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#### Supporting Online Material

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Materials and Methods

Table S1  
References

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# Decoupled Plant and Insect Diversity After the End-Cretaceous Extinction

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Food web recovery from mass extinction is poorly understood. We analyzed insect-feeding damage on 14,999 angiosperm leaves from 14 latest Cretaceous, Paleocene, and early Eocene sites in the western interior United States. Most Paleocene floras have low richness of plants and of insect damage. However, a low-diversity 64.4-million-year-old flora from southeastern Montana shows extremely high insect damage richness, especially of leaf mining, whereas an anomalously diverse 63.8-million-year-old flora from the Denver Basin shows little damage and virtually no specialized feeding. These findings reveal severely unbalanced food webs 1 to 2 million years after the end-Cretaceous extinction 65.5 million years ago.

There is little direct evidence from the fossil record about food web recovery after mass extinction. One theoretical model describes the rebuilding of diversity, after a lag period, first for primary producers and then for successively higher trophic levels after additional time lags (1). Consistent with this pattern is a 3- to 4-million-year recovery period for pelagic food webs after the Cretaceous-Paleogene boundary (K-T), inferred from isotopic depth gradients (2-4).

Insect damage on compressed fossil leaves provides abundant information about terrestrial food webs, because the diversity of plants and their insect feeding associations can be directly compared using the same fossils, at high sample sizes and in fine stratigraphic context (5-7). Modern ecological observations generally show positive correlations between insect herbivore diversity and plant diversity (8-10), and the evaluation of fossil insect damage can test whether past extinctions disrupted this linkage. In southwestern North Dakota, for example, the

K-T event caused a significant floral extinction (11) accompanied by a major extirpation of insect feeding morphotypes (6). These included diverse and abundant leaf mines and galls, whose extant analogs are typically made by host-specialized insects (12, 13). No significant recovery of specialized feeding was found in 80 m of local section representing the first ~0.8 million years of the 10-million-year Paleocene (6), prompting us to examine the geographic and temporal extent of the Paleocene ecological dead zone.

We investigated the recovery of plant-insect associations in the western interior United States, with emphasis on the Paleocene. We focused on insect mines (hereafter "mines") because they are a specialized feeding category commonly preserved in fine morphological detail (Fig. 1) (14, 15). We compared four latest Cretaceous, nine early and late Paleocene, and one early Eocene megafloral sites (Table 1, table S1, and fig. S1) from warm temperate and subtropical fluvial paleoenvironments, selected to optimize preservation and diversity, sample size, stratigraphic control, and temporal and geographic coverage. The sites are located in several basins, forming a composite regional data set. Nearly all the Paleocene samples have similar taxonomic composition and the low floral diversity that is typical of the time period and region (Fig. 2 and tables S2 and S3). The major exception is the Castle Rock flora from the

Denver Basin: a highly diverse and compositionally distinct early Paleocene assemblage with tropical rainforest characteristics, located in a warm and humid, apparently geographically restricted, belt on the eastern margin of the Laramide Front Range (16-20).

For taphonomic consistency, we analyzed only identifiable specimens of angiosperm leaves (excluding monocots) and avoided fragmentary leaves when possible. Samples came from single stratigraphic horizons whenever feasible, and biases were greatly reduced by either making quantitative census collections in the field (7) or using museum collections that had at least 400 identifiable specimens (Table 1). We also considered, where indicated below, more than 15,000 additional specimens that did not meet these criteria (table S4). These come from the North Dakota K-T study, Castle Rock, the late Paleocene and early Eocene of southwestern Wyoming, and one Late Cretaceous and two additional early Paleocene sites in the Denver Basin.

We scored each specimen for the presence or absence of 63 distinct insect damage morphotypes (DTs) found in the total data set, allocated to the four functional feeding groups of external foliage feeding, galling, mining, and piercing-and-sucking as described elsewhere (5, 14, 15) (table S2). Plant richness and DT diversity on bulk samples were standardized to 400 leaf specimens by means of rarefaction and randomized resampling, respectively (Fig. 2). Separately, we evaluated mining morphotype diversity for each of 89 species-site pairs with at least 25 leaf specimens (Fig. 3 and table S2).

The Cretaceous floras are rich, whereas all Paleocene assemblages are depauperate except Castle Rock (Fig. 2A), where plant diversity exceeds that of the Cretaceous samples. Insect damage diversity on bulk samples approximately tracks plant diversity, dropping across the K-T and remaining low until the latest Paleocene (Fig. 2 and table S4). However, insect damage shows a striking inversion with respect to plant richness at Castle Rock and Mexican Hat (Fig. 2). The diverse Castle Rock flora has some of the lowest feeding diversity in our data set. This result holds for all damage

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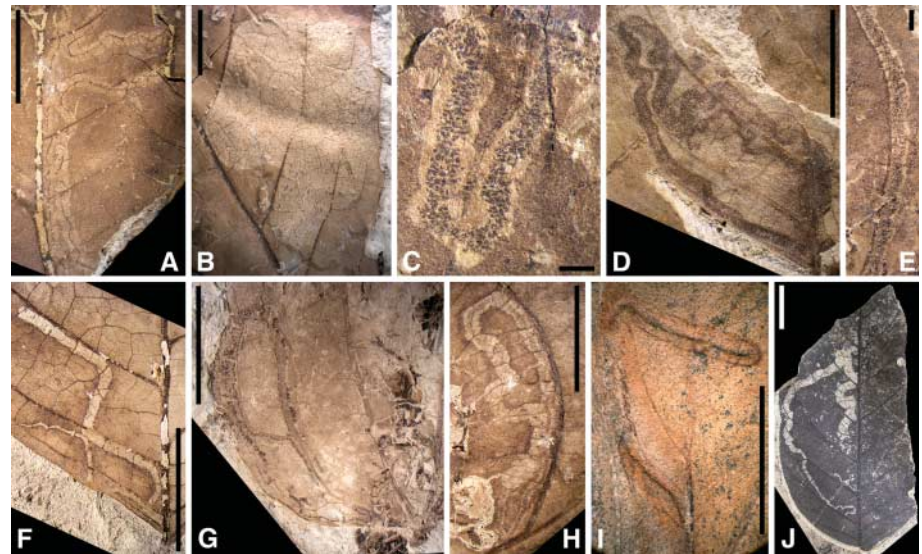
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morphotypes, for specialized damage only, and for mines alone (Fig. 2). Only two mines occur in the Castle Rock sample: two morphotypes on two hosts (Fig. 1, I and J) (21).

In contrast, feeding diversity on the depauperate Mexican Hat flora is comparable to that of considerably more diverse Cretaceous floras (Fig. 2). Mining at Mexican Hat is unlike that of

any other Paleocene flora we have observed, in its abundance and in its prevalence, diversity, and taxonomic breadth among host plants. Mining occurs on 2.6% of leaves, which is more than double

**Fig. 1.** Representative leaf mines on the botanically depauperate Mexican Hat [(A) to (H)] flora and the diverse Castle Rock [(I) and (J)] flora, both early Paleocene (Table 1). Scale bars, 1 mm in (C) and (E), 1 cm in the other panels. (A) Elongate, serpentine, agromyzid dipteran mine (DT104) characterized by a hairline trail of fluidized frass and occurring only on *Platanus raynoldsi* (Platanaceae) [USNM specimen 498154 (National Museum of Natural History)]. (B) Blotch mine on *P. raynoldsi* with small ellipsoidal frass pellets (DT36), probably made by a tenthredinid hymenopteran, USNM 498155. A similar mine also occurs on a rare unidentified host at Mexican Hat (not shown in the figure). (C) Moderately sinusoidal to linear lepidopteran mine on *P. raynoldsi* with pelleted frass trail of variable width and undulate mine margins (DT91, USNM 498156). (D) Sinusoidal mine, probably lepidopteran, on *Juglandiphyllites glabra* (Juglandaceae; fragment, not included in analyses) with frass trail of dispersed rounded pellets oscillating across the full mine width (DT92, USNM 498157). (E) Mine on "*Populus*" *nebrascensis* (Trochodendrales) with distinct pelleted frass trail occupying the median 80% of the mine width (DT91, USNM 498158). (F) Curvilinear aborted mine lacking frass (DT105) on *J. glabra*, USNM 498159. (G) Serpentine lepidopteran mine with thick, initially intestiniform but subsequently looser frass trail (DT41), common throughout the Paleocene in the western interior United States and shown here on *Zizyphoides flabella* (Trochodendraceae), USNM 498160. (H) Serpentine lepidopteran mine (DT91) displaying frass detail of early instar stages at bottom, on *Cercidiphyllum genatrix* (Cercidiphyllaceae), USNM 498161. (I) Aborted mine on host morphotype CR9, showing confined, linear, median frass trail with lateral reaction rim [DT43, DMNH specimen 26060 (Denver Museum of Nature and Science)]. (J) Complete, serpentine, straight-margined mine lacking frass (DT45) on host morphotype CR59, DMNH 26039.



**Table 1.** Sampling summary. All insect-damage data are new between Mexican Hat and Lur'd Leaves, inclusive. The Cretaceous and Pyramid Butte samples were reanalyzed from our K-T data set (6), with the addition of >700 newly analyzed leaf specimens. Data are not adjusted for sample size as in Fig. 2 (see also fig. S1 and table S1).

Sample and time interval	Location	Age (Ma)	Leaf specimens	Leaf species
Early Eocene				
Sourdough* (5)	Great Divide Basin, SW WY	53.5	792	22
Latest Paleocene				
Clarkforkian† (5)	Washakie Basin, SW WY	56.5	749	10
Late Paleocene				
Lur'd Leaves‡§	Polecat Bench, Bighorn Basin WY	57.5	1360	15
Skeleton Coast‡§	Polecat Bench, Bighorn Basin WY	59.0	835	7
Persites Paradise‡§	Great Divide Basin, SW WY	59.0	963	10
Kevin's Jerky‡§	Washakie Basin, SW WY	59.0	1319	7
Haz-Mat‡§	Washakie Basin, SW WY	59.0	749	4
Early Paleocene				
Castle Rock lower layer* (19)	Denver Basin, CO	63.8	2309	130
Mexican Hat‡§ (30)	Powder River Basin, SE MT	64.4	2219	16
Pyramid Buttell (11)	Williston Basin, SW ND	65.5	549	23
Latest Cretaceous				
Battleshipll (11)	Williston Basin, SW ND	65.6	459	40
Dean Streetll (11)	Williston Basin, SW ND	65.7	743	74
Somebody's Garden levelll (11)	Williston Basin, SW ND	66.3	1525	46
Luten's 4H Hadrosaur levelll (11)	Williston Basin, SW ND	66.5	428	26

\*Field census, two or more quarries from the same level. †Field census, two quarries from approximately the same level. ‡New collection. §Field census, single quarry. llMuseum collection from single quarry or multiple quarries at same level, >400 specimens total.

the frequency of any other Paleocene sample (table S1). Most distinctively, the four most abundant host species, which together account for 91% of specimens and are also abundant in our other Paleocene samples (table S2), each have either two or three mine morphotypes (Figs. 1 and 3); mining also occurs on two other locally rare hosts [Fig. 1, B (caption) and E]. The sycamore *Platanus raynoldsi* has mines attributable to three insect orders, namely Hymenoptera (Fig. 1B) and Lepidoptera (Fig. 1C) and numerous mines (on 32 leaves, with up to six mines per leaf) assignable to Agromyzidae within the Diptera (Fig. 1A); the association of agromyzid leaf-miners and Platanaceae does not occur today (22).

The only other examples of more than one mine morphotype per species in our data set occur on two Cretaceous hosts from two different sites and on two latest Paleocene and early Eocene Betulaceae (*Corylites* and *Alnus*, respectively) (Fig. 3). Only one of the Mexican Hat mine morphotypes (DT41, Fig. 1G) has been found in the latest Cretaceous of North Dakota, on host plants unrelated to the Mexican Hat dominants (6), and three (DT91, DT92, and DT104; Fig. 1) have not been observed in any other North American fossil floras to date. This suggests that the Mexican Hat miners included more newly and regionally evolved taxa, or alternatively long-distance migrants, than regional K-T survivors.

Excepting Mexican Hat and the latest Paleocene, our Paleocene floras have few mines by comparison to the Cretaceous (Figs. 2C and 3), a finding corroborated by abundant supplemental data from the Denver Basin and North Dakota (table S4). The five late Paleocene sites from Wyoming (Table 1) contain significant numbers of all four dominant host plants found at Mexican Hat (tables S2 and S3) but yielded only seven mines on 5226 specimens, all of the DT41 type. Five of these occur on *Cercidiphyllum genetrix*, the only regional continuation of a mining association found at Mexican Hat (Fig. 1H).

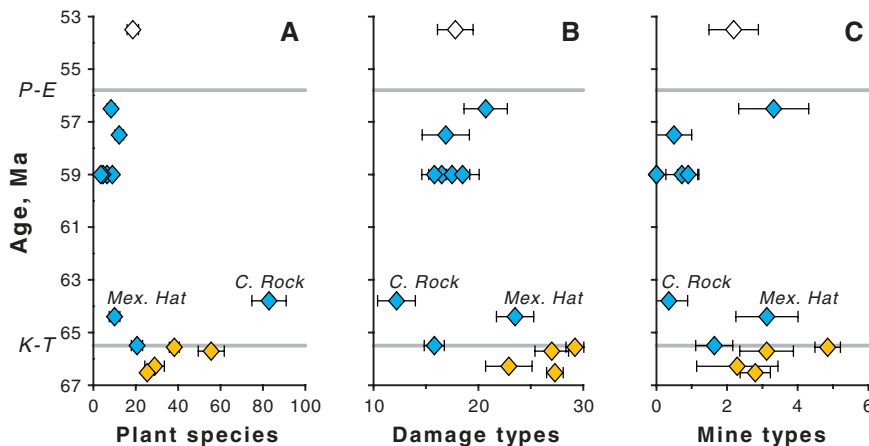
Sustained recovery of both plant and insect-herbivore diversity began during the warm latest Paleocene (5, 23), wherein herbivory apparently led ahead of plant diversity (Fig. 2). In contrast to Mexican Hat, however, latest Paleocene mining mostly occurred on a single host lineage, the Betulaceae (Fig. 3), which first appeared regionally in the late Paleocene and supported diverse and abundant herbivory through the early Eocene (5, 24, 25).

The Castle Rock flora is one of the oldest reliable examples of tropical rainforest vegetation (16, 17, 26), typified today by tough thick leaves with low nutritional value and high tannin content (27). The extraordinary but temporary diversification recorded at Castle Rock appears to be related to favorable climatic conditions, the establishment of unpalatable vegetation, and low herbivore pressure in a post-extinction setting. This scenario contrasts with living rainforests, where herbivores are implicated in maintaining and possibly promoting plant diversity (28, 29). Unlike Castle Rock, our other Paleocene samples are dominated by thin-leaved deciduous hosts (table S2) that we infer to have had relatively low defenses and thus to have been vulnerable to opportunistic colonization when herbivore pressure was present, as observed at Mexican Hat.

The Mexican Hat and Castle Rock floras show marked, apparently localized and transient, deviations from theoretical patterns of staged food web recovery (1), indicating much greater variance than has previously been considered in the relative numbers of producer and consumer species. Temporally and geographically isolated occurrences of severely unbalanced food webs may be a widespread feature of ecological recovery from mass extinction, resulting from instability, incumbency, and opportunism in drastically simplified ecological landscapes.

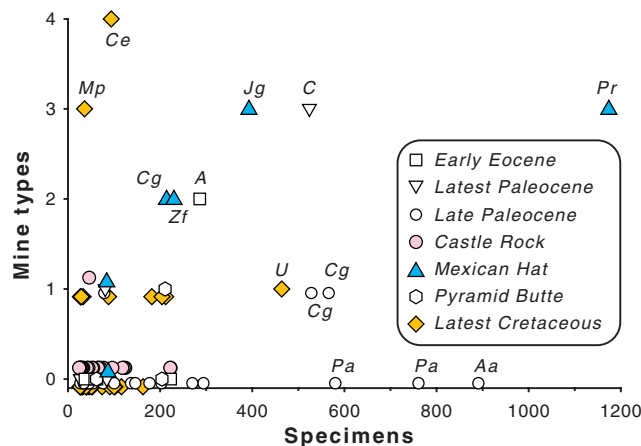
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**Fig. 2.** Plant and insect-feeding diversity for bulk floras (Table 1 and table S1), standardized to sample sizes of 400 leaf specimens each. Orange-yellow data points are Cretaceous floras; blue data points are Paleocene floras. Ma, million years ago. Plant richness (A) was standardized by means of rarefaction (31), with error bars indicating 95% confidence intervals. Insect damage was standardized by means of random resampling without replacement (5, 32), with  $\pm 1\sigma$  error bars around the mean of 5000 iterations, both for (B) all damage morphotypes and (C) mine morphotypes only. There is a strong negative correlation of plant and insect-damage richness for Mexican Hat (Mex. Hat) and Castle Rock (C. Rock). A separate analysis (not shown in the figure) excluded most external feeding and other “generalized” damage morphotypes as in (6) but yielded results nearly identical to (B). P-E, Paleocene-Eocene boundary.

**Fig. 3.** Leaf-mine morpho-type diversity plotted against number of leaf specimens for the 89 species-site pairs in our full data set (Table 1) that had a minimum of 25 leaf specimens at a site. There is high mining diversity on all four common host plants and one relatively rare host in the early Paleocene Mexican Hat flora. A sixth mined host represented by only 11 leaf specimens is not shown, and *Z. flabella* at Mexican Hat was previously found to have an additional morphotype, a blotch mine equivalent to our DT36 (30). Labeled outliers are as follows: A, *Alnus* sp. (Betulaceae); Aa, “*Ampelopsis*” *acerifolia* (?Cercidiphyllaceae); Ce, *Cercidiphyllum ellipticum* (Cercidiphyllaceae); Cg, *C. genetrix*; C, *Corylites* sp. (Betulaceae); Jg, *Juglandiphyllites glabra* (Juglandaceae); Mp, *Marmarthia pearsonii* (Lauraceae); Pa, *Persites argutus* (Lauraceae); Pr, *Platanus raynoldsi* (Platanaceae); U, *Urticales* sp. HC81; Zf, *Zizyphoides flabella* (Trochodendraceae). (See references in Table 1 for additional nomenclature.)



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32. We randomly resampled all leaves, rather than only damaged leaves as in (7). The latter approach is effective for floras with high damage diversity, but in Paleocene floras insect damage is generally rare, and many specimens and species would be lost from analysis.
33. We thank Harding Land and Cattle Company for land access; P. Anderson, R. Barclay, C. Brown, E. Currano, D. Danehy, R. Dunn, R. Horwitt, F. Marsh, T. Menotti, M. Nowak, M. Reynolds, J. Thomasson, K. Werth, S. Wing, and Western Wyoming Community College for field and technical assistance; three anonymous reviewers; K.C. Beard, E. Currano, D. Erwin, R. Horwitt, M. Patzkowsky, and J. Zachos for discussion; P. Lang, who noted insect mines at Mexican Hat; and I. Winkler for assistance in identifying Agromyzidae mines. Support was provided by the American Philosophical Society, the Colorado Department of Transportation; the Petroleum Research Fund (grant 35229-G2); the National Geographic Society, the Ryan Family Foundation; the Walcott Fund of the Department of Paleobiology, National Museum of Natural History (NMNH); NSF (grants EAR-0345910, EAR-9805474, DEB-0345750, and EAR-0236489); and the David and Lucile Packard Foundation. This is contribution 120 of the Evolution of Terrestrial Ecosystems Consortium at the NMNH.

#### Supporting Online Material

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Fig. S1

Tables S1 to S4

References

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# Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?

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Despite recent progress in understanding mechanisms of tree species coexistence in tropical forests, a simple explanation for the even more extensive diversity of insects feeding on these plants has been missing. We compared folivorous insects from temperate and tropical trees to test the hypothesis that herbivore species coexistence in more diverse communities could reflect narrow host specificity relative to less diverse communities. Temperate and tropical tree species of comparable phylogenetic distribution supported similar numbers of folivorous insect species,  $29.0 \pm 2.2$  and  $23.5 \pm 1.8$  per 100 square meters of foliage, respectively. Host specificity did not differ significantly between community samples, indicating that food resources are not more finely partitioned among folivorous insects in tropical than in temperate forests. These findings suggest that the latitudinal gradient in insect species richness could be a direct function of plant diversity, which increased sevenfold from our temperate to tropical study sites.

**L**arge numbers of herbivore species in the Tropics relative to temperate communities might reflect differences in (i) host plant species diversity, (ii) numbers of herbivore

species per host, and/or (iii) host specificity, the number of plant species hosting each insect species. The tropical maximum in plant species richness is well documented. For instance, there are 5 to 10 times as many plant species per 10,000 km<sup>2</sup> in tropical than in temperate areas (1), and woody plant species richness per hectare in the Tropics is on average six times as high as that in temperate forests ( $156.8 \pm 63.6$  and  $25.2 \pm 19.7$  species with diameter at breast height  $\geq 10$  cm; fig. S1). However, latitudinal differences in host specificity and numbers of insect species per host plant species are more difficult to assess (2, 3).

A recent proliferation of quantitative studies on tropical insect herbivores that include feeding and rearing experiments (4–9) have not been matched by comparable activity in temperate

forests (10, 11), perhaps because patterns of host use are believed to be well documented for temperate herbivores. Much qualitative data on host associations of herbivores accumulated during the past two centuries, particularly in Great Britain and Central Europe, are not directly comparable to recent, quantitative studies in the Tropics (12). A temperate-tropical comparison of herbivore communities is further complicated by differences in the phylogenetic diversity of the vegetation. Temperate forests are dominated by a relatively small number of woody plant lineages as compared to tropical forests (13).

We compared temperate and tropical communities of folivorous insects using identical sampling protocols and phylogenetically comparable sets of local tree species (14). All externally feeding folivorous insects were hand collected from the foliage of 14 woody plant species in a lowland floodplain forest in Moravia, Central Europe, and 14 species in a lowland hill forest in Madang, Papua New Guinea. Caterpillars (Lepidoptera) were also collected from eight woody species in an oak-hornbeam forest in Slovakia, Central Europe, and compared with caterpillars from eight tree species in Papua New Guinea (Madang). Samples of tree species from the local vegetation included both close relatives (i.e., congeneric species) and distantly related plant lineages (i.e., multiple families and orders) at each site (table S1). Molecular phylogenetic relationships among species sampled at each locality were compiled from the recent literature, and branch lengths were estimated from the large subunit of ribulose-1,5-bisphosphate carboxylase-oxygenase (rbcL) gene sequences. The diverse vegetation of lowland New Guinea provided an opportunity to select subsets of tree species with phylogenetic patterns closely matching those of temperate forest tree

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