No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France

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Insect herbivores are considered vulnerable to extinctions of their plant hosts. Previous studies of insect-damaged fossil leaves in the US Western Interior showed major plant and insect herbivore extinction at the Cretaceous–Palaeogene (K–T) boundary. Further, the regional plant–insect system remained depressed or ecologically unbalanced throughout the Palaeocene. Whereas Cretaceous floras had high plant and insect-feeding diversity, all Palaeocene assemblages to date had low richness of plants, insect feeding or both. Here, we use leaf fossils from the middle Palaeocene Menat site, France, which has the oldest well-preserved leaf assemblage from the Palaeocene of Europe, to test the generality of the observed Palaeocene US pattern. Surprisingly, Menat combines high floral diversity with high insect activity, making it the first observation of a ‘healthy’ Palaeocene plant–insect system. Furthermore, rich and abundant leaf mines across plant species indicate well-developed host specialization. The diversity and complexity of plant–insect interactions at Menat suggest that the net effects of the K–T extinction were less at this greater distance from the Chicxulub, Mexico, impact site. Along with the available data from other regions, our results show that the end-Cretaceous event did not cause a uniform, long-lasting depression of global terrestrial ecosystems. Rather, it gave rise to varying regional patterns of ecological collapse and recovery that appear to have been strongly influenced by distance from the Chicxulub structure.

Keywords: Palaeocene; Europe; herbivory; plant–insect interactions; end-Cretaceous extinction

1. INTRODUCTION

The Palaeogene was a time of profound reorganization of the biosphere, following the catastrophic Cretaceous–Palaeogene (we use the traditional acronym K–T) bolide impact at 65.5 Ma (e.g. Jablonski & Raup 1995; Alroy 1999; Pearson et al. 2002; MacLeod et al. 2006; Benton & Harper 2009). Among the many consequences was substantial turnover for North American plants and herbivorous insects (Tschudy et al. 1984; Wolfe & Upchurch 1986; Johnson et al. 1989; Hotton 2002; Labandeira et al. 2002a,b; Nichols 2002; Wilf & Johnson 2004), expressed in a general pattern of low-diversity floras throughout the 10 Myr of the Palaeocene and a nearly complete loss of specialized insect-feeding damage on leaves until the last approximately 1 Myr of the Palaeocene (Wing et al. 1995; Labandeira et al. 2002a,b; Wilf et al. 2006; Currano et al. 2008).

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There are two known exceptions to the general Palaeocene depression: an extremely diverse (used here synonymously with rich, speciose) flora with little insect damage, from Castle Rock, Colorado, and a typically depauperate flora with extremely rich and abundant insect damage, from Mexican Hat, Montana (Johnson & Ellis 2002; Ellis et al. 2003; Wilf et al. 2006). However, at no time during the Palaeocene was there a diverse flora together with diverse insect damage in North America, indicating either depressed or decoupled development of plants and insect herbivores in perhaps unbalanced ecosystems (Wilf et al. 2006; Currano et al. 2008; Wilf 2008). These patterns have been recorded and quantified as a certain range of feeding-type diversity and specialized damage (e.g. insect mining) on Maastrichtian through Eocene floras in the Western Interior of North America (Labandeira et al. 2002b; Wilf et al. 2006).

The extent of this ecological catastrophe in terrestrial ecosystems outside the Western Interior remains poorly known because the quantity and stratigraphic resolution of continental sequences with abundant plant or insect fossils covering the relevant time intervals diminishes dramatically elsewhere (Nichols & Johnson 2008).
Palaearctic floristic patterns for the Northern Hemisphere outside North America have been described by various authors (e.g. Wolfe 1985; Mai 1995; Collinson 2000; Tiffney & Manchester 2001; Collinson & Hooker 2003; Akhmetiev & Beniamovski 2009). Herein, we present the first analysis of fossil plant–insect interactions from the Palaearctic of Europe. Our data derive from the middle Palaearctic Menat fossil site (Menat basin, Puy-de-Dôme, France; approx. 60–61 Ma), which has the European macroflora that is stratigraphically closest to the K–T event (Piton 1940; Mai 1995; we note that there are no suitable macrofloras known from the European terminal Cretaceous). In sharp contrast to the US data, we find high values of insect-feeding damage coupled with elevated floral richness. These results, though from a single site, are the first evidence for more robust, undepressed plant–insect systems during the Palaeocene.

2. GEOLOGICAL SETTING AND LOCALITY

INFORMATION

The geological setting, stratigraphy, depositional environment and age of the middle Palaeocene fossil-lagerstätte Menat are reviewed in detail elsewhere (Vincent et al. 1977; Kedves & Russell 1982) and summarized here in the electronic supplementary material. The Menat Pit fossil site is located within the Department Puy-de-Dôme, France, near the town of Gannat in the northwestern part of the Massif Central (46°06′N, 02°54′E). It represents a fossil lake with sedimentary infill, interpreted as a maar lake, created by volcanic activity (Vincent et al. 1977). The geology, geochemistry and composition of the fossil assemblages clearly indicate a warm palaeoclimate and a forested palaeoenvironment in the lake catchment, dominated by Lauraceae, Plantaginaceae and Fabaceae (Fritel 1903; Laurent 1912, 1919; Piton 1940), the same higher groups that are common at nearly all of the US sites (e.g. Will et al. 2006). Plants from Menat are preserved as impressions and compressions in thinly laminated, bituminous shales (spongio-diatomite). The typical leaf assemblage is shown in Mai (1995, fig. 134) and in figs S3–S7 in the electronic supplementary material. There is no evidence for climate being an important factor affecting the interpretation of results from Menat (see fig. S2 and table S1 in the electronic supplementary material).

3. MATERIAL AND METHODS

(a) Databases

We compare the Menat flora with the pre-existing dataset of latest Cretaceous through earliest Eocene insect-feeding damage on fossil leaves in the US Western Interior basins; the US data have provided abundant information regarding how extinction, as well as climate change, affects plant–insect systems (Will & Labandeira 1999; Johnson 2002; Labandeira et al. 2002a,b; Will et al. 2006; Currano et al. 2008). With Menat included, the total dataset considered here comprises a total of 16,846 fossil leaves from 16 sites with well-resolved stratigraphic ages, spanning approximately 11 Myr from the latest Cretaceous (66.5 Ma, terminal Maastrichtian) to the Palaeocene–Eocene boundary (55.8 Ma, Ypresian, Palaeocene–Eocene Thermal Maximum; see table S1 in the electronic supplementary material).

(b) Data acquisition

European fossil plants were examined from field collections done by the Musées Association Rhinopollis, Gannat, in 2006 and 2007, and every identifiable dicot leaf with at least half of the blade preserved was collected. Field collections, used in the statistical analyses, were supplemented with relevant historical collections from the Muséum National d’Histoire Naturelle, Paris (Coll. Piton, Coll. Saporta, Coll. Gimenis). A total of 1130 specimens of leaves, fruits and flowers were preserved (figure 1). As for the US sites, all specimens of leaves, or leaflets in the case of compound leaves, thought to be from woody, non-monocot (‘dicot’) angiosperms, were identified to species when possible (or to morphotypes when taxonomy was ambiguous), and non-angiosperm plants were not included in the analysis. Unidentified specimens (15.7% of the collections) had poor preservation and/or a lack of diagnostic characteristics. These were excluded from analysis, resulting in a total of 792 applicable dicot leaves. Piton’s (1940) monograph and subsequent taxonomic revisions of the flora (Knobloch & Kvaček 1965; Jones et al. 1988; Kvaček & Walther 1989; Manchester 1989; Hably 2006; Wang et al. 2007) were used to identify the plants. In our opinion, this taxonomy remains slightly oversplit, especially for Lauraceae, and there is the possibility of collection bias in the historical samples. All specimens are housed in the palaeobotanical collections of the Muséum National d’Histoire Naturelle. We recorded the presence and absence of 39 discrete morphologies of insect damage, or ‘damage types’ (DTs), within four functional feeding groups (FFGs: external foliage feeding, mining, galling and piercing-and-sucking). We used the scoring system of Labandeira et al. (2007; see also the electronic supplementary material), which was also used on the US sites.

We also considered insect herbivory on individual host plants (figure 2f–i). Species-level damage data should be less affected by the overall floral richness and by the increased spatial and temporal averaging at Menat (see Currano 2009 and also Novotny et al. 2007 for limited beta diversity of herbivores over large host-plant ranges). Therefore, although we present both, we feel that species-level herbivory data are more suitable for comparison than bulk floral data.

(c) Taphonomic bias

Previous studies indicate that the depositional environment has an effect on recovered floral diversity (Wing & DiMichele 1995). Menat represents a more or less isolated lacustrine system that originated in a deep maar lake with a highly diverse taphocoenosis trapped (Piton 1940). In contrast, the studied North American sites are more or less parautochthonous and were formed in a range of fluvial depositional settings (abandoned channel beds, floodplain ponds, flooded forest floors or river channels in the case of the Cretaceous sites; Wing et al. 1995; Johnson 2002). The North American floras are not analogous to Menat in that they represent low-relief, floodplain palaeo-environments and perhaps less than 100 years of accumulation, whereas lacustrine assemblages such as Menat represent significantly more temporal averaging than all the US sites and more
spatial averaging than the US Palaeocene and Eocene sites (e.g. Wing & DiMichele 1995).

(d) Statistical analyses
All analyses were performed from census data using the R statistical environment (R Development Core Team 2008). The complete census data for the Menat megafossil site and further details on the statistical analyses are provided in the electronic supplementary material.

4. RESULTS
The Menat megaflora had 76 dicot-leaf species, which represent a much higher diversity than any of the sites studied here from the Western USA, except the Castle Rock rainforest site (Johnson & Ellis 2002; Ellis et al. 2003). Menat’s richness may be inflates relative to that of the USA owing to the differing depositional environments and, to some extent, from taxonomic splitting, but the difference is nevertheless obvious and highly significant (see figs S3–S7 in the electronic supplementary material). To underscore this point, we note that the richest Palaeocene or Eocene lacustrine leaf flora known from the USA is the early Eocene Republic flora from Washington State (Wolfe & Wehr 1987; Pigg et al. 2007). When sampled using very similar collecting methods, Republic yielded a much lower total of 58 dicot-leaf species from approximately 1000 specimens, equivalent to 51.6 ± 4.3 species when rarefied to the sample size of Menat (Wilf et al. 2005).

Total damage and mine-damage diversity on the Menat bulk flora parallel the high plant diversity (figure 2a–e), making Menat outstanding in comparison with all the North American Palaeocene floras. Total frequency shows little pattern throughout the dataset, whereas mine frequency shows the same general pattern as the diversity data. If the sites are split into two groups based on damage diversity, mine diversity and mine frequency, the Cretaceous sites, Mexican Hat, Menat and the latest Palaeocene and Palaeocene Eocene thermal maximum (PETM) sites fall in a high-diversity and high-frequency group (figure 2g–d), whereas the remaining early and middle Palaeocene sites show only depressed insect damage.

The species-level data reveal an unexpectedly high degree of host specialization for Menat (e.g. mining; figure 2g,h), in sharp contrast to the conspicuous drop following the K–T boundary at the US sites (Labandeira et al. 2002b; Wilf et al. 2006). Unlike most of the Palaeocene US sites, mining at Menat occurs on more than one host lineage. The only other sites in which this pattern is observed are the Cretaceous suite, Mexican Hat and the PETM sites (figure 2g,h). The betulaceous Corylus macquarrii (figures 1b,c,h,i and 2g,h) is particularly rich in mines, with four mine DTs and 12 occurrences. The species–damage diversity data indicate that the bulk data (in which damage diversity at Menat is higher than all the early to early–late US Palaeocene sites) reflect a true diversity pattern, even though overall floral richness can be taphonomically influenced (vide infra). The diversity and prevalence of host-specialized mining morphotypes on so many different host plants is especially striking, indicating well-developed specialized feeding
associations on a broad spectrum of host lineages (table 1).

As expected, ordinations using non-metric multi-dimensional scaling (NMS) emphasize the exceptional position of Menat (figure 3). The points closest to it are the two most highly diverse Cretaceous floras (Battleship and Dean Street) and the latest Palaeocene Daiye Spa, which, as shown in figure 2, reflects some rebound from the extinction related to climatic warming (Currano et al. 2008). Menat has greater mining richness and frequency than Daiye Spa, which, in turn, has a high mining percentage for the Western Interior.

Because the Menat plant species are not found in North America, we estimated leaf mass per area (LMA) to test whether the US sites have significantly different leaf properties that may affect herbivores. Leaves with high LMA are thicker, tougher and generally have lower nutrient concentrations (Wright et al. 2004). These leaves are therefore less palatable to insect herbivores and have less insect damage (Coley & Barone 1996; Royer et al. 2007). We estimated LMA for plant species from Menat and five North American sites using the methodology of Royer et al. (2007). An ANOVA of LMA by site yielded an F-value of 0.16 and p = 0.97.

Figure 2. Insect damage on (a–e) bulk floral assemblages and (f–i) individual plant hosts from Menat compared with US Western Interior floras. (a) Number of dicot species at each site rarefied to 400 leaves; error bars represent the standard error of Heck et al. (1975). (b) Total damage diversity (number of DTs) on each flora standardized to 400 leaves by averaging damage diversity for 5000 random subsamples of 400 leaves without replacement. Error bars represent ± 1σ of the mean of the resamples. (c) Sampling-standardized mine diversity on the bulk floras, calculated as in (b). (d) Percentage of leaves at each site with mines. Error bars represent ± 1σ, based on a binomial sampling distribution. (e) Percentage of leaves with damage at each site with damage; error bars as in (d). (f) Damage diversity on individual species at each site, standardized to 25 leaves. Each × represents a single plant host, which was randomly resampled without replacement as in (b). The filled symbols are the among-species means for the site, and the thick grey lines delineate one standard deviation. (g) Sampling standardized mine diversity on individual host plants, as in (f). (h) Percentage of leaves of each species (with at least 25 leaves in the flora) with mines. Symbols as in (f). (i) Percentage of leaves of each species with damage, as in (h). P–E, Palaeocene–Eocene boundary; K–T, Cretaceous–Palaeogene boundary. (a–e) Bulk flora: black triangle, Eocene; grey diamond, Palaeocene; red diamond, Menat; white square: Cretaceous. (f–i) Host species: triangle, diamonds and square, site average; cross, single host.
Table 1. Summary of plant hosts from Menat with at least 25 leaves; errors represent the 95 percent prediction intervals. dam., damaged; DT, damage type.

<table>
<thead>
<tr>
<th>species</th>
<th>plant group</th>
<th>number of leaves</th>
<th>% of flora</th>
<th>total DTs</th>
<th>% dam.</th>
<th>% mined</th>
<th>total DTs*</th>
<th>mine DTs*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corylus macquarrii</td>
<td>Betulaceae</td>
<td>139</td>
<td>14.8</td>
<td>22</td>
<td>28.8 (+3.84)</td>
<td>8.6 (+2.19)</td>
<td>7.4 (+2.29)</td>
<td>1.7 (+0.92)</td>
</tr>
<tr>
<td>Dryophyllum denalquei</td>
<td>Fagales</td>
<td>99</td>
<td>10.6</td>
<td>12</td>
<td>24.2 (+4.30)</td>
<td>2.0 (+1.41)</td>
<td>4.4 (+1.37)</td>
<td>0.5 (+0.62)</td>
</tr>
<tr>
<td>Salix lamottei</td>
<td>unknown</td>
<td>38</td>
<td>4.1</td>
<td>8</td>
<td>31.6 (+7.54)</td>
<td>0</td>
<td>6.2 (+1.13)</td>
<td>0</td>
</tr>
<tr>
<td>Cinnamomum sp.</td>
<td>Laurales</td>
<td>31</td>
<td>3.3</td>
<td>8</td>
<td>19.4 (+7.10)</td>
<td>3.2 (+4.43)</td>
<td>6.8 (+1.49)</td>
<td>0.8 (+0.39)</td>
</tr>
<tr>
<td>Fraxinus sp.</td>
<td>unknown</td>
<td>29</td>
<td>3.1</td>
<td>10</td>
<td>58.6 (+9.15)</td>
<td>3.4 (+3.37)</td>
<td>9.3 (+0.87)</td>
<td>0.9 (+0.35)</td>
</tr>
</tbody>
</table>

*Standardized to 25 leaves.

5. DISCUSSION

Previous studies indicate that, in the majority of cases, plant and insect-feeding diversity on a per-leaf basis were high during the Cretaceous and low during the Palaeocene in the US Western Interior (e.g. Labandeira et al. 2002a,b; Wilf et al. 2006). The two remarkable exceptions, Mexican Hat and Castle Rock, show either rich and abundant insect feeding (in the former) or high floral diversity (in the latter), but not both. This indicates severe ecosystem depression and ecological imbalance throughout much of the Palaeocene in the US Western Interior. The exceptionally high floral diversity and DT richness at Menat argue for a balanced and fully functional middle Palaeocene ecosystem completely unlike any known from the US Palaeocene, even for Castle Rock, which grew under tropical rainforest-like conditions (Johnson & Ellis 2002; Ellis et al. 2003; Wilf et al. 2006). Furthermore, the high mining diversity is indicative of extensive host specialization on many different host species, such as C. macquarrii, which has 22 DTs coupled with an elevated mining activity.

The cause of the observed pattern is probably complex. Possible factors include reduced impact effects as distance from the Chicxulub crater in Mexico (Hildebrand & Boynton 1991) increases, a higher Cretaceous floral diversity in Europe, or higher Palaeocene immigration or origination rates. Further investigations of potential Palaeocene floras (e.g. Sézanne, Gelinden; Collinson & Hooker 2003) will be necessary to better characterize plant–insect associations following the K–T boundary in Europe, especially with respect to the specialized feeding groups. Suitable latest Cretaceous floras for comparison are not yet known. However, the Menat data are consistent with palaeoecological findings from the early Palaeocene in Chubut, Argentina (7700 km modern distance from Chicxulub) and West Coast, New Zealand (12 300 km). Like Menat (8500 km), these areas are far from the impact site and show higher Palaeocene plant diversity (Igléias et al. 2007) or a more rapid ecosystem recovery (Vajda et al. 2001) than occurring in the Western Interior USA (e.g. southwestern North Dakota, 3100 km) or is indicated by approximately 58 Ma Cerrejón flora of northern Colombia (2100 km; Wing et al. in press). Thus, the diversity of plants and plant–insect associations at Menat contributes to an emerging global pattern of more robust Palaeocene terrestrial ecosystems at great distance from the Chicxulub structure.

We are grateful to Carlos A. Jaramillo and two anonymous reviewers for their insightful comments on an earlier draft of this manuscript. This research received support from the SYNTHESYS Project (http://www.synthesys.info), which is financed by European Community Research Infrastructure Action under the Structuring the European Research Area Program (to T.W.), and a grant from the German Science Foundation (RU 665/4-1, 4-2, to J.R. and T.W.). Additional support was provided by the American Philosophical Society and the David and Lucile Packard Fellowship (to E.D.C.). We especially thank Beth Ellis and Kirk Johnson for their untiring work on Cretaceous and Palaeogene floras in the Western Interior, supported by NSF grant EAR-0345910, to acquire data cited here.


