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Plant–insect interactions from the mid-Cretaceous at Puy-Puy (Aquitaine Basin, western France) indicates preferential herbivory for angiosperms amid a forest of ferns, gymnosperms, and angiosperms

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ABSTRACT

Plants and insects are the two dominant groups in terrestrial ecosystems, and insect damage on fossil plants is the only direct evidence documenting the past ecological history between these two, hyperdiverse groups. We describe, analyze, and interpret plant–insect interactions of a lower Cenomanian paleoforest from western France – the Puy-Puy Quarry of the Nouvelle-Aquitaine Region. We examined 1605 fossil leaves, axes, and reproductive material of bennettitalean, pinalean, and ginkgoalean gymnosperms; lauralean and magnolialean angiosperms; and pteridophyte fronds. We identified functional feeding groups (FFGs) and insect damage types (DTs) preserved on this foliage and data were rarified to indicate sample completeness. By employing *R*, various statistical parameters were calculated. We established 71 DTs for the nine FFGs of hole feeding, margin feeding, skeletonization, surface feeding, oviposition, piercing and sucking, galling, mining, and pathogens, and 1292 feeding event occurrences. Of the specimens examined 22.2% exhibited one or more DT, with angiosperms the most affected plant group. The most diverse interactions were mining and galling, indicating a mosaic of humid and xeric habitats, respectively, for the Puy-Puy paleoforest, a conclusion consistent with previous paleontological and sedimentological interpretations. Elevated DT richness suggests long-standing ecological relationships between the plants and insects, representative of a mature forest.

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1. Introduction

Today, plants and arthropods together represent more than 80% of the species that have been established on the planet (Mora et al. 2011; Zhang 2011; Roskov et al. 2013; Stork 2018). Currently, plants represent about 80% of the biomass of the planet and arthropods 0.18%, the latter accounting for about half of all animal biomass (Bar-On et al. 2018). The abundance and diversity of these two groups throughout Earth history makes their relationships extensive, intense, and complex. In co-associational terms, the abundant and well-documented relationships of predation, commensalism, mutualism, parasitism, parasitoidism, and herbivory between plants and arthropods characterize the trophic history of terrestrial ecosystems and attests to the close ecological links between these two groups (Zhang 2011; Currano et al. 2021;

Labandeira and Li 2021). **Perhaps**, the most important of these interactions is the herbivory between plant hosts and their arthropod (and pathogen) herbivores.

The Cretaceous Period is an interval of profound and rapid change in terrestrial ecosystems at a global level that was especially intense during the Cretaceous Terrestrial Revolution (KTR) of the mid-Cretaceous (e.g. Barba-Montoya et al. 2018). Plants clearly were the protagonists during this great revolution due to the demise of many gymnospermous lineages and the rapid diversification of angiosperms; however, it also was an important time for the expansion of adversarial arthropods and pathogens representing a variety of herbivorous groups (Xiao et al. 2022a, 2022b, 2022c). These groups, present during the KTR, included Orthoptera (grasshoppers, katydids) (Song et al. 2015), Hemiptera (cicadas, aphids, scale insects,

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70 planhoppers, bugs) (Szwedo 2002; Yao et al. 2012; Song and Liang 2013; Vea and Grimaldi 2016; Xiao et al. 2021b), buprestid beetles (Evans et al. 2015), weevils (McKenna et al. 2009; Wang et al. 2013), ditrysian moths (Wahlberg et al. 2013), and sawflies (Leppanen et al. 2012). There also was an expansion of mutualisms, especially insect pollinators (Perris et al. 2020; Xiao et al. 2021a). These shifts in herbivore and pollinator insect taxa that populated ecosystems during the KTR (Labandeira 2014) had such an influence on relationships among plants, arthropods, and pathogens during this approximate 30-million-year-long interval that it ushered a major shift in plant–insect interactions and marks the beginning of Phase 4 of the global herbivore expansion (Labandeira 2006; McCoy et al. 2021). During this phase, the ecological and evolutionary displacement of gymnosperms by angiosperms comprised complex patterns of adaptation within ecological networks, wherein various groups of herbivorous insects shifted their feeding strategies from gymnosperms to angiosperms. Most of these re-accommodations in the ecological relationships between plants and insects occurred during the Aptian–Albian interval (Labandeira 2006, 2014; McCoy et al. 2021). During this shift from gymnosperm to angiosperm hosts, there also was a shift of insect sublineages within the dominant herbivorous hemipteroid, holometabolous, and to a lesser extent orthopteroid lineages in local plant assemblages (Labandeira 2006).

Previous examinations of plant–insect interactions from the Cretaceous (Table 1) are scarce compared to those of the Cenozoic (Labandeira et al. 2006; Wappler et al. 2009; Knor et al. 2012, 2013; Gunkel and Wappler 2015; Currano et al. 2021), and the vast majority are limited to a few specimens (e.g. Fritch 1882; Genise 1995; Banerji 2004; Pires and Sommer 2009; Petrov 2013; Ding et al. 2015; Klymiuk et al. 2015; Estévez-Gallardo et al. 2018; Filho et al. 2019; Maccracken et al. 2019, 2021). Equally important, the few studies documenting local plant assemblages indicate many interactions, but do not use the functional feeding group–damage-type evaluation system and derivative quantitative analyses (Stephenson 1991; Krassilov 2007a, 2007b, Krassilov 2008a, 2008b), disallowing relevance for our study.

From the mid-Cretaceous of Europe, the only reported plant–insect interactions are single instances or limited occurrences of external foliage feeding, galling, piercing and sucking, oviposition, and mining on angiosperms, typically on one or a few specimens. Examples include the Cenomanian of the Czech Republic (Fritch 1882, 1901; Stephenson 1991), and external feeding, surface feeding, mining, and galling, on aquatic angiosperms from the Albian of Spain (Estévez-Gallardo et al. 2018; Santos et al. under review). Currently,

there is minimal direct evidence for associations between plants and insects in the mid-Cretaceous of Europe, despite it being a key moment in the evolutionary and ecological history of these two groups. This knowledge gap for the presence of paleoecological interactions is likely due to the absence of study, rather than limitations of the fossil record.

The abundance of gymnosperm and angiosperm foliage in the Puy-Puy *Konservat-Lagerstätte* allow us to analyze in detail the incidence and intensity of various kinds of damage caused by arthropods that consumed plants of this Cenomanian forest from western France. This work represents the first complete study of plant–insect interactions from the mid-Cretaceous of Europe that provide the volume of fossils sufficient to implement statistical interpretations at a larger, bulk-floral scale. Our study extends similar studies of a gymnosperm-dominated plant assemblage from the earliest Albian of northeastern China (Xiao et al. 2022a), and an angiosperm-dominated plant assemblage from the latest Aptian of the midcontinental United States (Xiao et al. 2022b), and collectively represent only three such studies that examine Cretaceous floras during the early ascendancy of angiosperms.

Accordingly, the objective of the present work is to (a), carry out the first plant–insect interaction study of the Cenomanian forest at Puy-Puy; (b), identify the quantity, diversity (richness), and intensity of herbivory as expressed by damage types (DTs) and functional feeding groups (FFGs) in this paleoecosystem; and (c), provide new statistical data for interpretation of the paleoecological meaning of plant–insect interactions in this plant assemblage.

2. Geographical and geological setting

The Puy-Puy quarry is in the Aquitaine Basin of the Nouvelle-Aquitaine Region, in southwestern France (Figure 1), near the town of Tonnay-Charente in the Department of Charente–Maritime. The outcrop in which the quarry lies is a succession of sands and fossiliferous clays. The lowermost part (lithological unit A1) is uppermost Albian in age and contains plant cuticle accumulations and amber (Néraudeau et al. 2005, 2020) (Figure 2). The upper part (lithological unit A2) is of lower Cenomanian age, and the shale beds are very rich in plant impressions of various dimensions, ranging from a few mm to several dm). The present study concerns the lower Cenomanian plant impressions of lithological unit A2. The sedimentological structures of the sandstone beds, such as large cross stratifications, and the paleontological assemblage of the claystone beds of Unit A2 that bears dragonfly/damselfly and cockroach wings, theropod

Table 1. Evidence of arthropod damage on Cretaceous individual plants and plant assemblages from 29 studies (after Labandeira et al. 2002).

Age	Geographic area	Formation/Basin	Damage type	References
Late Cretaceous (Maastrichtian)	Patagonia (Argentina)	Lefipán Formation	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 Formation	Leaf mine of <i>Leucopteropsa spiratae</i> in an angiosperm leaf	Mackracken et al. (2021)
Late Cretaceous (Campanian)	Southern Utah (USA)	Kaiparowits Formation	Acarodomatia interactions on angiosperm leaves	Mackracken et al. (2019)
Late Cretaceous (Coniacian)	Vancouver island (Canada)	Dunsmuir Member of the Comox Formation	Feeding galleries and damage (putative lepidoptera) on cones of <i>Acanthostrobus edenensis</i> (Cupressaceae)	Klymiuk et al. (2015)
Late Cretaceous (Turonian)	Negev (Israel)	Upper Shale Member of the Ora Formation	Hole feeding, margin feeding, mining, galling, oviposition, skeletonization. Mainly on angiosperms	Krassilov (2007), Krassilov (2008a), 2008b); Krassilov et al. (2007); Krassilov and Rasnitsyn (2008); Krassilov and Shuklina (2008)
mid Cretaceous (Cenomanian)	Kachin (Myanmar)	Hukawng Valley, Noije Bum Range	Pollen-feeding beetle in amber associated with gymnosperm and angiosperm pollen grains	Peris et al. (2020)
mid Cretaceous (Cenomanian)	Tonny-Charente (France)	Puy-Puy quarry (Aquitaine Basin)	Quantitative/semiquantitative study of plant-insect interactions on 1605 plant remains. 71 different DTs	This study
Late Cretaceous	Gobi (Mongolia)	?	Gallery system of a bark beetle in Araucaraceae wood	Petrov (2013)
Late Cretaceous	Patagonia (Argentina)	Unnamed Formation	6 ichnospecies in wood remains (<i>Cycalichnus garciorum</i> ; <i>Stipitichnus koppae</i> ; <i>Xylonichnus</i> , <i>Carpotichnus maximus</i> ; <i>C. berthaeorum</i> , and <i>C. minimus</i>)	Genise (1995)
mid Cretaceous (Albian)	Patagonia (Argentina)	Piedra Clavada Formation	A new petalurid ichnospecies: <i>Maichnus wetkarooae</i>	Genise et al. (2020)
mid Cretaceous (Albian)	Cantabria (Spain)	Las Peñas Formation?	Diptera in amber with grains of pollen (<i>Exesipollenites</i>)	Penalver et al. (2015)
mid Cretaceous (Albian)	Teruel (Spain)	Utrillas Fm.	Margin and hole feeding on Nymphaeaceae leaves	Estévez-Gallardo et al. (2018)
Early Cretaceous (Aptian)	Nabraska, United States	Dakota Fm.	Margin feeding, surface feeding, skeletonization, hole feeding, oviposition, piercing and sucking, leaf-mining, galling, seed predation, borings; and pathogens (14 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 (65 DTs)	Ding et al. (2015); Xiao et al. (2022a)
Early Cretaceous (Berriasian)	Araripe Basin (Northeast Brazil)	Missão Velha Formation	Isoptera galleries in wood of conifers	Pires and Sommer (2009)
Early Cretaceous	Araripe Basin (Northeast Brazil)	Crato Formation	Margin feeding, galling, oviposition and piercing and sucking on ferns; margin feeding, skeletonization and galling on angiosperms	Filho et al. (2019)
Early Cretaceous	Rajmahal Hills (India)	Rajmahal Formation in the Rajmahal Basin	Margin feeding on <i>Ptilophyllum</i> sp., oviposition on <i>Phyllopteroides</i> ; galling on <i>Nipaniophyllum</i>	Banerji (2004)
Early Cretaceous (Berriasian)	Bornholm, Denmark	Rabekke Formation	Insect boring (putative fungus-farming beetle) on wood	Mikuláš et al. (2020)

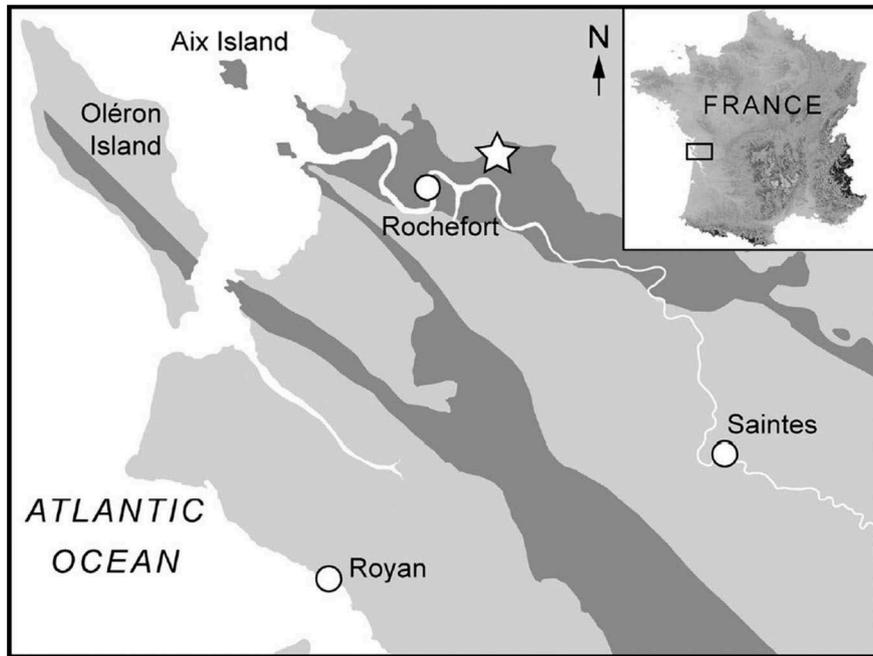


Figure 1. Geographical map of France indicating with a star indicating the location of the Puy-Puy Quarry. The dark grey signifies uppermost Albian-Cenomanian outcrops. Modified from Néraudeau et al. (2020)

180 feathers, mechochirid crustaceans, and linguloid brachiopods, collectively display depositional evidence for both continental and marine influence (Girard et al. 2011; Néraudeau et al. 2020).

185 The analyzed plant specimens originate from the lowermost fossiliferous claystone bed P1 of lower Cenomanian Unit A2, although two other fossiliferous clays beds, P2 and P3, are known but they contain only small plant debris. The P1 bed constitutes the major facies of the Lagerstätte, displaying exceptional preservation of various plant macroscopic remains, and the presence of other exquisite fossil specimens of insect wings, feathers, and shark eggs (Figure 2). From palynological studies, Unit A1 was dated as uppermost Albian to earliest Cenomanian (Polette et al. 2019), and unit A2, near the Puy-Puy quarry, was dated as earliest Cenomanian (Néraudeau et al. 2002, 2020). The Unit A2 was barren of palynomorphs at the Puy-Puy quarry, but the fossiliferous clay is located between the amber and lignite beds of the uppermost Albian–lowermost Cenomanian Unit A1, and the first calcareous marine beds of the lithological Unit B1, very rich in the lower Cenomanian foraminifer *Orbitolina plana* d’Archiac and rudist *Ichthyosarcolites triangularis* Desmarest (Néraudeau et al. 2005, 2020; Peyrot et al. 2005; Polette et al. 2019). Consequently, the plant assemblage of P1 can be dated as lower Cenomanian. No formational name has been formally assigned to the strata bearing the afore-mentioned plant fossils.

210 Plant fossils are abundant at the Puy-Puy Quarry. Plant megafossils from Unit A2 are dominated by leafy axes principally affiliated with the needleleaved conifer

Geinitzia reichenbachii (Geinitz) Hollick & Jeffrey (Geinitziaceae) and isolated leaves of the broadleaved conifer *Dammaphyllum* sp. (?Araucariaceae). 215 Conifers are also represented by a male cones such as *Classostrobus* Alvin, Spicer & J. Watson of the Cheirolepidiaceae), isolated ovuliferous scales, and rare winged seeds. Unit A2 occasionally yields leafy axes of the xerophytic, fleshy-leaved conifer *Glenrosa carentonensis* Moreau, Néraudeau, Tafforeau & Dépré (incertae sedis). Gymnosperm remains from Unit A2 also include isolated leaves of Ginkgoales (*Eretmophyllum* Thomas), leaflets of Bennettitales assigned to *Zamites* sp. (Williamsoniaceae), and cuticles of putative Cycadales (Gomez et al. 2004; Le Diouron 2005). In addition to gymnosperms, angiosperms represent the second most abundant plant macrofossils, constituting about 20 leaf morphotypes (Le Diouron 2005). The angiosperms are dominated by magnoliids, principally Lauraceae, and possible basal eudicots such as Platanaceae of the Proteales (Néraudeau et al. 2005). The most abundant leaf in the plant assemblage is *Eucalyptolaurus depreii* Coiffard, Gomez, Thiébaud & Kvaček (Lauraceae) 220 (Coiffard et al. 2009). Other angiosperm leaves were tentatively assigned to cf. “*Grevillea*” *dvorakii* probably of the Lauraceae (Friis et al. 2011), and cf. *Debeya coriacea* (Néraudeau et al. 2005), of unknown taxonomic affinities (Krassilov et al. 2008). Angiosperm 225 remains are composed of rare and exquisitely preserved inflorescences, flowers, and fruits (Néraudeau et al. 2020). Paleobotanical material from Unit A2 includes isolated and fragmented pinnae and pinnules of ferns, such as cf. *Osmunda cretacea* Samylinia 230 235 240 245

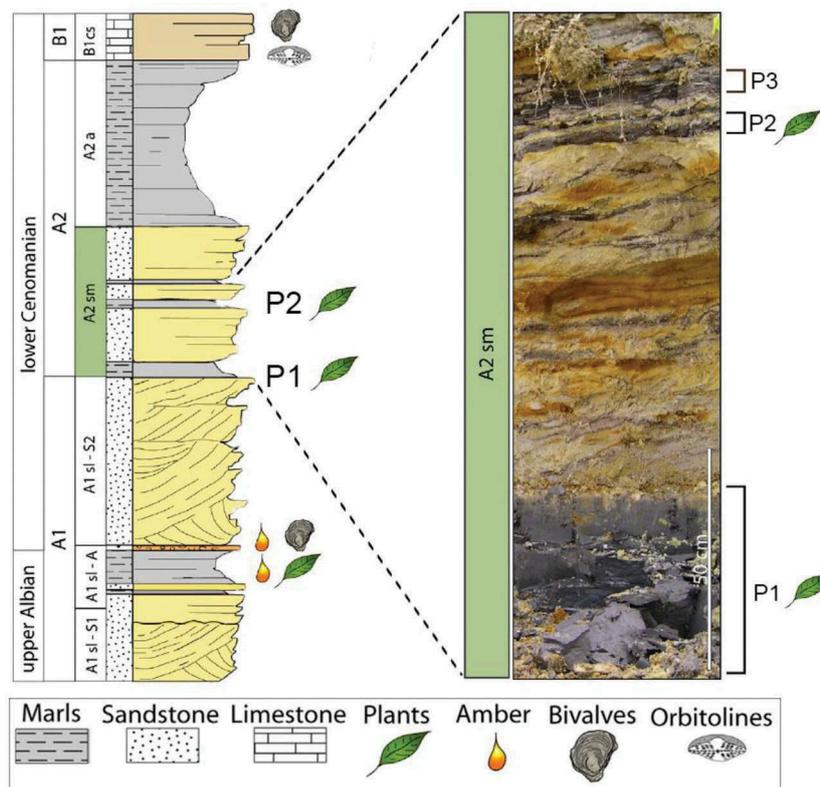


Figure 2. Stratigraphic section indicating the sedimentological features of the three studied levels at the Puy-Puy Quarry. Modified from Néraudeau et al. (2020)

(Osmundaceae). Unit A2 also yields wood remains ascribed to *Agathoxylon* Hartig, *Protopodocarpoxyton* Eckhold emend. Vogell. (Coniferales indet.), and basal or eudicotyledonous angiosperms (Perrichot 2005; Philippe et al. 2008). Recently, a preliminary study of Puy-Puy plant–insect interactions was provided (Néraudeau et al. 2020, pp. 8–9), which we develop in greater detail in this work.

A variety of insect taxa have been found in the Puy-Puy Lagerstätte. These taxa include specimens of Hemiptera and Dictyoptera entombed in amber from lithological Unit A1 (Perrichot et al. 2006; Néraudeau et al. 2020) positioned immediately below Unit A2, and from impressions of Odonata, Trichoptera, Dictyoptera, and Neuroptera found in the shale of Unit A2 (Nel et al. 2008; Néraudeau et al. 2020). In addition to insect body fossils, coprolites attributed to termites (Isoptera) have been reported in Unit A2 (Colin et al. 2011; Néraudeau et al. 2020). The Puy-Puy site contains other invertebrate fossils, such as putative nematodes and brachiopods, crustaceans, and annelids or cephalochordates, as well as vertebrate remains that include shark eggs and theropod feathers (Vullo et al. 2013; Néraudeau et al. 2020).

The depositional environment of the plant-bearing clay from Puy-Puy was coastal, consisting of continental and marine influences, but deposited in a regionally protected area (Néraudeau et al. 2005, 2020; Girard et al. 2011). Notably, the P1 plant assemblage contains

Ploufolia specimens, an aquatic angiosperm affiliated to Nymphaeales, suggesting continental freshwater input rather than solely a marine littoral influence. Moreover, our interpretation of the well-preserved leaves is more compatible with minimal transportation of the plant material prior to deposition in an area likely adjacent to a forest. Nevertheless, the presence of a marine to brackish fauna of brachiopods, decapods, and sharks indicates that the depositional environment was a paralic basin with a marine connection, suggesting that the deposit was a parautochthonous continental plant assemblage (Vullo et al. 2013; Breton et al. 2015; Néraudeau et al. 2020). Based on the co-occurrence of freshwater plants with marine/brackish organisms, we cannot exclude that the taphocoenosis is composed of plants from several (but close) areas. During the late Albian to early Cenomanian, the Puy-Puy forest probably developed during a period when the climate was warm (Néraudeau et al. 2020). Such an interpretation is supported by plants, such as *Glenrosa* Watson & Fisher or *Frenelopsis* Schenk emend. Wats that possess leaf stomata exhibiting morphologies adapted for a xeric environment (Gomez et al. 2002). Nevertheless, in Unit A2 *Glenrosa* is rare and *Frenelopsis* is absent. In addition, echinoids and vertebrates from the lower Cenomanian of the Tonny-Charente region exhibit Mediterranean–Tethyan affinities and similarities with low latitude, warm-temperate faunas (Vullo et al. 2003; Néraudeau et al. 2005, 2020; Vullo and Néraudeau 2008).

3. Material and methods

For the present study, 1605 leaves of angiosperms, leafy axes, leaves, and leaflets of gymnosperms that include Bennettitales, Coniferales, and Ginkgoales, as well as fragmented pinnae and pinnules of ferns were analyzed for plant–insect interactions. This material originated from the lower Cenomanian lithological bed P1 in unit A2. Only those specimens that were well preserved and allowed observation of more than 50% of the lamina were selected for examination. Most of the plant specimens and insect interactions were preserved as compressions or impressions that display exceptional preservation typical of a Lagerstätte site.

Identification of most of the plants was carried out *in situ*. However, some specimens could not be identified at the genus or family level. Those specimens that were taxonomically indeterminate were assigned to a paleobotanical morphotype, based on the system of Le Diuron (2005). For identification of plant–insect interactions, the guide of Labandeira et al. (2007) was used, supplemented by updates in subsequent publications. Based on this guide, each interaction morphotype was assigned to a specific damage type (DT), followed by an identifying number. Each DT was grouped with similar DTs into a functional feeding group (FFG) that we identified as hole feeding, margin feeding, skeletonization, surface feeding, oviposition, piercing and sucking, galling, mining, and pathogens, representing the nine FFGs present at the Puy-Puy Quarry. In addition, each DT has a DT host-plant specificity (HS) value, indicated by 1 (generalized), 2 (intermediate specificity), and 3 (specialized), based on the specificity relationships that the plant hosts have for each DT interaction. It is important to note that the modern insect–host-plant specificities of polyphagous, oligophagous, and monophagous diets are similar, respectively, to the DT host-plant specificity values of generalized, intermediate specificity, and specialized used for fossil material. However, for fossil material, DT host-plant specificity (HS) is based on the specificity of the DT distribution on plant species, rather than the situation for modern material, where direct evidence for the specificity level of insect feeding on host-plants is determined by the breadth of feeding patterns of extant herbivorous insects (Xiao et al. 2021a).

3.1 Evaluation of sample size

The interaction data were sample standardized and statistically treated with R i386 3.6.0 (R Development Core Team) and R Commander, following the procedure of Gunkel and Wappler (2015). The richnesses of different interactions were analyzed and compared by calculating their rarefactions and their respective

standard deviations based on Heck et al. (1975). Rarefactions were calculated for all DTs, FFGs, and specialized DTs. The richnesses of interactions also were calculated for different species or groups of plants that exceeded 10 specimens (Knor et al. 2012; Adroit et al. 2021).

4. Results

4.1. The Puy-Puy plant assemblage

The 1605 studied plant specimens consisted overwhelmingly of leaves, but also fruits, seeds, and cones. Gymnosperm specimens constituted 62.6% of the total analyzed plant assemblage and were represented principally by *Dammarophyllum* Velen. and *Geinitzia* Endl., followed by angiosperms that expressed a distinct dominance of *Eucalyptolaurus* comprising 32.4% of the total, and pteridophytes consisting of 5% of the plant assemblage that was represented mostly by *Osmunda* L. The Puy-Puy plant study is the only extensive, major plant assemblage examined to date that has gymnosperms, representing about two-thirds of specimens, angiosperms representing about one-third of specimens, and ferns, representing 5% that are all present in the same deposit (Table 2).

The most abundant taxon is *Dammarophyllum* sp. (Coniferales, incertae sedis), with a total of 744 specimens, approaching almost half of the specimens studied (46.3%). The second most abundant taxon was *Eucalyptolaurus depreii* (Laurales: Lauraceae) with 285 specimens and 17.8% of the total plant assemblage, followed by *Geinitzia reichenbachii* (11.3%) (Coniferales: Geinitziaceae). No other taxon exceeds 3% of the plant assemblage analyzed, and all other taxa together constitute 24.5% of the taxa and morphotypes (Table 2). Overall, this plant assemblage is dominated by gymnosperms (62.24% of specimens) and angiosperms (32.7%), whereas ferns (5.0%) form a minor element (Table 2; Appendix S1).

Among the analyzed leaves, the presence of *Ploufolia* sp. (three specimens), an aquatic angiosperm related to Nymphaeales (Sender et al. 2010), is notable for its paleoenvironmental implications. For gymnosperms, in addition to conifers, the presence of Bennettitales of the genus *Zamites* Brongn. is prominent, as well as the ginkgoalean leaf *Eretmophyllum*. In addition to leaves, there were many fewer specimens of seeds (13 specimens), conifer cones (23 specimens), and an angiosperm fruit (Table 2), which were analyzed for plant–insect interactions.

4.2. Plant-arthropod interactions

A wide variety of arthropod damage was encountered on the Puy-Puy plants. The damage occurred on ferns and broadleaved conifers (Figure 3), lanceolate, entire-

margined angiosperm (Figure 4), and wider, symmetrical and asymmetrical leaved angiosperms (Figure 5). The damage consists of hole feeding (Figures 4C; 5A), margin feeding (Figure 5A,F), surface feeding (Figure 3C), oviposition (Figures 3D; 4A,D; 5E), piercing and sucking (Figure 3A), mining (Figures 3E; 4C), and galling (Figures 4E–G; 5C). Much of this damage is very well preserved, and is represented by distinctive differences in the color, texture, microtopography, and micromorphological detail between the damage and the ambient unaffected plant tissue.

4.2.1. By major plant hosts

Angiosperms were the group in the plant assemblage with the highest incidence of plant–insect interactions (DTs), in which 34% of the specimens displayed evidence of herbivory (Table 2). The incidence of herbivory was 17.8% of specimens for gymnosperms, and 6.3% for pteridophytes. In addition, angiosperms displayed the highest incidence of external damage, consisting of 24.1% of all specimens, followed by mining (5.4%), oviposition (1.4%), and piercing and sucking (1%). Gymnosperms, despite presenting the lowest incidence of all interactions, presented the highest incidence of specialized damage (12.9%), although this is a value close to that of angiosperms (12%). Gymnosperms have almost twice the percentage of galls (8.7%), than angiosperms (4.7%).

By contrast, pteridophytes have low levels of interactions for all FFGs compared to gymnosperms and angiosperms. Conspicuous because of their absence, are low values for oviposition, piercing and sucking, and galling for these groups. Ectophytic feeding, or external foliage feeding, displayed the highest incidence of consumption, on pteridophytes with a 6.3% incidence, dominated by hole feeding, and constituting a value slightly higher than that of gymnosperms (6.2%), but this is well below that of angiosperms (24.1%).

4.2.2 By functional feeding group (FFG) and damage type (DTs) frequency

In the plant assemblage, 422 individual interactions were identified (Appendices S1 and S2) representing a total of 71 DTs (Figures 3–5 and Appendix S1) that belong to 8 FFGs (Appendix S2). There are 11 DTs of hole feeding; 5 DTs of margin feeding; 2 DTs of skeletonization; 7 DTs of surface feeding; 5 DTs of oviposition; 5 DTs of piercing and sucking; 13 DTs of galling; 20 DTs of mining; and 3 DTs of pathogens (Figures 3–5; Tables 2 and 3). Ectophytic damage, consisting of hole feeding, margin feeding, skeletonization, and surface feeding, accounted for more than half of the identified interactions (52.03%), followed

by the endophytic damage of galling (15.54%) and mining (20.94%), and ectoendophytic damage of piercing and sucking (4.73%), oviposition (4.05%).

Regarding the incidence of damage in the plant assemblage, 22.2% of the analyzed leaves (or leaf fragments) presented some type of plant–arthropod interaction, scored as at least one DT. The most frequent FFG was surface feeding, present in 7.10% of the plant specimens followed by galling (6.8%), mining (3.7%), margin feeding (3.2%), and hole feeding (2.7%); the least frequent FFGs were piercing and sucking (0.8%), oviposition (0.5%), and skeletonization (0.4%) (Tables 2 and 3). Evidence of pathogens was only present 0.003% of the plant specimens.

4.2.3. By surface area herbivorized

The total surface area measured was 11,569.60 cm² and the herbivorized leaf area is 128.59 cm², resulting in an herbivory index of 1.11% (Appendices S3 and S5). The first to third FFGs with the herbivorized surface area are surface feeding (31.85%), margin feeding (17.76%), and mining (15.86%) (Appendix S3), representing 65.47% of all surface area consumed. This pattern indicates that, for herbivorized surface area, a combination with a clear predominance of ectophytic (60.71%), and to a minor extent also endophytic feeding classes (28.70%) were the dominant consumers. The fourth to sixth ranked FFGs of galling (12.84%), hole feeding (9.66%), and pathogens (5.80%) are responsible for an additional 28.30% of surface area eaten. The seventh to ninth ranked FFGs of oviposition (2.90%), piercing and sucking (1.84%), and skeletonization (1.44%) are inconsistent.

4.2.4. By feeding event occurrences

Feeding event occurrences consists of 1292 separate feeding events in the total dataset (Appendices S1 and S4). When these data are partitioned by FFG, the first to third ranks are galling (37.69%), surface feeding (23.22%), and margin feeding (11.84%), accounting for 72.75% of feeding event occurrences, which display a pattern somehow comparable to DT frequency. Differences in rank order of FFGs suggesting that DT presence on a single leaf is tracking the multiple feeding event occurrences on the same leaf. The remaining ranks are distributed as follows: hole feeding (10.22%), piercing and sucking (2.01%), oviposition (5.65%); mining (5.80%), pathogens (2.36%), and skeletonization (0.93%).

4.2.5. By herbivore specificity for plant taxa

The examined DTs that have more three occurrences are classified into generalized (1), intermediated (2) or specialized (3) host–plant specificities (Xiao et al.

Table 2. Proportional representation of herbivorized specimens and their functional-feeding-group representation for the upper Albian–lower Cenomanian quarry of Puy-Puy, at Tonnyay-Charente (Charente-Maritime, SW France).

Foliar taxon (abundance ranked)	No. specimens in flora	Proportional representation in flora	No. herbivorized specimens in flora	Proportional representation of herbivorized specimens in flora											Pathogen
				with damage	external damage	Margin feeding	Hole feeding	Skeletonization	Surface feeding	Galling	Mining	Piercing & sucking	Oviposition		
<i>Dammarophyllum</i> sp.	744	46.36	175	23.52	7.93	1.21	0.94	.00	6.18	11.56	4.17	0.94	0.40	.00	
<i>Eucalyptolaurus dapeirii</i>	285	17.76	87	30.53	18.60	8.42	4.91	1.40	8.42	4.56	7.02	0.70	1.05	.00	
<i>Geinitzia reichenbachii</i>	182	11.34	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type 3-lobed	48	2.99	24	5.00	39.58	8.33	8.33	4.17	27.08	2.08	14.58	.00	.00	0.04	
cf. <i>Osmunda cretacea</i>	43	2.68	2	4.65	4.65	2.33	.00	.00	2.33	.00	.00	.00	.00	.00	
Angiosperm Type 6	41	2.55	12	29.27	19.51	7.32	7.32	.00	37.50	2.44	.00	2.44	2.44	0.05	
Angiosperm Type 9	32	1.99	18	56.25	56.25	6.25	21.88	.00	37.50	9.38	.00	.00	.00	.00	
Angiosperm indet.	29	1.81	7	24.14	17.24	3.45	10.34	.00	3.45	6.90	.00	.00	.00	.00	
<i>Weichsella</i> sp.	26	1.62	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type 7	17	1.06	5	29.41	29.41	.00	.00	.00	29.41	.00	.00	.00	.00	.00	
Angiosperm Type long	15	.93	1	6.67	.00	.00	.00	.00	.00	.00	.00	6.67	.00	.00	
Angiosperm Type i	10	.62	5	5.00	4.00	3.00	1.00	.00	2.00	1.00	.00	.00	.00	.00	
<i>Zamites</i> sp.	10	.62	1	1.00	1.00	.00	1.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type j	8	.50	5	62.50	5.00	25.00	.00	.00	37.50	.00	.00	12.50	.00	.00	
Pteridophyte Type 3	7	.44	3	42.86	42.86	.00	42.86	.00	.00	.00	14.29	.00	.00	.00	
<i>Glenrosa</i> sp.	6	.37	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type a	4	.25	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type d	4	.25	2	5.00	5.00	.00	5.00	.00	.00	.00	.00	.00	.00	.00	
<i>Dammarites</i> sp.	4	.25	1	25.00	.00	.00	.00	.00	.00	.00	25.00	.00	.00	0.25	
Angiosperm Type	3	.19	1	33.33	33.33	.00	.00	.00	33.33	.00	.00	.00	.00	.00	
<i>Cinnamomum</i>															
Angiosperm Type Q	3	.19	1	33.33	.00	.00	.00	.00	.00	33.33	.00	.00	.00	.00	
<i>Ploufolia</i> sp.	3	.19	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type g	2	.12	2	10.00	10.00	10.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type k	2	.12	2	10.00	5.00	5.00	.00	.00	5.00	.00	.00	.00	5.00	.00	
<i>Cunninghamites</i> sp.	2	.12	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Pteridophyte Type A	2	.12	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type 8	1	.06	1	10.00	.00	.00	.00	.00	.00	10.00	.00	.00	.00	.00	
Angiosperm Type b	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type c	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type e	1	.06	1	10.00	10.00	.00	.00	.00	10.00	.00	.00	.00	.00	.00	
Angiosperm Type f	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type h	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Angiosperm Type m	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Lauraceae indet.	1	.06	1	10.00	10.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
<i>Fretmophyllum</i> sp.	1	.06	0	.00	.00	.00	.00	.00	10.00	.00	.00	.00	.00	.00	
Pteridophyte Type 4	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Pteridophyte Type B	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Fruit indet.	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
winged seed	1	.06	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Conifer Type A	8	.50	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Conifer Type B	8	.50	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Conifer Type C	8	.50	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Seed indet.	13	.81	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Cone Type A	23	1.43	0	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	.00	
Totals and averages	1605	100.00	357	22.24	11.78	3.24	2.74	0.37	7.10	6.79	3.74	0.75	0.50	.003	

% Leaves with



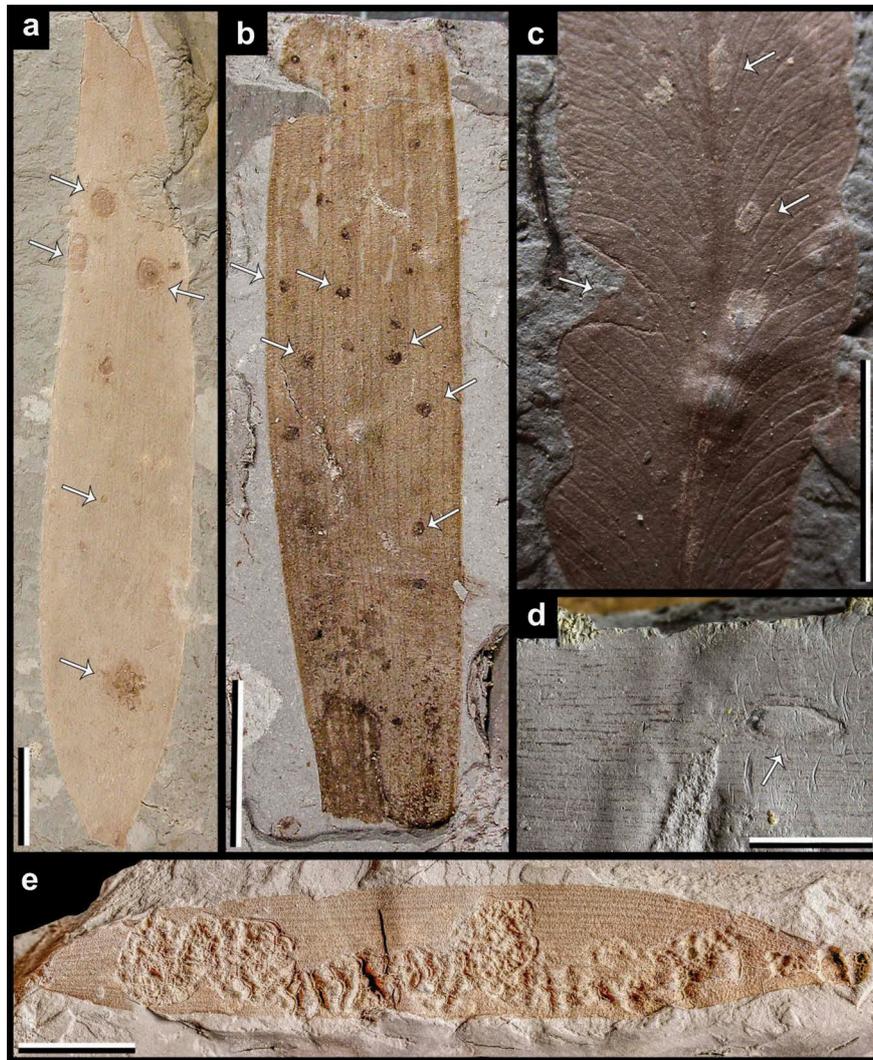


Figure 3. Plant-insect interactions in gymnosperms and pteridophytes from the Puy-Puy Quarry. **A)** *Dammarophyllum* sp. with DT128; scale bar = 1 cm; **B)** *Dammarophyllum* sp. with DT80; scale bar = 1 cm; **C)** *Osmunda cretacea* with DT130; scale bar = 5 mm; **D)** *Dammarites* sp. with DT102; scale bar = 1 cm; **E)** *Dammarophyllum* sp. with DT45; scale bar = 1 cm.

2022a) which is based on the distribution of the DTs on the different relationships of plant hosts (Appendix S6). Four main patterns of host-plant specificity can be summarized here: The first and broadest pattern at Puy-Puy plant assemblage is the dominant percentage of generalist (53.19%), over specialist (29.79%), and intermediated (17.02%) host-plant associations. The second is oviposition, and piercing and sucking, hole feeding associations, which displayed the highest level of host specificity of any FFG at Puy-Puy. The third is the unexpected absence specialized specificity among galling, and the only one specialized DT among mining, as modern gallers and leaf miners usually establish special associations with host plants. The rare host specialisms in galling and mining might be due to the lack of close relationships between gymnosperm and angiosperm lineages. The fourth is the surface feeding displayed by the five generalists, one intermediate specificity, and none specialists. By contrast skeletonization harbors two specialists, one

intermediate specificity, and lack generalists. The rest of the FFGs, such as margin feeding, and pathogen display only one specialists, and few generalists within one or two DTs.

4.3. Sampling issues

The sampling of plant taxa in the Puy-Puy plant assemblage proved to be highly variable when evaluated by rarefaction analyses, which compared the number of specimens to the surface area covered by those specimens. For taxa, such as *Dammarophyllum* sp., *Eucalyptolaurus depreii*, and Angiosperm type 3 lobed, it appears that sample size was sufficient, as these taxa reached asymptotic stability, even though the total plant assemblage was far from being asymptotically stable (Appendix S7). For rarefaction comparisons of plant taxa for the number of damage types (DTs) versus surface area, the same three taxa above displayed asymptotic stability (Appendix S8). With the



Figure 4. Plant-insect interactions in angiosperms from Puy-Puy. **A)** *Eucalyptolaurus deprerii* with DT67; scale bar = 1 cm; **B)** Detail of A (*Eucalyptolaurus deprerii*) with DT67; scale bar = 5 mm; **C)** *Eucalyptolaurus deprerii* with DT65 (lower white arrow) and DT5 (upper white arrow); scale bar = 1 cm; **D)** Angiosperm type k with DT12, 14; scale bar = 1 cm; **E)** *Eucalyptolaurus deprerii* with DT33; scale bar = 5 mm; **F)** Angiosperm type 6 with DT32; scale bar = 5 mm; **G)** Detail of D with DT77 (Angiosperm type k); scale bar = 5 mm.

exception of these three taxa, all other taxa in the plant assemblage were undersampled, as indicated by rarefaction analyses.

When DT richness, as aggregated into FFGs, were rarefied by the number of leaves, a pervasive pattern resulted (Figure 6A). Apparently, none of the functional feeding groups of reached an asymptote, resulting in the conclusion that added sampling was needed to inventory additional DTs for the five FFGs of external foliage feeding (a combined “super FFG” of hole feeding, margin feeding, skeletonization, and surface feeding), oviposition, piercing and sucking, mining, and galling. The rarefaction analysis for all DTs (Figure 6B), incorporating all FFGs, showed an even stronger deficiency in reaching an asymptote, indicating a substantial number of potential DTs were not

accessed in the collection due to insufficient sampling. When only specialized DT host-plant specificity was analyzed (Figure 6C), the pattern was very similar to that of all DTs. Collectively, the rarefaction analyses indicate that the Puy-Puy plant assemblage was substantially undersampled (Figure 6), and only three of the 44 plant species – *Damarophyllum* sp., *Eucalyptolaurus deprerii*, and Angiosperm type 3 lobed – were adequately sampled (Appendices S7–S8).

4.4. Nonmetric multidimensional scaling analyses

The association of insect herbivory and the major plant-host clades of Puy-Puy plant assemblage are shown at the NMDS plot (Appendices S9, S10),

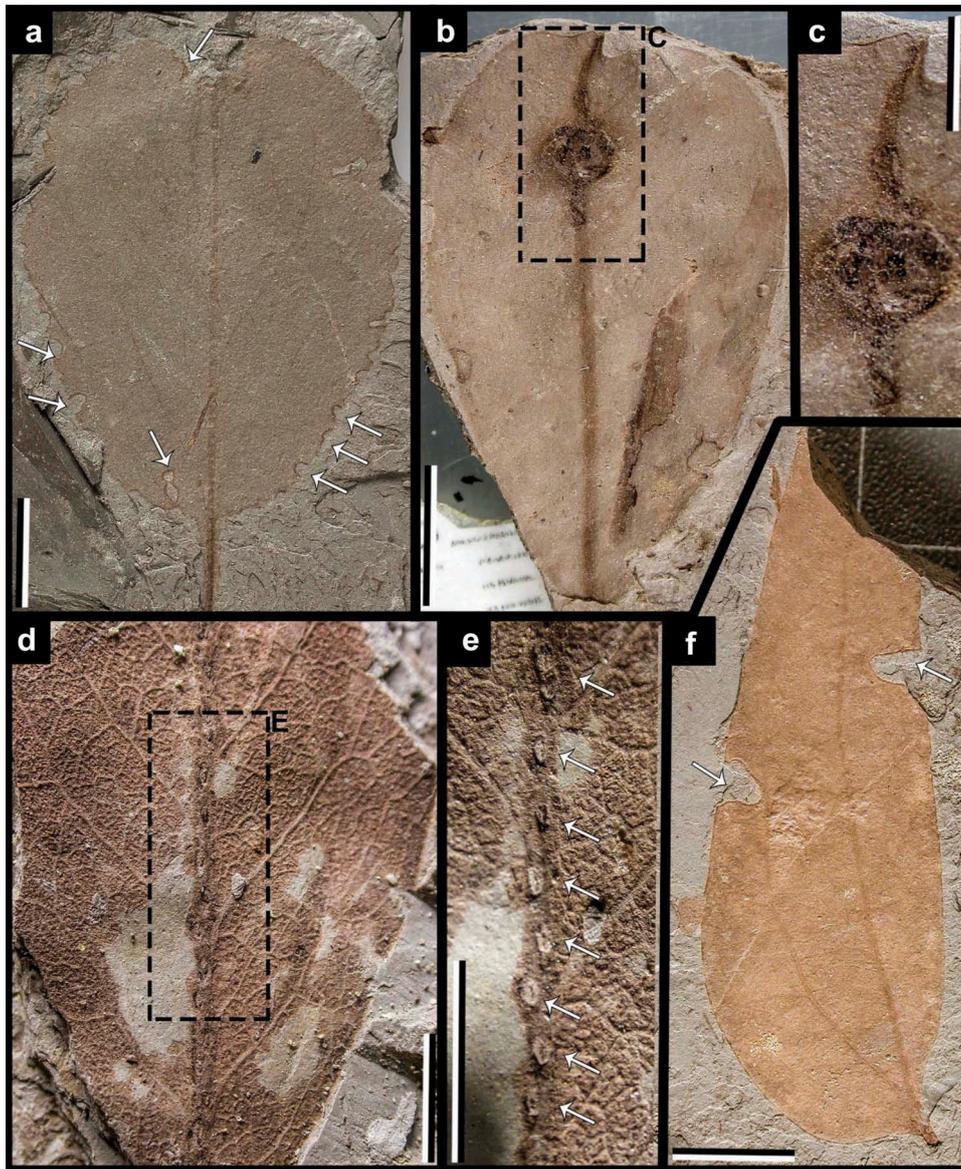


Figure 5. Plant-insect interactions in angiosperms from Puy-Puy. **A)** Angiosperm type g with DT143; scale bar = 1 cm; **B)** Angiosperm type Q with DT33; scale bar = 5 mm; **C)** Detail of B; scale bar = 2 mm; **D)** Angiosperm type k with DT216; scale bar = 5 mm; **E)** Detail of D with DT216 (Angiosperm type k); scale bar = 5 mm; **F)** Angiosperm type d with DT12; scale bar = 1 cm.

which indicates that the plant resources partitioning is influenced by the plant lineages. The gap between confidence ellipses for Filicales, and Pinales and Laurales represents the different insect herbivory patterns for ferns and Laurales, and Pinales (Appendix S9). **However**, the overlap showed between the Magnoliidae with the rest of **the plant hosts** implies the diversified FFGs in Magnoliidae hosts. When we focus on the major three plant species of Laurales, Pinales, and Magnoliidae (Appendix S10), a small overlap is evident between *Eucalyptolaurus depreii* and Angiosperm Type 3 lobed, and close to external foliage feeding, mining and pathogen. The obvious gap between *Dammarophyllum* sp. close to the galling, and piercing and sucking and angiosperm host, points to a highly disparate herbivore component community structure.

5. Discussion

5.1. Herbivory at the Puy-Puy forest

All analyzed plant species or morphotypes in the plant assemblage showed arthropod damage (Table 2). The total proportion of specimens exhibiting one or more DTs in the plant assemblage was 22.2%. However, the type and incidence of damage varied greatly among plant groups. Among the three major plant groups, angiosperms clearly suffered the highest level of damage with 34%, of specimens affected; compared to 17.8% for gymnosperms, about half of that for angiosperms; and 6.3% for pteridophytes, about a third of that for gymnosperms. This distribution could be related to the greater occurrence of leafiness and succulence, and hence palatability, among angiosperms, foliar conditions that are deemed preferable by

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Table 3. Damage-type occurrences (DTO) by functional feeding group, external damage, and specialized damage on the plant hosts from the upper Albian–lower Cenomanian quarry of Puy-Puy, at Tonny-Charente (Charente-Maritime, SW France).

Plant hosts	Hole feeding	Margin feeding	Surface feeding	Skeletonization	Piercing & sucking	Oviposition	Pathogene	Galling	Mining	Total	External	Specialized
Angiosperm Type 3-lobed	4	4	13	2	0	0	2	1	8	34	21	14
Angiosperm Type 6	3	3	3	0	1	1	2	1	0	14	9	6
Angiosperm Type 7	0	0	5	0	0	0	0	0	0	5	5	0
Angiosperm Type 8	0	0	0	0	0	0	0	1	0	1	0	0
Angiosperm Type 9	7	2	14	0	0	0	0	3	0	26	23	2
Angiosperm Type <i>Cinnamomum</i>	0	0	1	0	0	0	0	0	0	1	1	0
Angiosperm Type d	2	0	0	0	0	0	0	0	0	2	2	0
Angiosperm Type e	0	0	1	0	0	0	0	0	0	1	1	0
Angiosperm Type g	0	3	0	0	0	0	0	0	0	3	3	0
Angiosperm Type i	0	3	2	0	0	0	0	1	0	6	5	1
Angiosperm Type j	0	2	3	0	1	0	0	0	0	6	5	0
Angiosperm Type k	0	1	1	0	0	1	0	0	0	3	2	0
Angiosperm Type long	0	0	0	0	1	0	0	0	0	1	0	0
Angiosperm Type Q	0	0	0	0	0	0	0	1	0	1	0	1
Angiosperm indet.	3	1	1	0	0	0	0	2	0	7	5	2
<i>Dammarites</i> sp.	0	0	0	0	0	0	1	0	1	2	0	2
<i>Dammarophyllum</i> sp.	7	10	48	0	7	3	0	84	32	191	63	128
<i>Eucalyptolaurus depreii</i>	15	27	24	4	2	3	0	13	20	108	66	36
Lauraceae indet.	0	0	1	0	0	0	0	0	0	1	1	0
cf. <i>Osmunda cretacea</i>	0	1	1	0	0	0	0	0	0	2	2	1
Pteridophyte Type 3	5	0	0	0	0	0	0	0	1	6	5	1
<i>Zamites</i> sp.	1	0	0	0	0	0	0	0	0	1	1	0
Total	47	57	118	6	12	8	5	107	62	422	220	194
FFG %	11.12	13.51	7.10	1.42	2.84	1.89	0.12	25.36	14.69	100		

615 herbivorous arthropods, rather than the more coriaceous foliage of pteridophytes and gymnosperms that possess more structural tissues (Ruhnke et al. 2009; Caldwell et al. 2016). Gymnosperms also likely to have had greater physical and chemical defenses than angiosperms, a condition that has been demonstrated for modern conifers (Moreira et al. 2012), cycads (Schneider et al. 2002), *Ginkgo* L. (Mohanta et al. 2012), and gnetaleans (González-Juárez et al. 2020). These differential herbivory values are consistent with other studies suggesting that the higher palatability of angiosperms results in higher herbivory pressure compared to gymnosperms (Chabot and Hicks 1982; Farrell 1998; Wardle et al. 2002; Augusto et al. 2014)

620 Alternatively, although angiosperm origins remains a contentious issue (Wang 2010; Doyle 2012; Li et al. 2019), there is broad agreement regarding their pattern of early diversification and ecological extension into new environments. The first extensive records of angiosperm plant assemblages are from the Aptian–Albian interval (125–100 Ma) at the beginning the Cretaceous Terrestrial Revolution (KTR) that initiated global Phase 4 of arthropod herbivore expansion (Labandeira 2006; McCoy et al. 2021). This event is represented by plant assemblages such as those from the Dakota Formation (Xiao et al. 2021a, 2021b, 2022a, 2022b, 2022c). During this time, arthropods shifted their herbivory strategies by colonizing new plant groups, particularly angiosperms, and became integrated within ecosystems hosting new plant

645 lineages. For the Puy-Puy plant assemblage, although gymnosperms remain the dominant group and represent approximately two-thirds of the assemblage compared to one-third for angiosperms, the clear preference of arthropods was with the latter.

650 Nine FFGs are represented at Puy-Puy, with mining being the most diverse FFG (20 DTs) in richness, followed by galling (13 DTs) and hole feeding (11 DTs). However, the diversity of DTs contrasts with that of the DT feeding event occurrences and herbivorized area (Appendices 2 and 4). Despite the high DT richness of mining, 15.86% of plant specimen surface area exhibited mining damage, and galling was observed approaching almost twice the level of mining, at 12.84%. The DT host specificity index shows that specialized damage, at about 29.79%, is equivalent to less specialized damage, such as external damage (11.8%). It is usually assumed that specialized interactions are equated with monophagous insects, interactions of intermediate specificity equated with oligophagous insects (Currano et al. 2008, 2010; Adroit et al. 2016), while more generalized interactions are usually equated with polyphagous insects (Currano et al. 2008). However, these three DT plant-host specificity index categories have never been tested for equivalence to their counterparts of modern insect diet categories, and the fossil–modern correspondences likely are approximate at best.

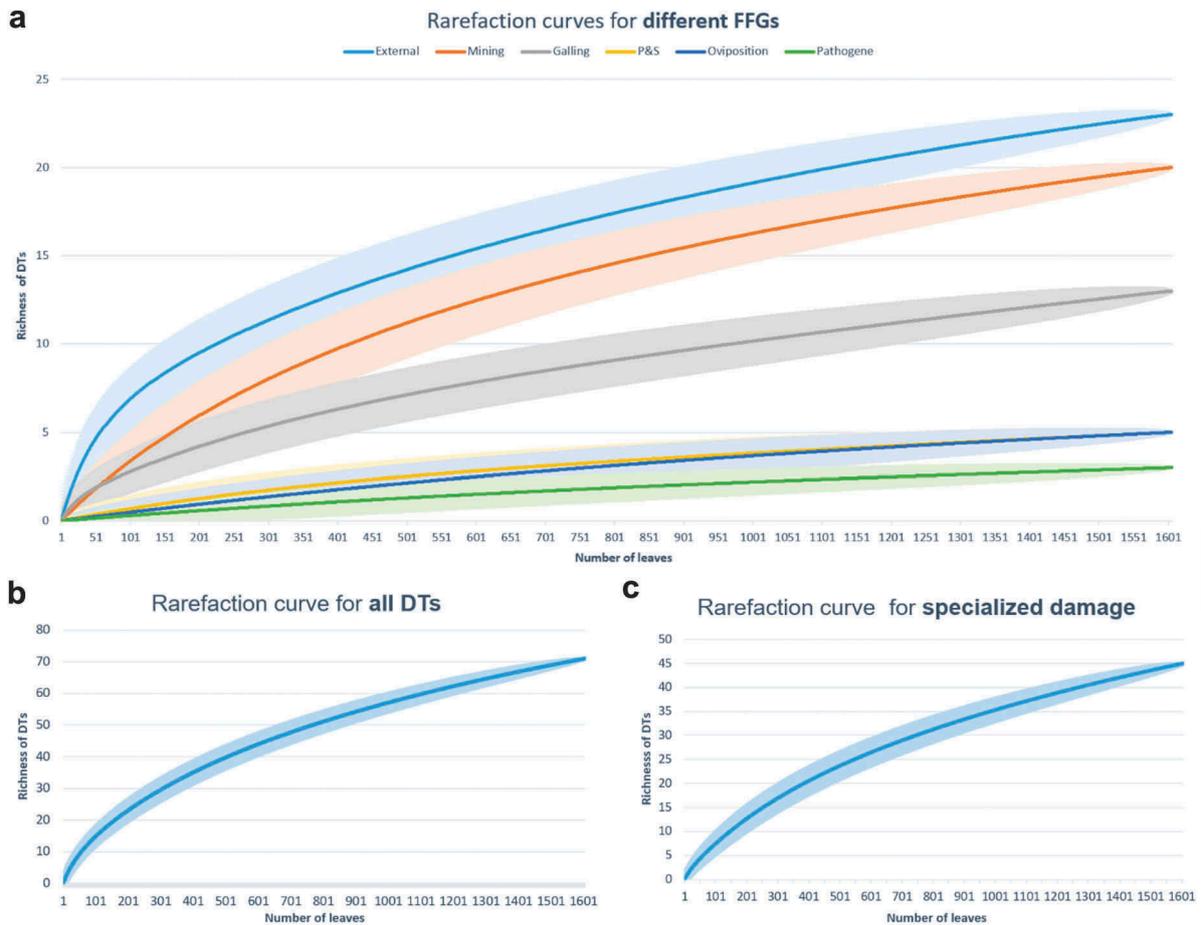


Figure 6. Rarefaction curves for Puy-Puy plant-insect interactions. from data for different FFGs (A), for all DTs (B), and for specialized damage (C).

675 At the Puy-Puy quarry, a variety of herbivorous
 insect taxa would have coexisted with the local plant
 assemblage. Insect specimens co-occurring in these
 deposits have been identified representing five orders:
 Odonata (dragonflies and damselflies), Dictyoptera
 680 (cockroaches and termites), Hemiptera (cicadas,
 aphids, scale insects, planthoppers, bugs), Neuroptera
 (antlions, lacewings, and relatives), and Trichoptera
 (caddisflies) (Perrichot et al. 2006; Nel et al. 2008;
 Colin et al. 2011; Néraudeau et al. 2020). Most of
 685 these orders contain few herbivorous lineages, but
 the diversity of observed interactions in the plant
 assemblage suggests the presence of additional orders
 of insects, such as Diptera (flies, e.g. DT120),
 Coleoptera (beetles, e.g. DT71), and Lepidoptera
 690 (moths, e.g. DT41, DT45, DT111). Linking the culprits
 of each interaction requires knowledge of how particu-
 lar groups of herbivores feed on plants, and estab-
 lishment of the entomological culprits for the more
 obvious and recognizable DTs would require
 695 a detailed analysis of the damage. However, even
 though a substantial number of plant specimens have
 been analyzed, rarefaction curves (Figure 6A, B, and
 C) show that the total number of potential DTs have

not been completely recovered, indicating that if
 a greater number of specimens were inventoried,
 700 new DTs would be discovered.

5.2. Paleoenvironmental and paleoclimatic implications

In most of Albian–Cenomanian plant-rich beds from
 western France, assemblages from paralic environ-
 705 ments with strong marine influence are dominated
 by conifers and ferns whereas angiosperms are poorly
 represented or absent (Néraudeau et al. 2005, 2009;
 Gomez et al. 2008; Moreau et al. 2014, 2017). Coastal
 floras from salt marsh-type habitats are characterized
 710 by conifer-dominated assemblages like
Eretmophyllum–Nehvizdyella, *Frenelopsis–Alvinia*
 (Uličný et al. 1997; Kvaček 2000; Kvaček et al. 2005)
 that commonly include also taxa such as
Brachyphyllum Brongn., and *Glenrosa* (Gomez et al.
 715 2008; Moreau et al. 2014). These taxa display xero-
 morphic features that include the presence of fleshy
 shoots, small leaves adpressed against axes, thick cuti-
 cles, stomatal crypts and sunken stomata (Gomez et al.
 720 2008; Moreau et al. 2015). Plants from these

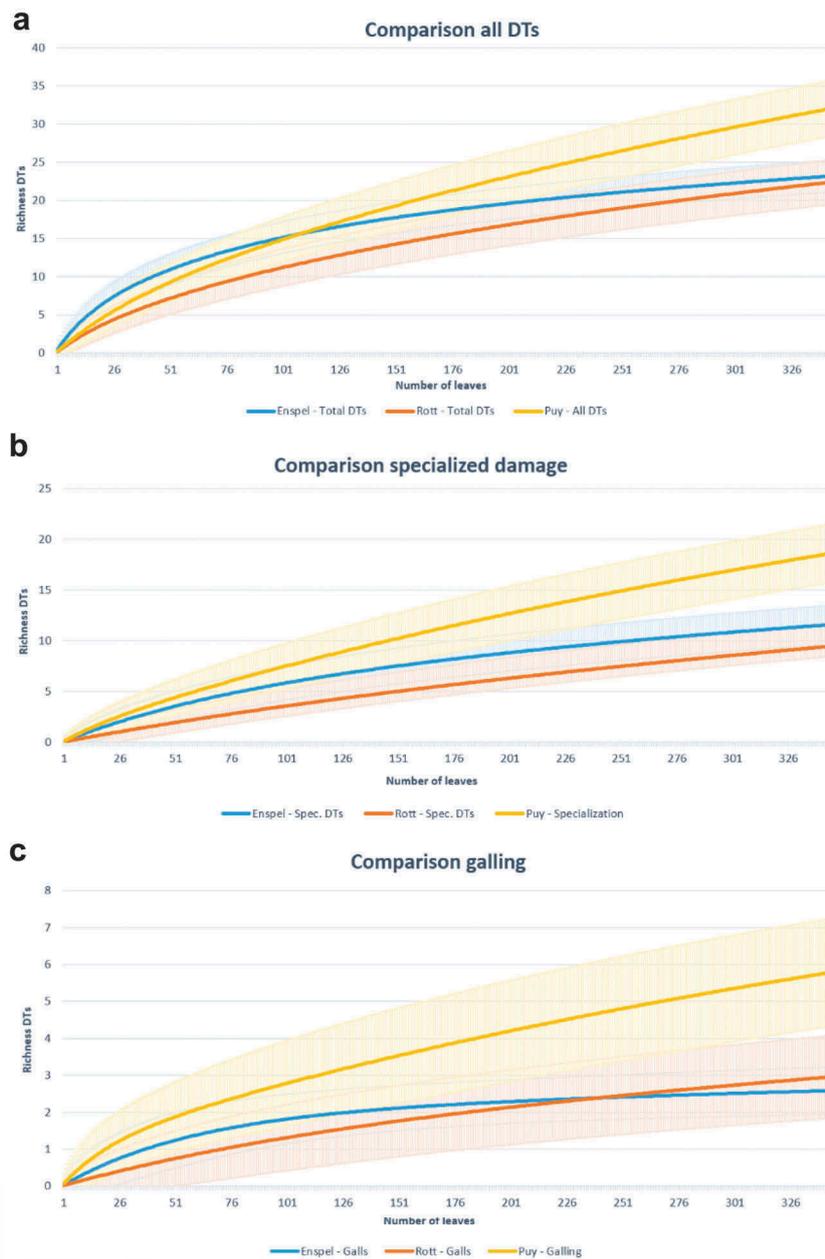


Figure 7. Rarefaction curves for Puy-Puy plant–insect interactions compared to the European Paleogene plant assemblages of Enspeil and Rott. Comparisons include all DTs (A), specialized damage (B), and galling (C).

environments were adapted to withstand intense sunlight and challenging coastal environments that exposed tissues to desiccating conditions amid an environment of saline seawater. By contrast, the paucity of xerophytic conifers and the abundance of angiosperms in the plant-rich shale from Unit A2 of the Puy-Puy Quarry suggests a protected brackish coastal environment heavily influenced by inland freshwater.

Vertebrate and invertebrate data from the Cenomanian of the surrounding Puy-Puy region has showed affinities with low latitude taxa (Vullo et al. 2003; Néraudeau et al. 2005, 2020; Vullo and Néraudeau 2008). The elevated diversity and abundance of plant–insect interactions, as indicated by

DTs, in the Puy-Puy paleoforest could be an indication of relatively high temperatures. Previous analyses of plant–insect interactions in the fossil record have found positive correlations between temperature and the diversity and intensity of interactions (Wilf and Labandeira 1999; Labandeira et al. 2002).

In addition to evidence for relatively high temperatures, the elevated occurrence of galls at Puy-Puy, representing 14 DTs and a presence in 6.9% of plant specimens, could be related to arid ambient environments (Fernandes and Price 1988). The abundance and diversity of galls is related to either regional arid environments, or local xeric conditions, such as the tops of forest canopies, in both extant and extinct ecosystems (Fernandes and Price 1992; Price et al.

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1998; Cuevas-Reyes et al. 2004, 2006; Wappler 2010; Moreno-Domínguez 2018). Local environmental conditions of this paleoforest are unclear nevertheless, some of the most abundant species, such as *Geinitzia reichenbachii* are represented by more than 10% of the examined plant specimens and possess a morphology and histology resilient against intense sunlight, hot temperatures, saliferous winds, and aridity (Moreau et al. 2021). Additionally, the less frequent occurrence of other genera such as *Glenrosa* sp. also have been linked to conditions of aridity (e.g. Gomez et al. 2002). The presence of species with resistance to aridity, elevated temperature, high solar exposure, as well as the great diversity of galls, would indicate presence of a xeric, ground based habitat in the Puy-Puy paleoforest analogous to those of today (Fernandes and Price 1988), or at the tops of tree canopies, similar to that of tropical Amazonian forest in present-day Brazil (Julião et al. 2014). For greater resolution of the environmental conditions at the Puy-Puy paleoforest, additional data will be needed.

Initially, the Puy-Puy plant assemblage was interpreted as accumulating within floodplain or levee deposits, as shown also by the occurrence of *Eucalyptolaurus* and *Debeya*, typical alluvial plain elements (e.g. Coiffard et al. 2006, p. 498). More recent studies have interpreted the Puy-Puy deposit as representing a coastal environment with continental and marine influences, and as a protected area with freshwater input (Néraudeau et al. 2005, 2020). The Charente-Maritime is considered to have been located at a latitude of 35°N during the Upper Cretaceous (Philip et al. 1993). Based on $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotopic data of bivalves from this area, Videt (2004) demonstrated that the climate of the Upper Cretaceous was tropical and strongly seasonal. Additionally, the low degree of fragmentation of leaves and leafy axes, as well as the superior preservation of delicate structures, such as flowers and inflorescences (Néraudeau et al. 2020), suggest short transport distances. Consequently, the Puy-Puy plant assemblage is best interpreted as a coastal forest occurring in a relatively warm climate, probably with xeric habitats or characterized by periods or seasons dominated by xeric conditions. Given this environmental context, the Puy-Puy paleoforest likely provided a secure and protected environment for many insect taxa that inhabited shady areas in tree canopies, higher rates of humidity attributable to the ambient vegetation, and abundant food resources.

5.3. Comparisons with another plant-insect assemblages of similar age

Another study has analyzed plant-insect interactions of the slightly older, latest Albian Rose Creek plant assemblage from southeastern Nebraska, U.S.A. (Xiao

et al. 2022b, 2022c). The Puy-Puy study provides an objective and quantitative comparison with this plant assemblage. The Puy-Puy plant assemblage has 44 plant species/morphotypes as hosts supporting 71 DTs assigned to 8 FFGs (excluding pathogens); by contrast, the North American Rose Creek plant assemblage has 49 plant species/morphotypes with 114 DTs assigned to 11 FFGs (including pathogens). Although the Puy-Puy paleoforest presents 62.3% of the DTs compared to the Rose Creek plant assemblage of similar age (Xiao et al. 2022b), it has an elevated diversity of DTs compared to Cenozoic European plant assemblages. These plant assemblages include the diverse Eocene Enspel locality containing 39 different DTs and the Oligocene Rott locality with 55 DTs in Germany, and the Pleistocene Bernasso locality with 39 DTs from France (Wappler 2010; Gunkel and Wappler 2015; Adroit et al. 2016) (Figure 7). The richness in plant-insect interactions at Puy-Puy over younger Cenozoic plant assemblages suggests that elevated insect speciosity was associated with a mature and complex food web (also see Dunne et al. 2014). In addition, evidently the Puy-Puy forest was well integrated biogeographically, since its diversity and specificity of interactions is comparable to other isolated ecosystems of the Mesozoic of Europe (Santos et al. 2021), but less than that of an equivalent but more completely sampled Rose Creek locality in midcontinental North America (Upchurch and Dilcher 1990).

Comparisons of the rarefaction curves of the Puy-Puy interactions, or DTs, with those of Rott and Enspel show that under complete sampling conditions, Puy-Puy would be slightly more diverse in total DTs and specialized DTs (*sensu* Labandeira et al. 2007) (Figure 7A and B), and notably richer in galling (Figure 7C), approaching the sampling levels at Rose Creek. Considering the positive correlation between galling and xeric habitat conditions (Fernandes and Price 1992; Price et al. 1998), the heightened diversity of galls at Puy-Puy likely is due to a more arid, seasonally xeric, or warmer habitat compared to the Rott and Enspel plant assemblages. Nevertheless, to address this question in greater detail, additional paleoenvironmental studies are necessary. The abundance and diversity of interactions at the Puy-Puy plant assemblage suggests a paleoforest with integrated ecological relationships between plants and insects, suggesting a mature ecosystem. Currently, this study represents the third quantitative, statistical study of mid-Cretaceous plant-insect interactions, and the first from Europe. Additional studies of plant-insect associations from this time interval are needed to indicate how general the conclusions are regarding the plant-insect interactions for this several million-year-long stretch of time during the mid Cretaceous.

6. Conclusions

The Puy-Puy plant assemblage exhibits a wealth of plant–insect interactions, consisting of 71 different damage types assigned to 9 functional feeding groups, 1292 feeding event occurrences, and a herbivory index of 1.11. Although gymnosperms are the dominant plant group, it is angiosperms that have the highest incidence of interactions and thus are the most herbivored. During the mid-Cretaceous angiosperms were still undergoing an evolutionary radiation of ecological expansion, and evidently insects already were diversifying their feeding options on angiosperms rather than gymnosperms. Importantly, mining and galling were the two most diverse types of interactions in the Puy-Puy plant assemblage, and the elevated diversity of these endophytic interactions indicate a mature forest with well-established ecological relationships between plants and their insect herbivores. The abundance of galling could be related to arid or seasonally **electric conditions**, at least locally, conducive to the presence of thermophilic plants such as *Geinitzia reichenbachii* and *Glenrosa* sp., whose anatomy was consistent with this warm period in earth history.

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Data availability

The data supporting the results are included in this article as supplementary file data and can be accessed here DOI: [10.5281/zenodo.6535148](https://doi.org/10.5281/zenodo.6535148)

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