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# 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).

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).

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Palaeogene 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 Palaeocene of Europe. Our data derive from the middle Palaeocene 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 and 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 palaeo-environment in the lake catchment, dominated by Lauraceae, Platanaceae and Fagales (Fritel 1903; Laurent 1912, 1919; Piton 1940), the same higher groups that are common at nearly all of the US sites (e.g. Wilf *et al.* 2006). Plants from Menat are preserved as impressions and compressions in thinly laminated, bituminous shales (spongo-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 (Wilf & Labandeira 1999; Johnson 2002; Labandeira *et al.* 2002a,b; Wilf *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 Rhinopolis, 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. Giniès*). 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 2*f–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



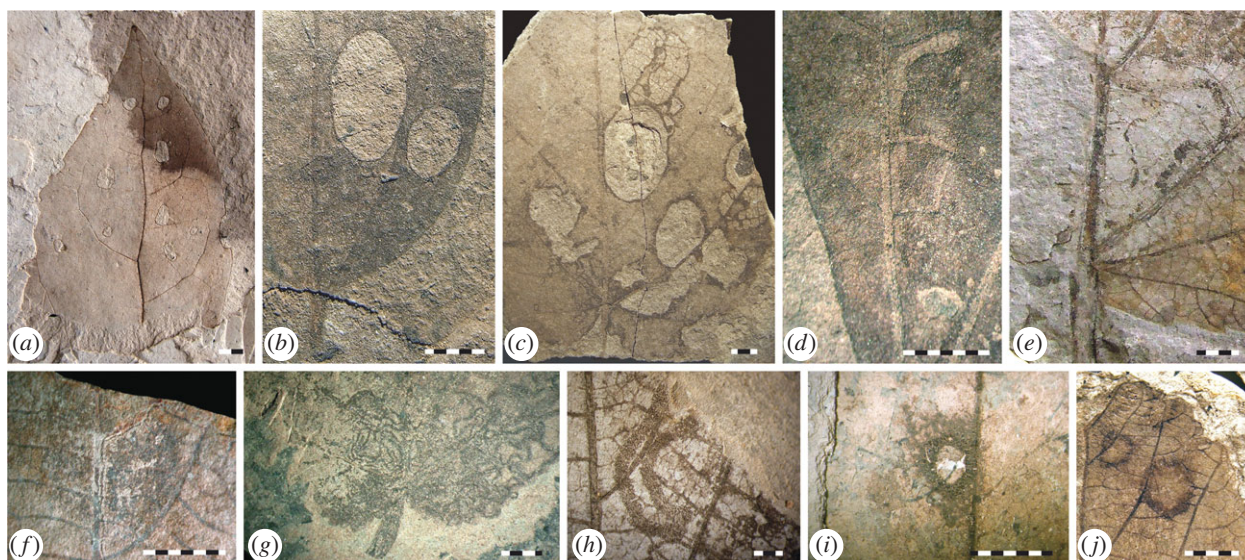


Figure 1. Representative insect damage from the Palaeocene of Menat, France. (a) Characteristic large, circular hole feeding (DT4 of Labandeira *et al.* 2007) on unidentified dicot sp. (Morphotype I; MNT 06 3493); (b) large, circular hole feeding (DT4) on *Cinnamomum* sp. (Lauraceae; 20 909); (c) skeletonization (DT16) and large, circular hole feeding (DT4) on *Corylus macquarrii* (20 816); (d) serpentine mine, parallel-sided, thin reaction rim (DT41) on *Luheopsis vernieri* (21 209); (e) serpentine lepidopteran mine with thick, initially intestiniform but subsequently looser frass trail (DT41) on *C. macquarrii* (Betulaceae; 15 083); (f) serpentine mine on *C. macquarrii* with confined, linear, median frass trail (DT41; 20 847); (g) sinusoidal mine, probably lepidopteran (Nepticulidae; DT92), on *C. macquarrii* with frass trail of dispersed rounded pellets oscillating across the full mine width (MNHN-LP-R 63 913); (h) undulating lepidopteran mine on *C. macquarrii* with pelleted frass trail (DT95; 20 747); (i) circular galling structure, surrounded by thick, dense, reaction tissue (DT11) on *Fraxinus* sp. (MNT 05 115.1); (j) circular galls on 3° veins, central chamber sharply separated from a wide, thick carbonized brim on *C. macquarrii* (DT110; MNHN-LP-R 63 917). Scale bars, 5 mm. MNT, collection number from the Musées Association Rhinopolis; MNHN-LP-R, collection number from the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France.

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 megafloora 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 inflated 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  $51.6 \pm 4.3$  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 2b–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 site (figure 2f,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

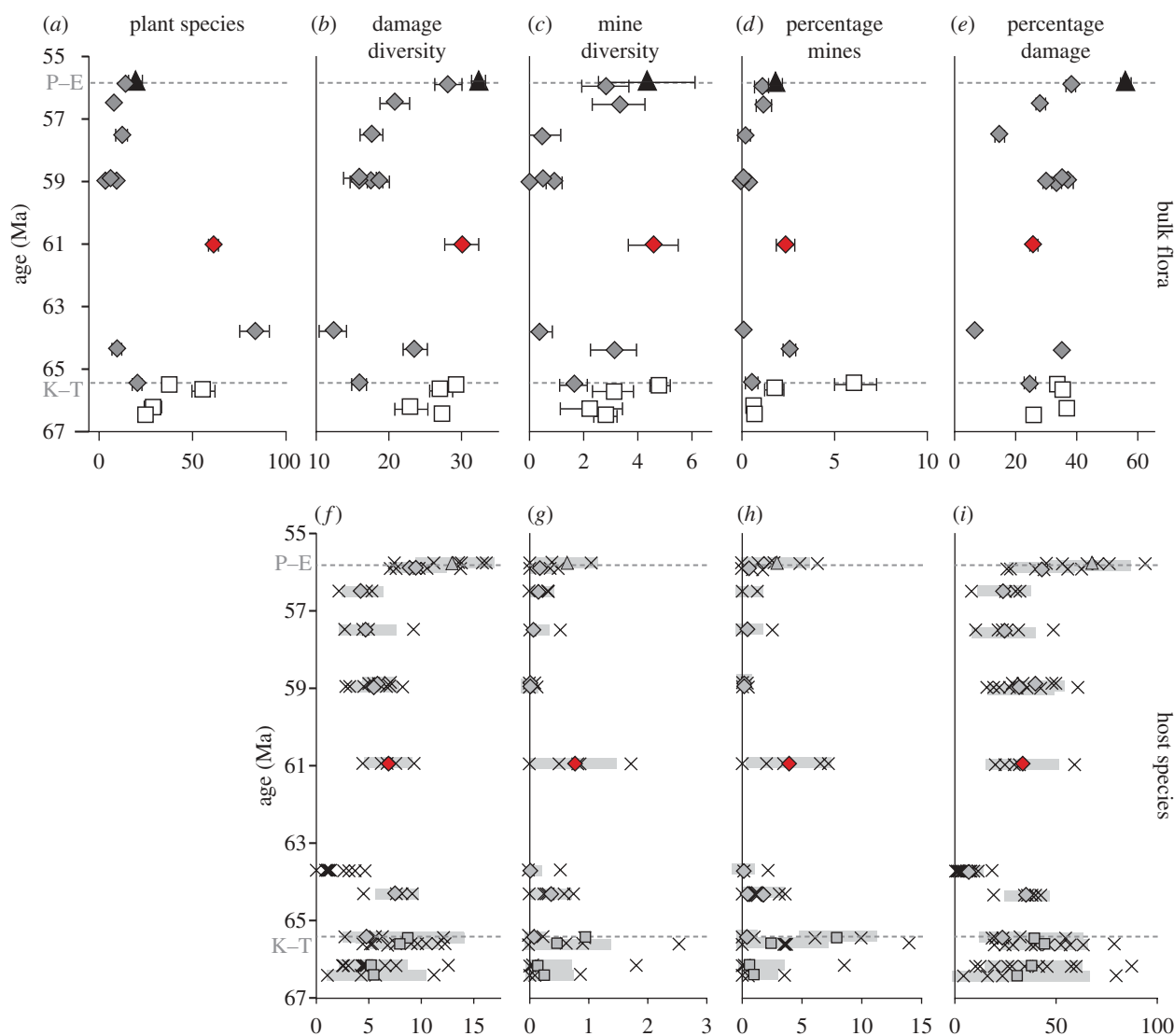


Figure 2. Insect damage on (a–e) bulk floral assemblages and (f–i) individual plant hosts from Menat compared with US Western Interior floras. (a) Number of dicot species at each site rarefied to 400 leaves; error bars represent the standard error of Heck *et al.* (1975). (b) Total damage diversity (number 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  $\pm 1\sigma$  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  $\pm 1\sigma$ , 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  $\times$  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.

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  $p = 0.97$

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.

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

<sup>a</sup>Standardized to 25 leaves.

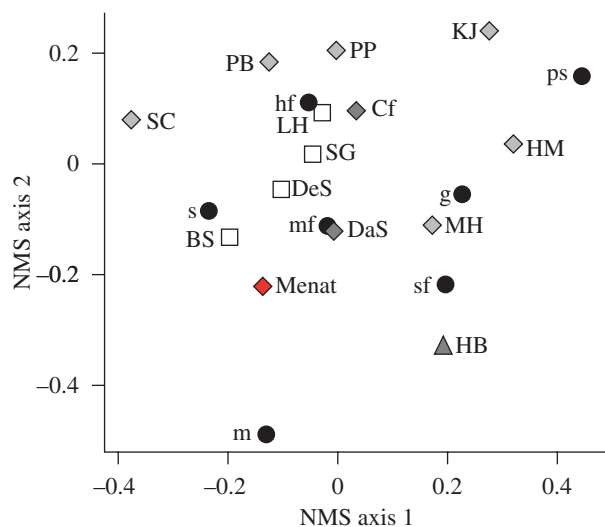


Figure 3. Non-metric multi-dimensional scaling (NMS) ordination of the insect damage on the bulk floras. The 14 sites were ordinated in NMS using a matrix of the percentage of leaves at each site with each FFG; FFGs were also ordinated based on their occurrences at the sites, and they are plotted on the same axis. Castle Rock and Lur'd leaves are not included in the analysis because their extremely low damage frequencies turn NMS axis 1 into a measure of damage frequency, thus limiting comparisons among sites based on damage composition. Dark grey triangle, Eocene site; dark grey diamond, late-late Palaeocene site; light grey diamond, early-late Palaeocene site; white square, Cretaceous site; black circle, FFG. For abbreviations of sites and FFGs, see the electronic supplementary material.

(five d.f.), indicating no significant differences in leaf properties (see table S2 and fig. S1 in the electronic supplementary material).

## 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 palaeobotanical 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 (Iglesias *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.

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