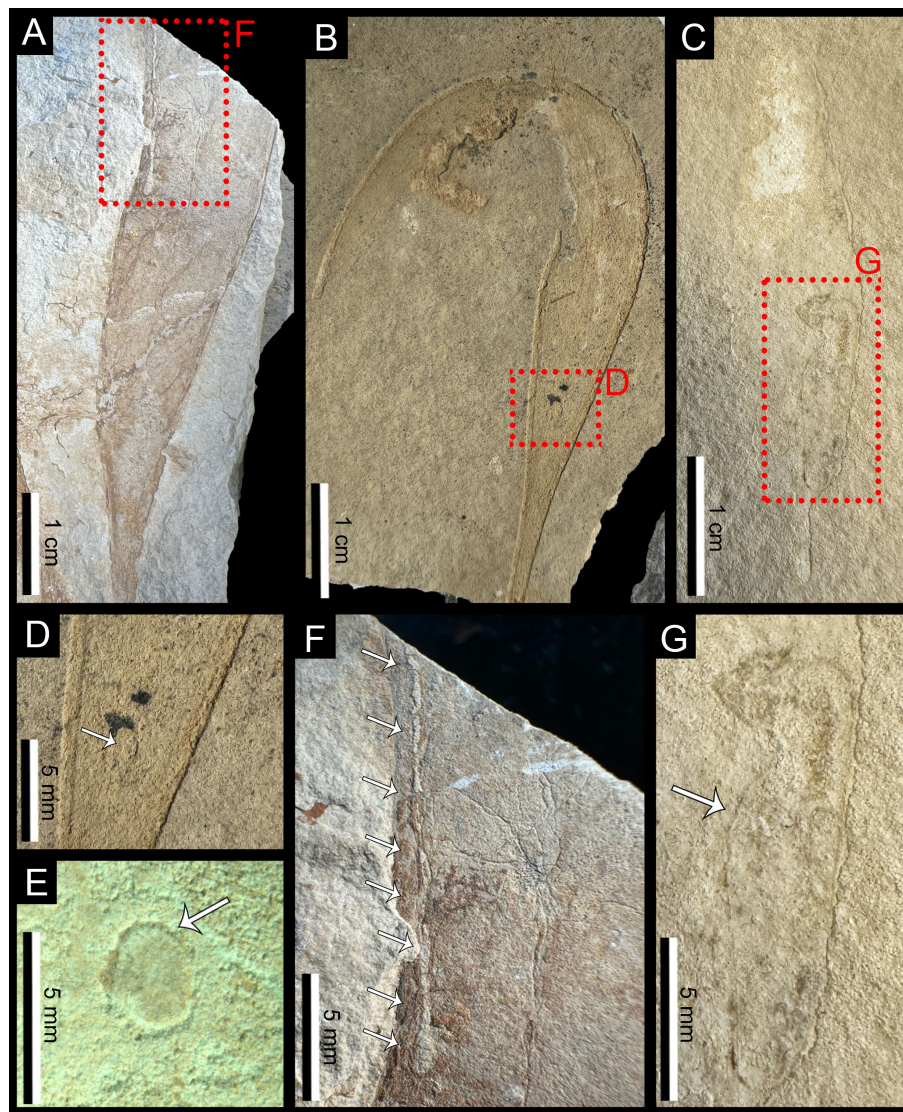
FIGURE 4

Various DTs of surface feeding, oviposition, piercing and sucking, and mining on basal angiosperms of El Chango site. **(A)** Angiosperm MF13 with linear mining in the right side of the leaf (DT129). Scale Bar = 10 mm; **(B)** aff. *Sapindopsis* sp. with an oviposition scar in the midvein (DT076; see detail of red square in **(D)**. Scale Bar = 10 mm; **(C)** Surface feeding on Angiosperm MF11 (DT030; Detail in **G**). Scale Bar = 10 mm; **(D)** Detail of the oviposition mark (see white arrow) in aff. *Sapindopsis* sp. Scale Bar = 5 mm; **(E)** Possible piercing and sucking interaction (aff. DT053) in Angiosperm MF11. Scale Bar = 5 mm; **(F)** Enlargement of A, showing details of the linear mining (DT129), white arrows indicate the reaction rim surrounding this interaction. Scale Bar = 5 mm; **(G)** Detail of the damage patch corresponding to Surface Feeding (DT030). Scale Bar = 5 mm.

pathogen damage, does not necessarily imply the absence of insects, fungi, or other micro-organisms with these feeding styles in the parent biota but may indicate taphonomic biases. We also note that the rarefaction curve for all DTs is not stabilized at the 536 specimen level (Figure 7C), suggesting that if more samples are recovered from El Chango more diversity of damage would likely be identified.

According to the host specificity index, the interactions from the El Chango site have similar diversity of specific damage (six DTs) to that of generalist damage (external damage; seven DTs). Specialized interactions in the fossil record are commonly attributed to monophagous and particularly oligophagous insects (Currano et al., 2008, 2010; Adroit et al., 2016). In contrast, polyphagous insects are generally associated with more general interactions (Currano et al., 2008). The similar levels of diversity and abundance between specific and generalist damage in the El Chango flora suggest that oligophagous and polyphagous insects were equally important in this gymnosperm-dominated mid-Cretaceous paleoforest.

The plant assemblage at the El Chango site shows a significant disparity in the richness of damage for each plant group and genus. Gymnosperms represent only 1.8% of the specimens with one or more DTs. This contrasts with the dominance of this group in the total flora (89.3%). In comparison, 35.6% of angiosperms were damaged by insects or other arthropods or mollusks, yet flowering plants constitute only 10.7% of the plant specimens in this Cretaceous flora. This indicates that the regional entomofauna targeted broad angiosperm leaves in preference to the available
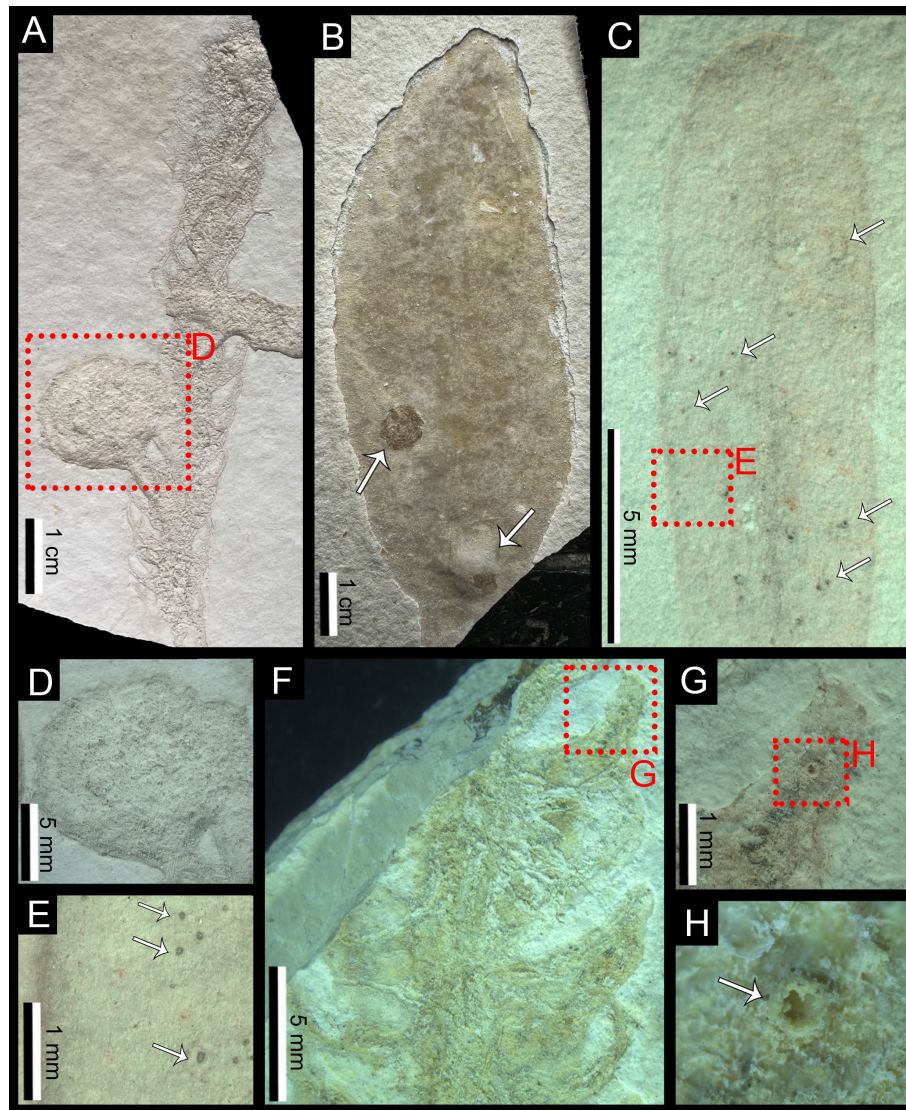
FIGURE 5

Various DTs of piercing and sucking, and galling on some gymnosperms and fruits from the El Chango site. **(A)** Gymnosperm branch of cf. *Geinitzia* sp. showing a putative gall (similar structure to DT336). Scale Bar = 10 mm; **(B)** Indeterminate angiosperm fruit showing an attached fish coprolite (upper white arrow) and a gall-like structure (lower white arrow). Scale Bar = 10 mm; **(C)** Piercing and sucking marks on a leaf of Angiosperm MF8 consisting of several slightly convex styletal punctures (DT047) Scale Bar = 5 mm; **(D)** Detail of the pedunculate gall emerging from a cf. *Geinitzia* sp. branch: Scale Bar = 5 mm; **(E)** Zoom on C, showing details on the styletal punctures (DT047). Scale Bar = 1 mm; **(F)** Specimen of cf. *Geinitzia* sp. bearing falcate leaves spreading from the axis, showing piercing and sucking marks on the upper leaf (see details on **G**). Scale Bar = 5 mm; **(G)** Detail of **(F)**, showing one falcate leaf of cf. *Geinitzia* sp. with a concave styletal puncture (DT046). Scale Bar = 1 mm; **(H)** Enlargement of the piercing and sucking mark (see white arrow).

scale-leafed gymnosperms, but it is not clear whether this differential distribution was due to preferences for broad leaf form or for flowering plants per se. No broad-leafed gymnosperms or scale-leafed angiosperms are available in the El Chango assemblage to test these alternative possibilities. In any case, the relatively abundance of damage on angiosperms is striking given that, during the Albian–Cenomanian, angiosperms had only recently emerged as a significant component of the vegetation and were still in their early phase of diversification (Friis et al., 2011). Insects, having adapted to interactions with pteridophytes and gymnosperms over hundreds of millions of years, might be expected to require significant time to adjust to herbivory on this

new plant group. However, our findings indicate that the entomofauna were already well adapted to feed on early angiosperms during the mid-Cretaceous in the tropics. This implies a relatively rapid adjustment of diverse insect clades to the emerging plant group that would soon dominate terrestrial ecosystems.

To resolve whether the insects from El Chango had a preference for feeding on angiosperms is challenging in the absence of broad-leafed gymnosperms, but we hypothesize that the small, thick and appressed leaves of the preserved conifers may have been inhibitory to some insect herbivores. Among the most dominant taxa in the El Chango assemblage were the conifers *Geinitzia* and *Brachyphyllum*
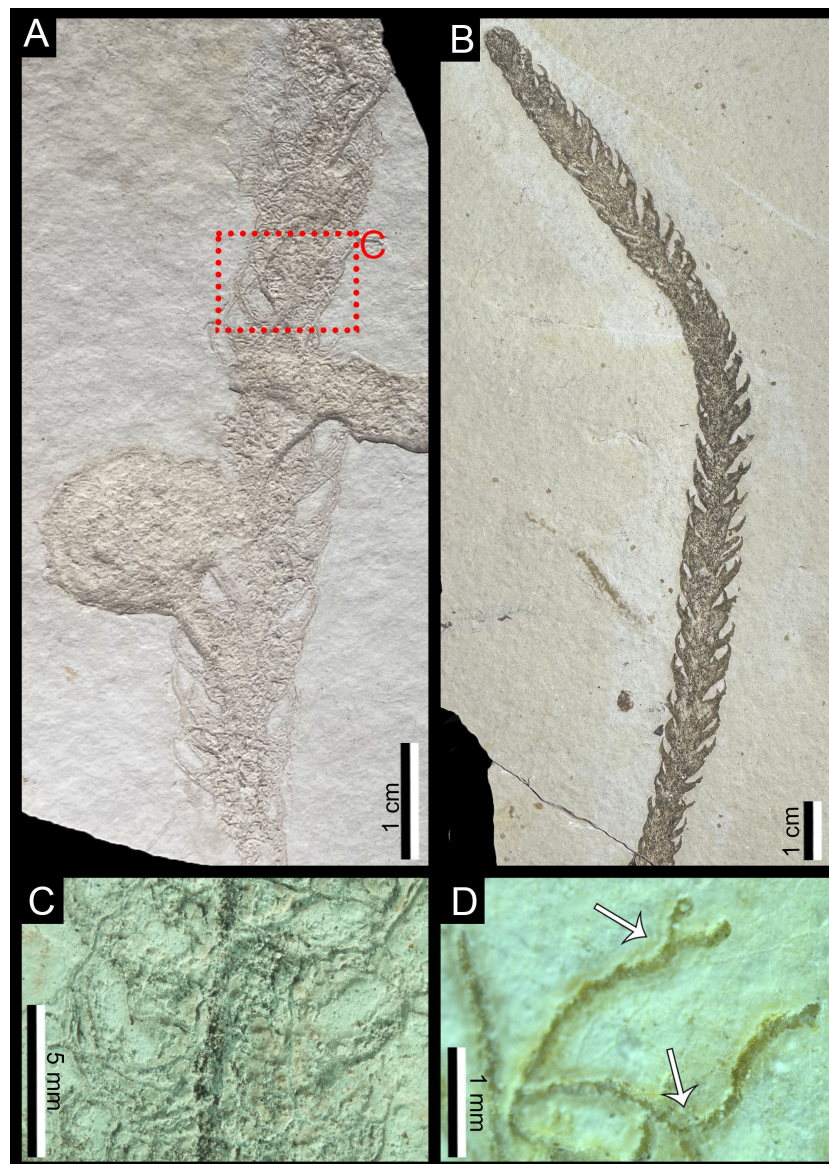
FIGURE 6
Putative plant-algae interaction (epibiont of marine/brackish algae on terrestrial gymnosperms from El Chango site. **(A)** Specimen of cf. *Geinitzia* sp. is affected by attached filaments of putative Chlorophyta *sensu lato* (see discussion). Scale Bar = 10 mm; **(B)** Unaffected specimen of cf. *Geinitzia* sp. from the same site). Scale Bar = 10 mm; **(C)** Detail of the putative algae filaments coating the leaves and the axis. Scale Bar = 5 mm; **(D)** Detail on the thin filaments that divide in a dichotomous pattern (see arrows). Scale Bar = 1 mm.

(collectively accounting for 72.4% of the flora), which have narrow and coriaceous leaves and thick cuticles. *Brachyphyllum* has been interpreted as coniferous (with various species affiliated to Araucariaceae, Cheirolepidiaceae, or Cupressaceae) and having xerophytic adaptations to semi-arid conditions (Moreau et al., 2022). *Geinitzia* sp. also bears reduced coriaceous leaves, and some low-palaeolatitude species of this genus have been linked by morphological adaptations and histology to high temperatures and aridity (Moreau et al., 2021; see also discussion by Santos et al., 2022a). These adaptations may have served as deterrents to herbivorous arthropods.

In contemporary plant studies, it has been established that environmental conditions play a pivotal role in determining plant palatability across various species (Münzbergová and Skuhrovec, 2013; Kuglerová et al., 2019). Specifically, arid and semi-arid conditions have been identified as factors that decrease plant palatability to insects across multiple plant species (e.g., Blumenthal et al., 2020). Consequently, the presence of plants adapted to semi-arid conditions may have contributed to a reduction in foliar palatability at El Chango. This reduction may have resulted in low insect populations and diversity, consequently contributing to the relatively low richness and diversity of DTs in this flora. This observation aligns with contemporary research on plant-insect interactions (e.g., Münzbergová and Skuhrovec, 2013; Kuglerová et al., 2019), indicating that aridity is associated with decreased network metrics related to plant-insect interactions.
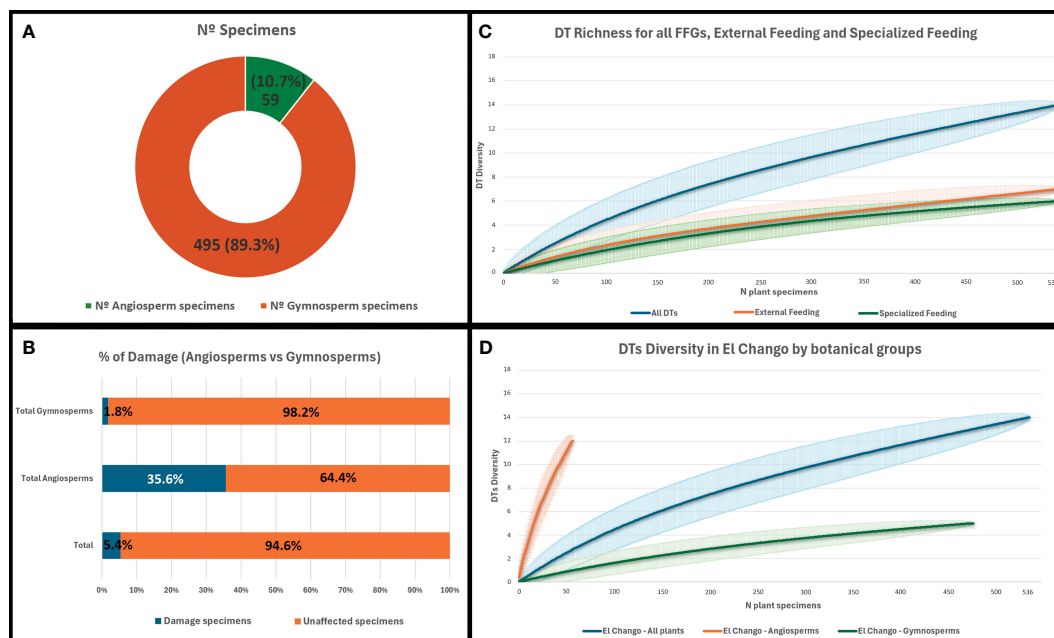
FIGURE 7

(A) Number of specimens used in this study indicating the total quantity of gymnosperms and angiosperms; **(B)** Incidence of affected specimens for angiosperms, gymnosperms, and the whole flora. **(C)** Rarefaction curves showing the diversity of all DTs, specialized feeding, and external feeding at El Chango. **(D)** Differences in the rarefaction of diversity damage in angiosperms and gymnosperms from the El Chango site.

Moreover, aridity negatively correlates with network specialization and the modularity of local webs (e.g., Santos-Neto et al., 2022). Furthermore, recent studies on herbivory have revealed that certain insects alleviate pressure on their host plants in response to rising temperatures (Laws and Belovsky, 2010). In this context, some of the discussed gymnosperms are indicative arid or semi-arid conditions, at least during certain parts of the year. This climatic influence might also contribute to the lower palatability observed in most specimens within this flora.

In the El Chango flora, various anti-herbivore adaptations have been identified, exemplified by the Papaveraceae-like fruit (Figures 3C, D). Features such as spines and thorns, found in multiple parts of the plants, are commonly interpreted as defences against herbivores (Hanley et al., 2007). Notably, spinescence is generally deemed more effective against vertebrates than invertebrates (Cooper and Owen-Smith, 1986; Hanley et al., 2007). Most plants in this assemblage bore leaves with at least some morphological feature(s) contributing to unpalatability and anti-herbivore defences. This aligns with the observed greater herbivory and trace diversity in angiosperms, which appeared more vulnerable to attacks by generalist insects.

5.2 Comparison with other mid-Cretaceous assemblages

The herbivory rates found in the El Chango fossil flora are relatively low (5.4% of affected specimens), especially when compared to quantitative data on plant-arthropod interactions from other Cretaceous sites, such as the Albian flora of Estercuel,

Spain (Santos et al., 2023), the Cenomanian flora of Puy-Puy, France (Santos et al., 2022a), which reach 20.4% and 22.2%, respectively, or the Albian flora from Rose Creek in USA (Xiao et al., 2022a), which has a higher proportion (45.6%) of damaged specimens. Only those three mid-Cretaceous floras from the North Hemisphere have been subjected to quantitative or semi-quantitative analyses of plant-insect interactions (Table 1). They are relatively close in age to the El Chango flora. Additionally, the fact that some authors of the current study participated in identifying interactions in two of the other floras reduces the potential human bias for detecting and interpreting different damage types. However, other influences, such as taphonomic bias, should be considered and may ultimately limit the scope of comparisons between these various mid-Cretaceous floras. Sampling limitations (only 72 specimens available) on the mid-Cretaceous flora from Spain (Santos et al., 2023) potentially bias the results from that assemblage. However, the interactions recorded in the mid-Cretaceous flora of France were based on an assemblage of more than 1500 plant specimens (Santos et al., 2022a), enabling more confident comparisons.

The richness of interactions at El Chango is relatively low if the flora is considered as a whole (5.4%), notably lower than the 20–22% observed in other paralic floras from the mid-Cretaceous of Spain (Santos et al., 2023) or France (Santos et al., 2022a). However, this percentage at El Chango must be considered in context. Although, superficially, it may seem like a low ratio, when the interactions are assessed by botanical groups, we note that these values reach percentages of around 36% in angiosperms, representing similar or even higher values than those found in other mid-Cretaceous floras. For example, the herbivory rate on the
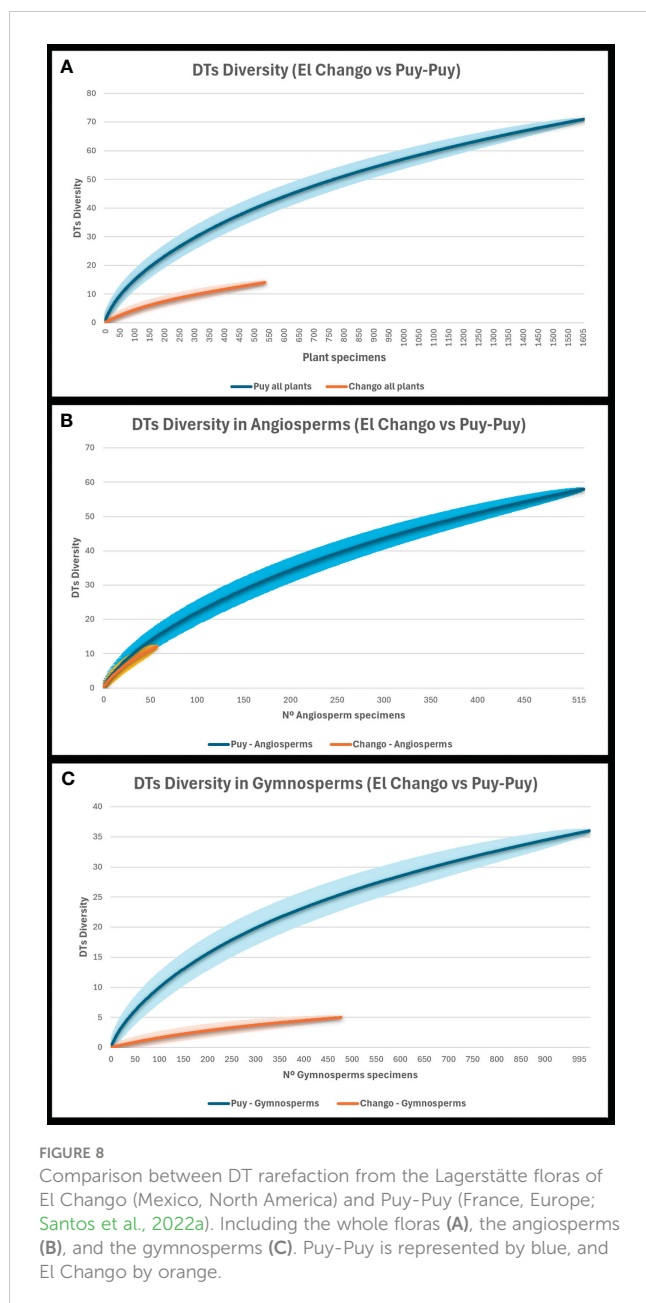
angiosperms of the Estercuel flora (East Spain) was 20.4%, and on the angiosperms of the Cenomanian flora at Puy-Puy was 34%. Nevertheless, the small number of angiosperms at El Chango might have influenced the results, and the patterns of herbivory should be interpreted cautiously. Ideally, more fossils of angiosperms from El Chango should be recovered from the site to support this interpretation.

The slightly older Albian flora from Rose Creek (USA) includes 114 DTs on about 2000 plant specimens (Xiao et al., 2022a), suggesting much greater diversity of herbivory styles than in the El Chango flora (14 DTs). This difference might be due to greater sampling effort (554 specimens vs 2084 at Rose Creek), but also to the higher plant diversity of the Rose Creek flora (about 24 species/morphotypes in El Chango vs 50 species/morphotypes in the Rose Creek flora). In addition, the Rose Creek flora includes a greater abundance of angiosperms (which are usually more herbivorized than gymnosperms; e.g.,

Santos et al., 2022a), whereas at El Chango, angiosperms are scarce. On the other hand, DT diversity in the early Cenomanian of France (coeval with the assemblage at El Chango) is significantly greater than that in the Mexican flora, with 71 DTs compared to 14 DTs. This evident disparity is linked to the difference in sample sizes, i.e., 1605 specimens analyzed from Puy-Puy versus 554 (536 leaves) specimens from El Chango. When considering rarefaction curves of DT diversity at an equivalent sampling level (554 specimens; 536 leaves), they confirm the heightened diversity of damage types in the Cenomanian of France (43 DTs) compared to Mexico (14 DTs; Figure 8A). Examining rarefaction curves specifically for DT diversity in angiosperms (Figure 8B) reveals a notable similarity in damage diversity at the same sampling level (approximately 13 DTs in France versus 11 DTs in Mexico at 50 angiosperms of rarefaction). Crucially, when considering the standard deviation of damage diversity in angiosperms, it is evident that the mid-Cretaceous assemblages demonstrate comparable variability at the same sampling level. The disparity in general DT diversity is attributed to differences in damage on gymnosperms. At an equivalent sampling level (about 500 specimens), gymnosperms from Puy-Puy host a higher diversity of traces than those from El Chango (26 DTs vs 4 DTs). The most parsimonious explanation lies in the anatomical differences in the gymnosperms between the two localities.

In Puy-Puy, gymnosperms are represented predominantly by the coniferous *Dammarophyllum* (constituting 46.3% of the assemblage), a genus characterized by broad leaves that are more susceptible to insect damage (Santos et al., 2022a). Most of gymnosperms at El Chango have small, appressed awl-shaped leaves with thick cuticles that are presumably less palatable. On this basis, angiosperms were a proportionately more significant food source for insects and other herbivorous arthropods and mollusks in the coastal paleoforests of North America than in equivalent settings in Europe during the mid-Cretaceous.

Despite the Puy-Puy flora hosting markedly more diverse and common interactions, potential taxonomic biases (owing to fewer plant species in El Chango) and taphonomic biases (greater preservational potential of robust conifers at El Chango) offer plausible explanations for these differences. Although marked differences exist between the assemblages, a common pattern is evident in the plant-insect interactions. In both gymnosperm-dominated floras from Europe and North America, insects clearly preferred angiosperms. Although there are variations in the specific compositions of the assemblages, the higher amounts of damage on angiosperms leaves in these mid-Cretaceous paleoforests prompts the need for further research. More comprehensive investigations into mid-Cretaceous plant assemblages and plant-insect interactions are essential to unravel the role that this apparent herbivory pressure on early angiosperms played in the radiation and dominance of terrestrial ecosystems by flowering plants during the KTR.

5.3 Plant-algae interactions

Other types of biotic associations have been found in El Chango assemblage, for example, the plant-algae interaction found on cf. *Geinitzia* sp. (Figure 6). Given their morphology and dichotomous

habit, we confidently exclude these filaments from constituting another part of the host plant, such as branches or roots of *Geinitzia* sp. (white arrows in Figure 6D). Additionally, the minute size of these filaments (around 0.1 mm in diameter) rules out the possibility that they are filaments from another parasitic angiosperm (such as *Cuscuta* sp.); and they are too large and robust to be fungal hyphae. Although the simple morphology of these tangled filaments makes their assignment to a specific taxonomic group impossible, we argue that the most parsimonious explanation is that they are filaments of some epibiont green algae growing on the robust branch in a marine setting before burial. Plants washed into fluvial, estuarine and marine systems can have long and complex taphonomic histories, developing interactions with a broad range of epibionts and saprotrophs (Philippe et al., 2022). The depositional environment at the El Chango site was a lagoon or estuary (e.g., Moreno-Bedmar et al., 2014). Hence, terrestrial plants may have been washed into this brackish water environment and submerged for extended periods before burial, allowing colonization by filamentous green algae epibionts.

6 Conclusions

The mid-Cretaceous El Chango Lagerstätte in Mexico provides unique insights into plant-insect interactions during a pivotal period of changes in the evolution of terrestrial ecosystems in the tropics of North America. A total of 554 fossil plant specimens were analyzed for plant-insect interactions. Our analysis revealed a relatively low overall herbivory rate of 5.4%. However, examination by botanical groups demonstrated a stark contrast between the insect damage on the available gymnosperms and the angiosperms from El Chango. Although gymnosperms dominated the palaeoflora (89.4% abundance), they hosted a low herbivory incidence of 1.8%. In contrast, despite constituting a smaller proportion of the El Chango flora (10.7%), early angiosperms were significantly more affected by herbivores, with 35.6% of specimens showing some form of damage.

The diversity of DTs was also relatively low in the flora, with 14 identified DTs and seven FFGs. Angiosperms hosted a higher diversity of damage (12 DTs), attributed to various FFGs, such as margin feeding, hole feeding, piercing and sucking, galling, oviposition, and mining. The available gymnosperms in the assemblage, in contrast, hosted a small range of interactions (five DTs belonging to galling and piercing and sucking, and hole feeding), potentially due to their anatomical structure and xeromorphic adaptations, making them less palatable to herbivores.

Comparison with coeval European plant assemblages, such as Puy-Puy (France), reveals similarities in gymnosperm dominance but notable differences in the diversity and frequency of plant-insect interactions. The Puy-Puy flora hosts more DTs and rates of herbivory, but potential biases in plant species diversity and taphonomy offer plausible explanations for the observed disparities. Nevertheless, a pattern emerges across these mid-Cretaceous ecosystems, with insects inflicting greater feeding damage on broad-leafed angiosperms than co-preserved scale/needle-leafed gymnosperms. These findings underscore the need

for further research on mid-Cretaceous plant assemblages and plant-insect interactions to unravel the relative roles of the targeting of angiosperms as a clade versus a potential preference of herbivores for feeding on broad-leafed plants in general during the mid-Cretaceous. Our study contributes to the broader understanding of coevolutionary dynamics between plants and insects during a critical phase in Earth's vegetation history.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

AS: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. SM: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. MR-K: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing – review & editing. AH-D: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing – review & editing. UV-A: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing. SC-F: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1381539/full#supplementary-material

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