Impact of the terminal Cretaceous event on plant–insect associations

Conrad C. Labandeira*†‡§, Kirk R. Johnson§¶, and Peter Wilf*§∥

*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0121; †Department of Entomology, University of Maryland, College Park, MD 20742; ¶Department of Earth Sciences, Denver Museum of Nature and Science, Denver, CO 80205; and ∥Museum of Paleontology and Department of Geological Sciences, University of Michigan, Ann Arbor, MI 48109

Evidence for a major extinction of insect herbivores is provided by presence–absence data for 51 plant–insect associations on 13,441 fossil plant specimens, spanning the Cretaceous/Paleogene boundary in southwestern North Dakota. The most specialized associations, which were diverse and abundant during the latest Cretaceous, almost disappeared at the boundary and failed to recover in younger strata even while generalized associations regained their Cretaceous abundances. These results are consistent with a sudden ecological perturbation that precipitated a diversity bottleneck for insects and plants.

One of the most scrutinized events in the history of life is the Cretaceous-Paleogene (K/T) mass extinction at 65.51 ± 0.3 million years before present (1, 2). This event has been linked to the impact of an extraterrestrial object (3) on the Yucatán Peninsula of Mexico (4) that resulted in the losses of numerous lineages within such disparate animal groups as pelagic vertebrates, dinosaurs, mammals, foraminifera, and marine and freshwater mollusks (5–11). Paleobotanical evidence indicates a drastic decline of seed plants in the Western Interior of North America, seen in both the megafloral and palynofloral records (11–17).

Several quantitative studies at the family level indicate that the diversity of insects suffered no decrease beyond normal levels of background extinction at the K/T boundary (18–20). The extinction resistance of insect families is probably attributable to the high diversity of their constituent species and the spatio-temporal plasticity of their geographic ranges, resulting in exceptional longevity in the fossil record (19, 21). Although few studies exist below the family level, the demise of Late Cretaceous aphidioid, beetle, and ant genera (20, 22, 23) provides some evidence for extinctions. Establishing a comprehensive test for the presence or absence of an insect extinction has been hindered by the worldwide lack of appropriate, local deposits that span the K/T boundary and contain well-preserved, diverse, and sufficiently abundant insect faunas (24). The deposits that come closest to meeting these criteria are: Canadian amber of the upper Campanian Foremost Formation, occurring approximately 10 million years before the K/T boundary (20); and the Fur Formation, a Danish unit that brackets the Paleocene to Eocene boundary and contains an assemblage of insect compression fossils from approximately 11 million years after the event (25). Even if more suitable deposits are found, taxonomic occurrence data are inherently limited for addressing the ecological aspects of extinction (26).

Here, we use an explicitly ecological approach that takes advantage of insect-damaged fossil plants (ref. 27; Fig. 1), which document the trophic associations between plants and their insect herbivores, the latter estimated as approximately half of all extant insect species (28). This approach also allows us to investigate a possible insect extinction at the K/T boundary by using a high sample size and stratigraphic resolution that are not available from body fossils of insects.

Study Area, Specimens, and Methods

The Williston Basin of southwestern North Dakota is ideal for our study because it contains a megafloral sequence that is the most intensively sampled across the K/T boundary worldwide (17). The floras occur in a well-characterized composite section of 183 m of strata, representing an estimated 2.2 million years (2, 17) and lacking significant hiatuses (13, 17). The boundary is defined locally by an iridium anomaly, shocked minerals, and palynofloral extinctions. It also is associated with dinosaur extinctions and the loss of ≈80% of megafloral species (11, 13, 15, 17). We studied 13,441 plant specimens collected from 143 localities, in turn derived from 106 stratigraphic levels The megafloras (17) consist predominantly of dicotyledonous angiosperms, which comprise 86.3% of the 380 organ morphotypes in the combined Cretaceous and Paleocene floras (29); 307 of the dicot morphotypes are leaves. Bryophytes, ferns, one horsetail, gymnosperms, and monocotyledons also are preserved. The collections include the full plant diversity found in the field for each locality (17). Only five insect body fossils have been found in the collections. All specimens were collected by K.R.J. and are housed as vouchers at the Denver Museum of Nature and Science and the Yale Peabody Museum, New Haven, CT.

The most significant bias in our data, typical of most museum collections, may be the tendency to overcollect rare and under-represent common plant taxa. However, this bias is partially compensated for by the large sample size. Fossil plants in our sample were preserved in a full range of floodplain environments, including active and abandoned channels, splays, ponds, and swamps, all of which were locally present during both the Cretaceous and Paleocene (17). The majority of Cretaceous specimens were derived from channels versus ponds and swamps for the Paleocene, and there does not yet exist sufficient material for a facies-equivalent study. Nevertheless, we do not consider the facies change near the K/T boundary to be a major impediment because the K/T plant extinctions in our section are well documented, and extirpated taxa, on which Cretaceous insects depended, do not reappear elsewhere (17); diverse insect damage is known to be recoverable from swamp and pond deposits (30); and grain size differences should bias against observing an extinction because of the presumably low potential for preservation of insect-damaged leaves in relatively energetic, allochthonous settings such as channels (30). The leaf-bearing horizons in our section appear to have originated as single episodic burial events ranging from hours to days in duration and representing samples of the original vegetation ranging from approximately 10^4 m^2 for parautochthonous to several square kilometers for allochthonous assemblages (31, 32).
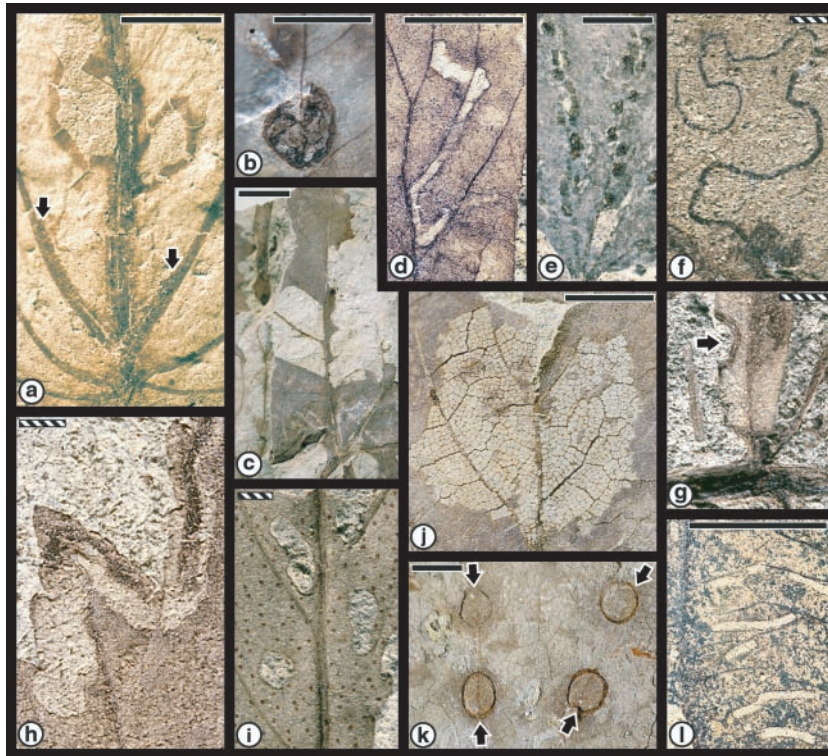
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Fig. 1. A spectrum of plant–insect associations from the Williston Basin of southwestern North Dakota. Associations range from the earliest Paleocene at upper left, 14.4 m above the K/T boundary, and continue to the older associations of the latest Cretaceous at lower right, 85.5 m below the boundary. All material is from the Denver Museum of Nature and Science (DMNH) or the Yale Peabody Museum (YPM). Following each plant host are, respectively, morphotype number (indicated by the prefixes HC or FU) (17), specimen number, DMNH locality number (loc.), and ± meter distances from the K/T boundary as in Fig. 2 (17). Damage types are indicated by the prefix DT (Fig. 2). (Scale bars: solid = 1 cm, backslashed = 0.1 cm.) (*a*) Two linear mines with oviposition sites (arrows), following secondary and then primary venation, terminating in a large pupation chamber (DT59), on the dicot *Paranymphaea crassifolia* (FU1), DMNH 20055, loc. 563, +14.4 m. (*b*) Single gall (DT33) on primary vein of *Cercidiphyllum genetrix* (Cercidiphyllaceae, FU5), DMNH 20042, loc. 562, +8.4 m. (*c*) Free feeding (DT26) on *Platanus raynoldsi* (Platanaceae, FU16), DMNH 20035, loc. 2217, +1.3 m. (*d*) Skeletonization (DT61) on a probable lauralean leaf (HC32), DMNH 19984, loc. 2097, −31.4 m. (*e*) Multiple galls (DT33) on *Trochodendroides nebrascensis* (Cercidiphyllaceae, HC103), DMNH 19976, loc. 1489, −33.7 m. (*f*) Initial phase of a serpentine mine (DT45) on *Marmarthia pearsonii* (Lauraceae, HC162), DMNH 7228, loc. 2087, −36.9 m. (*g*) Cuspate margin feeding (DT12, arrow) on *Metasequoia* sp. (Cupressaceae, HC35), DMNH 13108, loc. 567, −56.8 m. (*h*) Serpentine leaf mine (DT43) assigned to the Nepticulidae (Lepidoptera), on unidentified Rosaceae (HC80), YPM 6367a, loc. 567, −56.8 m. (*i*) Hole feeding pattern (DT57) on an unknown genus of Urticales (HC81), DMNH 19539, loc. 2203, −56.8 m. (*j*) General skeletonization (DT16) on *Erlingdorfia montana* (Platanaceae, HC57), DMNH 11013, loc. 571, −61.7 m. (*k*) Large scale-insect impressions (DT53) centered on primary veins of *E. montana*, DMNH 18829b. loc. 571, −61.7 m. (*l*) Slot hole feeding (DT8) on an unidentified genus of Platanaceae (HC109), DMNH 18658, loc. 434, −88.5 m. See Table 1, which is published as supporting information on the PNAS web site, www.pnas.org, for additional descriptions of damage types.

Each specimen was inspected for insect-mediated damage, which when present, was assigned to one or more of 51 insect damage types (Figs. 1 and 2). Herbivory was recognized on the basis of four explicit criteria, which were used singly or in combination. These criteria were: the presence of reaction tissue; anatomic details of the cut margin, such as excision cusps made by mandibles; stereotypy based on pattern, position, or size and shape of the damage; and plant-host specificity (24, 33). Each damage type then was classified into one of four functional feeding groups: external foliage feeding, subdivided into margin feeding, hole feeding, skeletonization, and special types of external feeding damage; galling; mining; and piercing and sucking; as well as a separate, nonfeeding damage type for oviposition. Additionally, we assigned each damage type to one of three categories based on the degree of plant-host specificity typically but not exclusively found in various insect species producing the same damage type today (24): generalized for polyphagy, intermediate for oligophagy, and specialized for monophagy. We note that some occurrences of damage types within our generalized category undoubtedly represent feeding by specialist as well as generalist insects, thus biasing toward a conservative estimate for specialist extinction. Host specificity assignments were based on published surveys of modern plant

damage linked to ecologically known insect taxa, including the spectra of host–plants consumed by descendant or otherwise related taxa (34–36), occasionally supplemented by plant–host specificity patterns observed in the fossils (24, 37). Our determinations (Table 1) are an expansion of previous work characterizing insect damage on latest Paleocene to middle Eocene floras (27, 30).

Of the examined 13,441 fossil plant specimens, 9,292 were Cretaceous and 4,149 were Paleocene. Although the Cretaceous was more heavily sampled than the Paleocene in the total specimen count, possibly biasing in favor of a greater apparent extinction, the critical lowest 5 m of the Paleocene was as well sampled as any 5-m portion of the Cretaceous, with 2,314 specimens. We also used two principal techniques to minimize sampling effects: confidence intervals on stratigraphic ranges that take varying sampling into account (Fig. 2) and bootstrap analyses, namely repeated and random resampling through a range of sample sizes (Fig. 3*b* and Table 3, which is published as supporting information on the PNAS web site).

The standard technique for computing classical confidence intervals (38) was inapplicable to our data because the distributions both of the fossil horizons and of sampling intensity are
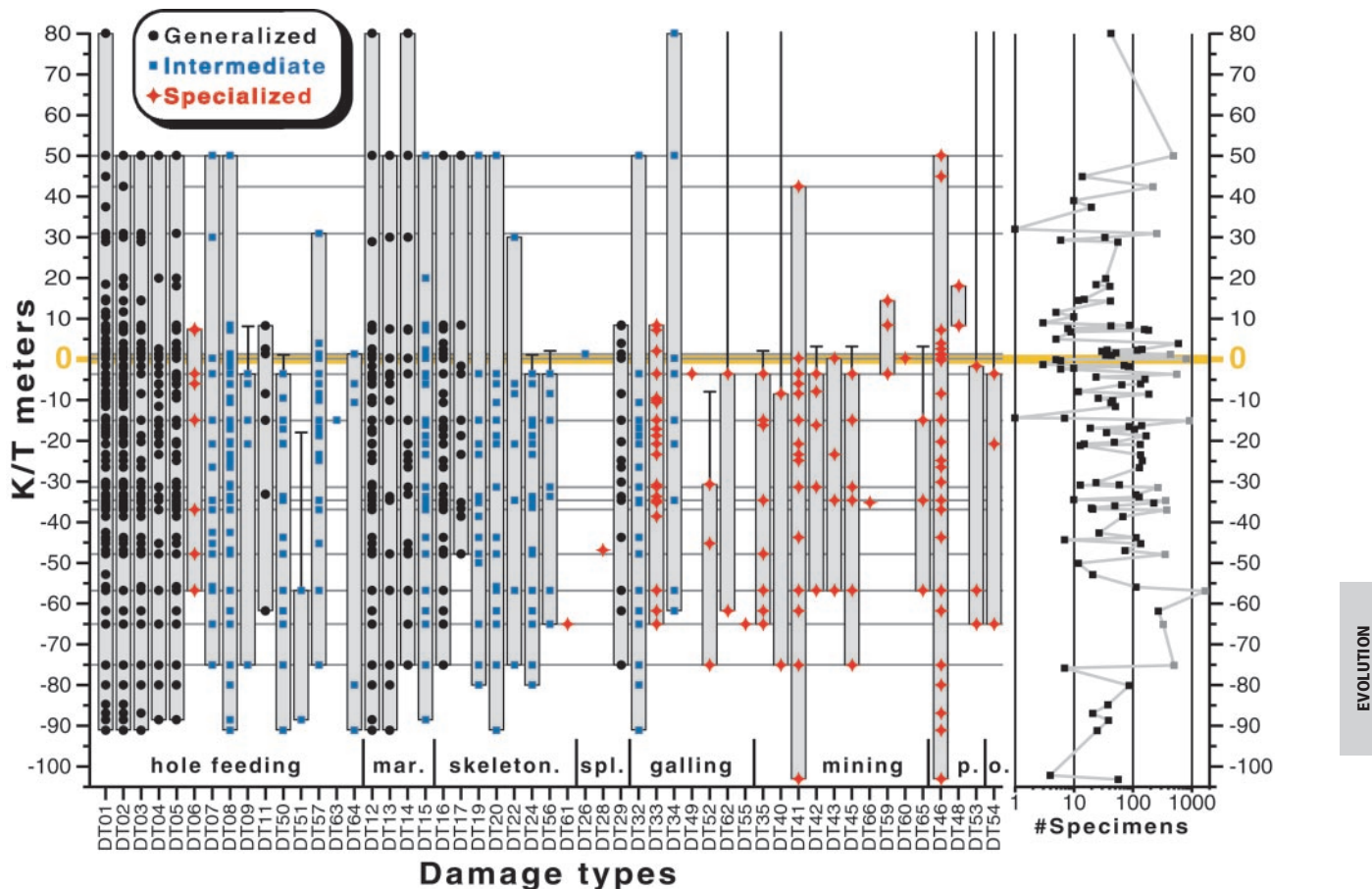
Fig. 2. Stratigraphic and sampling data for the 51 insect-mediated damage types from a 183-m composite section straddling the K/T boundary (orange bar), from the Williston Basin of southwestern North Dakota (Table 1 and Table 2, which is published as supporting information on the PNAS web site). The estimated time duration for this interval is 2.2 million years (my) before present, of which 0.8 my are assigned to the postboundary interval and 1.4 my are allocated to the preboundary interval (2). The Cretaceous strata are within the Hell Creek and Fort Union formations, and the Paleocene strata are entirely within the Fort Union Formation (2, 17). Placement of the zero datum is at the K/T boundary, not the Hell Creek/Fort Union formational contact, because the contact is diachronous with respect to the K/T boundary timeline (17). Depicted are the raw presence/absence data for damage types, categorized by functional feeding group and subgroup at the bottom, and representing 106 discrete horizons. Eight damage types have single stratigraphic occurrences (dots); the ranges of those with multiple stratigraphic occurrences are shown as vertical shaded bars, categorized by host specificity from the color scheme at upper left (see text). Confidence intervals of 50% are provided for the 14 damage types whose regional last appearances occur before the boundary, using a method that accommodates nonrandom distributions of fossil horizons and sampling intensity by allowing recovery potential to vary stratigraphically (39) (see text). Of the 14 specialized damage types with multiple stratigraphic occurrences that disappear at or below the K/T boundary, six (42.9%) reappear during the latest Paleocene to middle Eocene of Wyoming and Utah (27, 30). All associations are extant today. Four confidence intervals that exceed our sampling range are shown without end bars. Total specimen frequencies are given at right, including all plant organs; note logarithmic scale. The gray horizontal lines in the main figure and corresponding gray squares at right indicate the 14 horizons with more than 200 specimens of identified dicot leaves, used in Fig. 3; meter levels for these floras are: −75.0, −65.0, −56.8, −47.8, −36.9, −34.6, −31.4, −15.0, −3.6, +0.2, +1.3, +30.9, +42.4, +50.0. Abbreviations: mar., margin feeding; skel., skeletonization; spl., specialized external feeding types; p., piercing and sucking; o., oviposition. Limitations on graphical presentation cause the flora at +0.2 m, which is Paleocene, to appear within the orange line representing the K/T boundary.

nonrandom (Fig. 2). The fossil recovery potential, which is the relative likelihood of sampling a particular damage type at a certain horizon L, is therefore not uniform. However, the recent method of Marshall (39) allows for nonrandomness if fossil recovery potential can be defined in relation to stratigraphic level. In our data set, the recovery potential of a damage type at a particular L is well approximated by the number of plant specimens from L examined for insect damage. Specifically, all of the 14 damage types with range tops below the K/T boundary occurred exclusively on dicot leaves, so we defined the number of identified dicot leaves within each of 184 1-m bins to be the relative potential of sampling a damage type within that bin. The sum of the numbers of dicot leaves in each bin within the range of a damage type, inclusive, was considered to be the cumulative relative potential of recovery, CP. A proportionality factor α for the desired

confidence level, defined in equation 2 of ref. 39, was multiplied by CP to derive a scaled potential, SP, equal to the right side of equation 3 of ref. 39. The confidence interval must contain the same cumulative potential as SP, represented by the left side of equation 3 of ref. 39, and this potential was calculated in an analogous manner to CP: starting in the bin above the range top of a damage type and proceeding to sequentially higher bins. The number of dicot leaf specimens was summed until a number greater than or equal to SP was reached. The top of the highest bin summed was the top of the confidence interval.

Results

The stratigraphic structure of our presence–absence data is shown in Fig. 2. Generalized damage types are better represented than the intermediate and specialized types. Whereas all
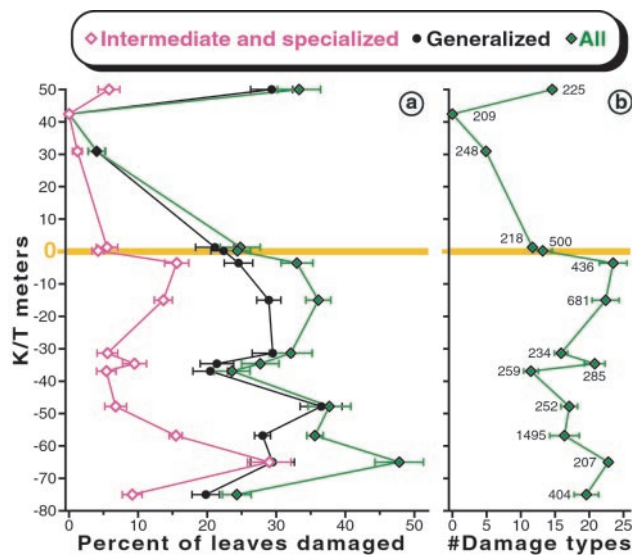
Fig. 3. (*a*) Frequency analyses (percentage basis) of insect damage for the 14 discrete horizons with at least 200 specimens of identified dicot leaves. The vertical scale shows the meter level with respect to the K/T boundary (orange bar). The horizontal scale is the percentage of leaves bearing insect damage. Binomial error bars of $\pm 1\,\sigma$ are placed on frequency data based on the number of specimens (30). In green are all damage types; black, generalized damage types only; and purple, lumped intermediate and most specialized damage types. Because some individual leaves contain more than one damage type, the total percentage (green) is usually less than the sum of the two other data series. (*b*) Damage diversity analysis of insect damage, with raw data bootstrapped to 5,000 replicates (27). Vertical scale and zero datum as in *a*; the data series shows the mean number of damage types for 200 specimens. The data labels show the number of leaves in each sample and also pertain to *a*. Limitations on graphical presentation result in the data from +0.2 m (500 specimens), which are Paleocene, to appear within the orange line representing the K/T boundary. Error bars represent $\pm 1\,\sigma$ around the mean and are mathematically forced to be small when the total number of specimens only slightly exceeds 200. Poor preservation is probably responsible for the lack of recovered insect damage around the 30- to 40-m interval. See Table 3.

12 generalized associations traverse the boundary, 37.5% (6/16) of the intermediate and 70.0% (14/20) of the specialized damage types present in the Cretaceous do not. Of the 14 Cretaceous associations that do not cross the boundary and occur at two or more stratigraphic levels, 10 have a last appearance in the uppermost Cretaceous horizon with a large sample size (Fig. 2), 3.6 m below the K/T boundary, or even higher in the Cretaceous. Therefore, at the limit of detection, these 10 damage types do not appear to have gone extinct before the boundary. These observations are reinforced by placement of 50% confidence intervals on the range tops of the 14 associations whose ranges terminate before the K/T boundary and whose apparent disappearances could be attributed to preservation or sampling (40) (Fig. 2). Only two of the 14 exhibit a 50% chance of extinction below the boundary. Of the remaining 12 associations, eight show a 50% chance of their real extinction occurring in the interval between the boundary and +8 m, and seven between the boundary and +3 m. Four of the 14 associations, with 50% confidence intervals that range above Fig. 2, are too rare for quantitative evaluation of their disappearance, yet three of these have a last appearance 3.6 m or closer to the boundary. The preceding observations, coupled with the major reduction of specialized insect damage immediately above the boundary that lasts throughout the sampled interval (Figs. 2 and 3), are consistent with a genuine extinction at the K/T boundary.

In addition to the presence–absence analyses (Fig. 2), we examined changes in the frequency and diversity of insect damage through the section (Fig. 3). Potential problems with such analyses are related to differential herbivory on various types of plant organs and to the lower likelihood of finding herbivory on the unevenly distributed fraction of unidentified plant specimens, which tend to be more poorly preserved. Following previous studies (27, 30), we avoided these biases by restricting the analyses for Fig. 3 to identified dicot leaves, which comprised 9,313 (69.3%) of the 13,441 specimens analyzed in Fig. 2. We further confined the analyses to the 14 discrete horizons containing at least 200 leaf specimens, which represented the best compromise between stratigraphic inclusiveness and sufficient sampling. Frequency (Fig. 3*a*) is expressed as the percentage of leaf specimens with insect damage, and damage diversity (Fig. 3*b*) is expressed as the bootstrapped number of damage types. Whereas the frequency data are not particularly affected by sample size once an adequate specimen count has been reached, damage diversity is quite sensitive to sampling intensity (27). Bootstrapping allowed comparisons at an equal sample size, in this case 200 leaves (Fig. 3*b*).

At the K/T boundary, all of the frequency analyses show a decrease in herbivory (Fig. 3*a*), with the most severe decrease among intermediate and specialized damage types, which decline from 16% to 4%. At +50.0 m, generalized feeding again rises to Cretaceous levels, but intermediate and specialized feeding remain relatively low (6%). The frequency data (Fig. 3*a*) are mirrored by the damage diversity data (Fig. 3*b*) near the boundary. Bootstrap values range from 12 to 24 damage types for Cretaceous samples, with particularly high diversity in the uppermost Cretaceous. These values decline, from 24 at −3.6 m to 13 at +0.2 m, with a modest rebound at +50.0 m.

Although there are also significant fluctuations before the boundary (Fig. 3), the combination of decreases together with parallel patterns in the presence–absence data (Fig. 2), the sustained low herbivory levels above the boundary, and the failure of specialized damage types to recover, appear to record a major extinction event. Given a positive correlation between herbivory and temperature (30), the high herbivory levels during the latest Cretaceous and low values during the Paleocene (Fig. 3) may be partly related to warming temperatures during the latest Cretaceous and cooling near the K/T boundary (14, 41). However, neither climatic nor local facies changes near the K/T boundary provides a sufficient explanation for the extirpation of specialized insect feeding (Fig. 2) that was coupled with a mass extinction of plants. Instead, the collapse of community structure is apparently analogous to the reduction in epifaunal tiering in marine habitats that followed the Permian/Triassic extinctions (42).

Discussion

Our data support two nonexclusive scenarios for the termination of intermediate and specialized associations. First is a primary extinction in which the insects were exterminated outright by adverse environmental conditions. Alternatively, a secondary extinction occurred after the demise of plant hosts (43). Most insect herbivores are host–plant specialists (28); estimates of the number of insect species that consume only one or a few chemically similar plant–host genera are typically more than 70% for major phytophagous insect clades (44, 45). In either scenario, our data probably underestimate the severity of extinction because of the broad taxonomic coverage represented by the generalized damage types, which include some damage made by host-specialized insects.**

**Given an ≈80% extinction for plant species at the end of the Cretaceous (17) and that ≈70% of herbivorous insects are oligophagous or monophagous (44), then a very rough estimate is that 55–60% of herbivorous insects were extirpated at the K/T boundary, with the simplifying assumption that every plant species had the same number of dependent herbivore species, 70% monophagous and 30% polyphagous. This finding compares favorably to our value of a 41.7% decrease in total associations.

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The simple demise of coupled plant and insect extinctions under the second scenario would be mitigated if some specialized herbivores were primarily tracking plant secondary chemistry (45–47), and thus survivors could colonize new but chemically similar host lineages (28). However, under conditions where approximately 80% of megafloral species were extinguished (13, 15), both continued host tracking and lateral transfer (43, 48) were largely unavailable. By contrast, generalist insects could have been significantly buffered from secondary extinctions by polyphagy, as suggested by studies of herbivore specificity on recently introduced plants (49, 50).

Our results, presently limited to a single basin, are potentially informative regarding the continuing debate over whether biotic changes at the K/T boundary were sudden (3, 7, 9, 11), gradual (51, 52), or indeterminate (40, 53). By comparison, even the dramatic climatic warming and vegetational changes associated with the Paleocene–Eocene boundary in nearby Wyoming did not incur a net loss of feeding associations (27, 30). Instead, only small turnovers of damage types occurred, demonstrating the capacity for insects to adapt to relatively gradual but cumulatively significant perturbations of the environment, shown also in studies of the Pleistocene (21). The sudden and sustained loss of many categories of feeding associations at the K/T boundary appears to be integrally related to the extinctions of about 80% of plant species (15) and stands in sharp contrast to the Paleocene–Eocene interval. This contrast supports a rapid and catastrophic failure of terrestrial ecosystems in the Williston Basin.

Theoretical explanations for plant–insect associations (28), including reciprocal genetic feedback that is inherent in true coevolution (46), would predict a bottleneck with lasting effects that would result from the decimation of both participants. In areas of the Northern Rocky Mountains and Great Plains sampled to date, plant diversity was not comparable to the latest Cretaceous until the early Eocene, more than 10 million years after the K/T event (54). Further, we reanalyzed late Paleocene and early Eocene herbivory data from nearby Wyoming (27), for direct comparison to Fig. 3. The resulting herbivory levels are lower than the latest Cretaceous, with values comparable to the highest stratigraphic horizon in Fig. 3.[††] Consequently, the possibility of a prolonged Paleocene interval of depauperate plant–insect associations deserves further investigation.

[††]The Wyoming data also are derived from plant fossils found in fine-grained, flood plain environments. The only difference in methodology is that the Wyoming data are from quantitative field censuses, not museum collections. Damage frequency for intermediate plus specialized damage types (Paleocene, Eocene): $3.87 \pm 0.705\%$, $5.30 \pm 0.796\%$; for generalized damage types: $24.8 \pm 1.58\%$, $31.2 \pm 1.65\%$; for all damage types: $28.3 \pm 1.65\%$, $34.8 \pm 1.69\%$. Bootstrapped number of damage types for 200 specimens: 15.0 ± 2.20, 13.9 ± 1.78 (27).

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