Tansley review

Insect-damaged fossil leaves record food web response to ancient climate change and extinction

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Contents

Summary

Plants and herbivorous insects have dominated terrestrial ecosystems for over 300 million years. Uniquely in the fossil record, foliage with well-preserved insect damage offers abundant and diverse information both about producers and about ecological and sometimes taxonomic groups of consumers. These data are ideally suited to investigate food web response to environmental perturbations, and they represent an invaluable deep-time complement to neoecological studies of global change. Correlations between feeding diversity and temperature, between herbivory and leaf traits that are modulated by climate, and between insect diversity and plant diversity can all be investigated in deep time. To illustrate, I emphasize recent work on the time interval from the latest Cretaceous through the middle Eocene (67–47 million years ago (Ma)), including two significant events that affected life: the end-Cretaceous mass extinction (65.5 Ma) and its ensuing recovery; and globally warming temperatures across the Paleocene–Eocene boundary (55.8 Ma). Climatic effects predicted from neoecology generally hold true in these deep-time settings. Rising temperature is associated with increased herbivory in multiple studies, a result with major predictive importance for current global warming. Diverse floras are usually associated with diverse insect damage; however, recovery from the end-Cretaceous extinction reveals uncorrelated plant and insect diversity as food webs rebuilt chaotically from a drastically simplified state. Calibration studies from living forests are needed to improve interpretation of the fossil data.

I. Introduction

How do food webs evolve through time, and how do they respond to major environmental perturbations? Despite the broad appeal of these questions, the deep-time (before *c.* 2 million years ago (Ma)) fossil record has virtually no assemblages wherein the diversity and composition of more than one level of a food web can be reasonably documented with directly preserved evidence of one group's feeding on another. Numerous productive examples exist of single associations (e.g. Collinson & Hooker, 2000; Richter & Baszio, 2001a; Tsujita & Westermann, 2001; Kowalewski, 2002; Prasad *et al.*, 2005) or, more rarely, diverse prey associated with typically undiverse representation of predator diversity such as shell drillhole or coprolite morphotypes (e.g. Richter & Baszio, 2001b; Vannier & Chen, 2005). Fossil food web research has thus emphasized a combination of reconstructions from paleontological inference (Chin & Gill, 1996), isotope geochemistry (Quade *et al.*, 1992; D'Hondt *et al.*, 1998; Schweizer *et al.*, 2007), and theoretical modeling (Solé *et al.*, 2002; Roopnarine, 2006).

The paleobotanical record offers a bright spot in this challenging landscape because bulk assemblages of fossil plant organs frequently bear diverse and well-preserved tissue damage that is diagnostic of insect herbivores. Thus plant fossils, uniquely in the fossil record, present abundant and diverse information about at least two, and sometimes more (when there is evidence of predation) levels of a food web. The abundance of fossil plant–insect associations is particularly fortuitous because they represent the two dominant clades of macroscopic organisms and their trophic associations (Schoonhoven *et al.*, 2005). The insect body-fossil record is episodic, being heavily biased towards the exceptional preservation found in some amber and lake deposits (Labandeira & Sepkoski, 1993; Grimaldi & Engel, 2005). Fossil plants occur much more evenly through time and space, including many important intervals and regions that lack any significant quantity of insect body-fossils. Even when insect fossils are present in the same deposits as plants, both are dispersed and extremely infrequently found in direct trophic association (Nishida & Hayashi, 1996), whereas insect damage offers direct ecological evidence that complements body fossils. Highly stereotyped insect damage can diagnose particular insect clades feeding on well-defined plant hosts in the past, offering unique calibration data for coevolutionary hypotheses, as seen for rolled-leaf hispine beetle feeding on latest Cretaceous gingers (Wilf *et al.*, 2000 and discussions in: Grimaldi & Engel, 2005; McKenna & Farrell, 2006; Chaboo, 2007; Gómez-Zurita *et al.*, 2007).

The fossil record of plants eaten by insects has been recently treated elsewhere (see below), although there is much less literature than in mainstream paleobotany and paleoentomology. Damaged plant tissues comprise one portion of a spectrum of evidence for ancient associations that also includes coprolites,

gut contents, insect mouthparts, and plant reproductive structures. My focus here is on how insect-damaged fossil plants can be used to interpret past environmental change, and for other aspects of the rich and informative associational record I refer the reader to an incomplete selection of reviews and particularly significant papers (Opler, 1973; Hickey & Hodges, 1975; Crane & Jarzembowski, 1980; Rozefelds, 1985; Scott *et al.*, 1992, 1995, 2004; Stephenson & Scott, 1992; Labandeira & Sepkoski, 1993; Labandeira *et al.*, 1994; Ash, 1996; Labandeira & Phillips, 1996a,b, 2002; Labandeira, 1997, 1998, 2005, 2006, 2007a,b; Glasspool *et al.*, 2003; Erwin & Schick, 2007).

As shown in the above contributions and summarized most recently by Labandeira (2006, 2007b), there is evidence for insect herbivory as early as the Late Silurian (Edwards *et al.*, 1995; 417 Ma; spores and other plant matter in coprolites). Folivory, in particular, has been a major feature of terrestrial ecosystems since at least the Late Carboniferous (305 Ma). By this time, most functional feeding groups were present (but mostly perpetrated by extinct insect clades such as Palaeodictyoptera): external feeding, piercing-and-sucking, boring, galling, seed predation, and oviposition, which is not a feeding group in the strict sense but makes comparable use of plant tissues. By the Late Triassic, the remaining feeding group, leaf mining, had appeared in Gondwana (Rozefelds, 1985; Scott *et al.*, 2004), and the dominant herbivores belonged to the major extant clades of Orthopterida, Hemiptera, and Holometabola.

Although fossil insect damage has been found on all plant organs, compressed leaves offer the most consistently abundant, diverse, widespread, and accessible record through time (Fig. 1); however, other modes of preservation, including the three-dimensional, anatomical preservation found in cherts and coal balls, can be extremely prolific in certain time intervals and settings (Labandeira & Phillips, 1996a,b, 2002). Compressed leaves are by far the most common type of plant macrofossil. For example, 66% of more than 46 300 plant macrofossil occurrences in the Paleobiology Database (paleodb.org, queried 16 July 2007) are leaves, and these overwhelmingly come from compression floras (technically termed adpression or compression-impression floras). Leaf compression floras, compared with wood, fruit, and seed assemblages (and most other types of fossil such as bone and shells), typically represent very little time-averaging (10^{0-2} yr for fluvially deposited leaf assemblages, or 10^{2-4} yr for lake deposits, vs 10^{3-6} yr for bone beds) and, with very rare and easily detected exceptions, cannot be reworked into younger sediments (Wing & DiMichele, 1995). Moreover, compression floras are taphonomically consistent through time because they typically represent a limited number of fluvial and lacustrine paleoenvironments (Wing & DiMichele, 1995; Behrensmeyer *et al.*, 2000). Leaf fossils can be collected with relative ease to sample sizes in the thousands from surface outcrops, where they are often associated with detailed
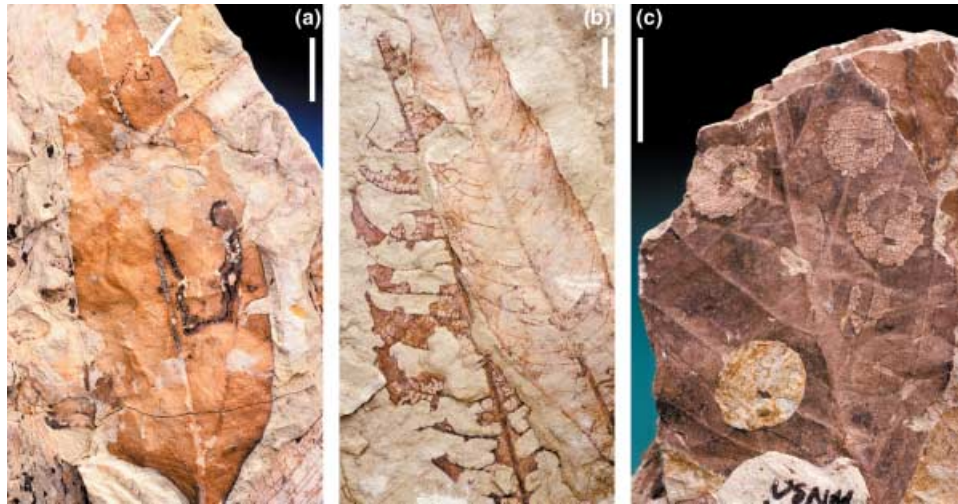
Fig. 1 Selected examples of fossil insect damage from the early Eocene Sourdough (a, b) and late Paleocene Clarkforkian (c) floras of southwestern Wyoming (Table 1). Bars, 1 cm. (a) Serpentine mine (damage type 44) on a Lauraceae leaf. Note oviposition site near apex (arrow; the fossil leaf is missing a fragment under the initial and above the mature portion of the mine); increase in mine width towards base of leaf; dark, medially confined, undulatory frass trail; necrotic reaction tissue, generated by the leaf, on mine border; and circular termination chamber near margin. Likely culprit: Nepticulidae, Lepidoptera. Specimen: National Museum of Natural History (USNM) 498162, USNM locality 41352. (b) *Platycarya americana* (Juglandaceae, two specimens), specimen at left skeletonized with extensive removal of high-order (fine) venation (damage type 21; USNM 498163, USNM loc. 41332). (c) Series of circular skeletonized areas with leaf case shelter sites preserved as unskeletonized zones in centers (damage type 38) on *Corylites* sp. (Betulaceae). Note incomplete feeding site at center right and completely excised area at lower left, used to make a leaf case. This feeding syndrome is typical of fairy moths (Incurvariidae, Lepidoptera; USNM 498164, USNM loc. 41270). See Labandeira *et al*. (2007b) and references therein for a complete inventory of fossil damage types. Photography by Chip Clark, National Museum of Natural History.

stratigraphic context and other ecologically or biostratigraphically informative fossils such as palynomorphs and vertebrates (Clyde *et al.*, 2007). The same leaf assemblages that hold the insect damage also provide a wealth of highly relevant proxy information for past climates, environments, and plant traits that greatly enriches the context of paleoherbivory data. For example, mean annual temperature and precipitation are routinely estimated from leaf margin characteristics and leaf size, respectively (Wolfe, 1971; Wilf *et al.*, 1998; Wing *et al.*, 2000; Jacobs & Herendeen, 2004), and multivariate approaches using additional leaf shape and climatic variables have great potential (Wolfe, 1993; Royer *et al.*, 2005; Greenwood, 2007). A new method reconstructs leaf mass per area, an important trait for interpreting folivory, from fossil petiole width and leaf area, using the extant scaling relationship of petiole width^2 and leaf mass, normalized for leaf area (Royer *et al.*, 2007a). To a much greater extent than other preservational modes of fossil plants, compressed leaf floras that are well preserved nearly always bear an ecologically representative suite of insect herbivore damage, and many types of damage often occur on a single specimen.

Most literature (as cited above) on fossil plant–insect associations has focused on iconic floras or single associations from widely separated (10^7 to 10^8 yr) time periods and regions. However, the stratigraphic approach reviewed here allows us to investigate how plant–insect food webs respond to significant, geologically short-term (10^5 to 10^6 yr) events,

such as rapid climate change and significant extinctions or evolutionary radiations documented from other fossil biota. The questions and hypotheses are framed and informed by ecology, but the ability to address them is made possible by advances in geochronology, paleobotany, and the quantification of insect damage that are not widely known to nonspecialists.

Below, I review this core toolkit, outline critical hypotheses that can be tested using insect-damaged leaves, and summarize progress to date in testing these hypotheses using several case studies from a 20 million year (Myr) time slice of the latest Cretaceous to middle Eocene, Western Interior USA (Table 1; Fig. 2). This time interval and place are dramatically suited to the hypotheses, including outstanding preservation within a single region of the end-Cretaceous mass extinction and recovery, followed *c*. 10 Myr later by the most significant global warming interval of at least the past 70 Myr. I also briefly mention recent work from the early Eocene of Patagonia, Argentina because it uses the same methods within the same time interval and allows interesting comparisons. Progress is being made in other intervals and regions with well-resolved floral sequences such as the Permian of Texas (Beck & Labandeira, 1998; Labandeira & Allen, 2007), the Permian-Triassic of South Africa (Gastaldo *et al.*, 2005), the middle to late Eocene of Colorado (Smith, 2000; Hodgkins & Smith, 2002), and the Oligocene to Pliocene of Central Europe (Titchener, 2000). However, the Cretaceous to middle Eocene interval in the Western Interior USA is currently the
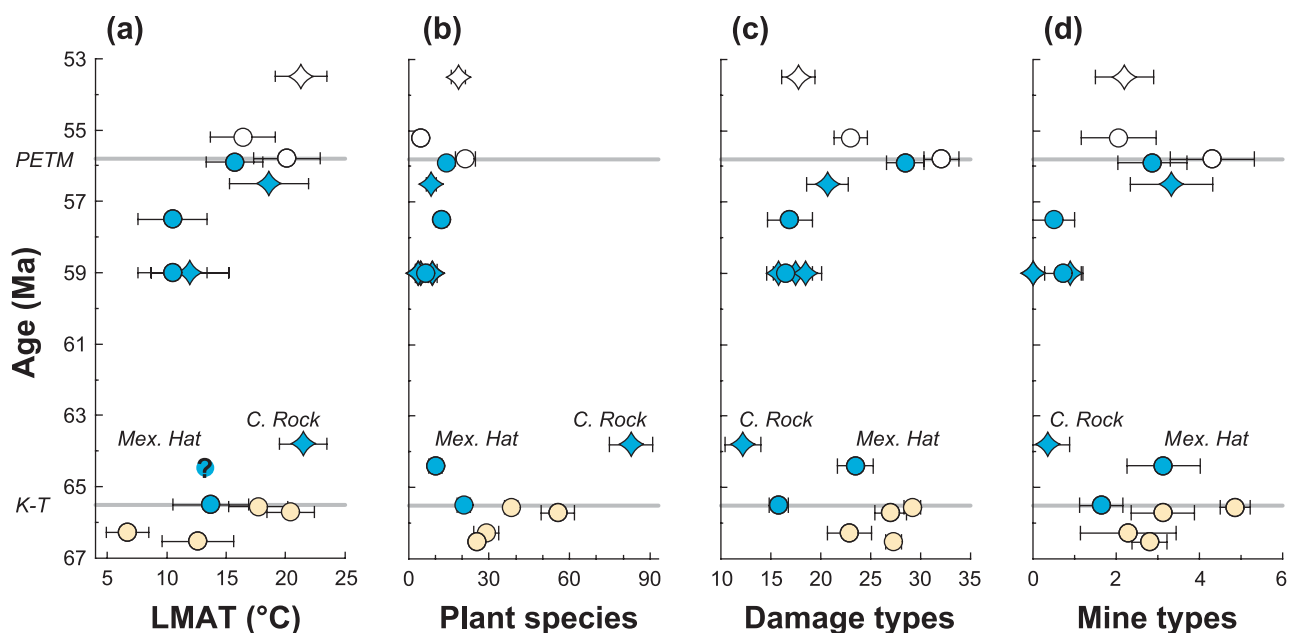
Fig. 2 Estimated paleotemperature (a), plant alpha diversity (b), total insect-damage richness (c), and mine richness (d) for dicot leaves from the bulk floras listed in Table 1, including fluvially deposited and excluding the environmentally dissimilar fossil lake floras. Circles, samples from the relatively uniform latitudes of northwestern Wyoming, Montana, and North Dakota. Concave diamonds, samples from relatively southern locations: southwestern Wyoming and the Denver Basin. LMAT, mean annual temperature estimated from leaf-margin analysis ± 1σ (Wilf, 1997: eqns 2 and 4) of the floras in (b), (c) and (d) and their stratigraphic correlates (Wing *et al*., 2000; Wilf, 2000; Wilf *et al*., 2003b; Currano *et al*., 2008). Most of the LMAT estimates are corroborated from independent proxies (Wing *et al*., 2000; Wilf *et al*., 2003b). The Mexican Hat flora has too few species for reliable climate analysis and is shown with a question mark in (a); because of similar species composition and location, it is probably very close climatically to the underlying Pyramid Butte sample. All data in (b), (c) and (d) are statistically adjusted to a sample size of 400 leaves, using rarefaction (b), shown with 95% confidence intervals (Tipper, 1979), or using random resampling of leaves without replacement (Wilf *et al*., 2001), shown as the means of 5000 iterations ± 1σ (c, d). Oviposition damage is not included. Symbol colors are used for visual separation of Cretaceous (below K-T line), Paleocene, and Eocene (within Paleocene–Eocene Thermal Maximum (PETM) line and above) samples that are closely spaced. Much additional detail is revealed in the species-level analyses discussed in the text and cited papers.

most thoroughly studied and offers a well-integrated introduction to the broad appeal of the approach.

II. Tools

1. Not your father's geologic time scale

When a flora is selected for insect-damage investigation, highest priority must be given to its chronologic and stratigraphic context. Recent order-of-magnitude improvements in telling geologic time throughout the rock record are revolutionizing all areas of paleobiology, which is in turn a major motivator for the improvements. These are most recently encapsulated in the dramatically improved 2004 geologic time scale (Gradstein *et al*., 2004). 'No dates, no rates' is a popular community saying that summarizes the importance of accurate ages, without which no fundamental questions can be asked about how fast life evolves and goes extinct. Errors are rapidly diminishing as techniques and instruments employed in both of the major absolute dating systems, Ar-Ar and U-Pb (both derived from radioactive decay series of minerals found in volcanic ashes), improve and

geochronologists neutralize inter-laboratory discrepancies and share techniques (www.earth-time.org; see Dalton, 2006). The state of the art is now moving towards and below 0.1% error at 95% confidence (Furin *et al*., 2006).

Accompanying the geochronologic improvements have been a suite of associated advances that complement the somewhat rare datable ashes. These include improvements in the quality of paleomagnetic stratigraphy (Clyde *et al*., 2007), which is widely applicable in continental (of nonmarine origin) rocks bearing fossil plants; refined calibration of magnetic reversals in deep-sea sediments to astronomical forcing cycles (Westerhold *et al*., 2007) that allow precise age models for magnetic chrons to be developed and also applied to continental sediments (Hicks *et al*., 2002); continued development of isotopic geochemical techniques that pinpoint the timing and correlation of significant environmental events on land and sea (Koch *et al*., 1992; Hesselbo *et al*., 2003; Montañez *et al*., 2007); the introduction of differential global positioning systems, which allow highly accurate measurements of rock attitudes and thickness and the rapid placement of new fossil localities into a rigorous framework (Secord *et al*., 2006); and significant improvements in the quality of biostratigraphic data, notably including (for

Table 1 Principal fossil floras discussed in text

Flora	Age (Ma)	Rock unit and location	Paleobotany references, selected	Insect damage references
Early and middle Eocene				
Bonanza*	47.3	Green River Fm., Uinta Basin, NE Utah	MacGinitie (1969); Wilf *et al*. (2001)	Wilf *et al*. (2001)
Republic*	49.4	Klondike Mountain Fm., NE Washington	Wolfe & Wehr (1987); Pigg *et al*. (2007)	Labandeira (2002); Wilf *et al*. (2005b)
Laguna del Hunco*	51.9	Laguna del Hunco Tuffs, NW Chubut, Argentina	Berry (1925); Wilf *et al*. (2005a); Zamaloa *et al*. (2006)	Wilf *et al*. (2005b)
Sourdough	53.5	Wasatch Fm., Great Divide Basin, SW Wyoming	Wilf (2000)	Wilf & Labandeira (1999); Wilf *et al*. (2001)
South Fork of Elk Creek	55.2	Willwood Fm., Bighorn Basin, NW Wyoming	Wing (1998); Currano *et al*. (2008)	Currano *et al*. (2008)
Hubble Bubble	55.8	Willwood Fm., Bighorn Basin, NW Wyoming	Wing & Lovelock (2007); Currano *et al*. (2008)	Currano *et al*. (2008)
Late Paleocene				
Daiye Spa	55.9	Fort Union Fm., Bighorn Basin, NW Wyoming	Currano *et al*. (2008)	Currano *et al*. (2008)
'Clarkforkian'	56.5	Fort Union Fm., Washakie Basin, SW Wyoming	Wilf (2000)	Wilf & Labandeira (1999); Wilf *et al*. (2001)
Lur'd Leaves	57.5	Fort Union Fm., Bighorn Basin, NW Wyoming	Wilf *et al*. (2006)	Wilf *et al*. (2006); Currano *et al*. (2008)
Skeleton Coast	59.0	Fort Union Fm., Bighorn Basin, NW Wyoming	Wilf *et al*. (2006)	Wilf *et al*. (2006); Currano *et al*. (2008)
Kevin's Jerky, HAZ-MAT, and *Persites* Paradise	59.0	Fort Union Fm., Washakie (KJ, HM) and Great Divide (PP) basins, SW Wyoming	Wilf *et al*. (2006)	Wilf *et al*. (2006)
Early Paleocene				
Castle Rock lower layer	63.8	D1 unit, Denver Basin, Colorado	Johnson & Ellis (2002); Ellis *et al*. (2004)	Wilf *et al*. (2006)
Mexican Hat	64.4	Fort Union Fm., Powder River Basin, SE Montana	Manchester & Dilcher (1997); Wilf *et al*. (2006)	Lang (1996); Wilf *et al*. (2006)
Pyramid Butte	65.5	Fort Union Fm., Williston Basin, SW North Dakota	Johnson (2002)	Labandeira *et al*. (2002a,b); Wilf *et al*. (2006)
Latest Cretaceous				
Battleship	65.6	Hell Creek Fm., Williston Basin, SW North Dakota	Johnson (2002)	Labandeira *et al*. (2002a,b); Wilf *et al*. (2006)
Dean Street	65.7	Hell Creek Fm., Williston Basin, SW North Dakota	Johnson (2002)	Labandeira *et al*. (2002a,b); Wilf *et al*. (2006)
Somebody's Garden level	66.3	Hell Creek Fm., Williston Basin, SW North Dakota	Johnson (2002)	Labandeira *et al*. (2002a,b); Wilf *et al*. (2006)
Luten's 4H Hadrosaur level	66.5	Hell Creek Fm., Williston Basin, SW North Dakota	Johnson (2002)	Labandeira *et al*. (2002a,b); Wilf *et al*. (2006)

*Floras deposited in lakes. The other floras were deposited in fluvial environments (see text).

our purposes) the North American land-mammal zonations that have stood for decades as reasonably accurate markers of time (Wood *et al*., 1941; Woodburne, 2004; Secord *et al*., 2006).

2. Sampling fossil leaf diversity

Surprisingly, although the evolutionary radiations of many major plant clades are well timed from fossils (Kenrick & Crane, 1997; Crane *et al*., 2004), very little reliable information exists about global plant diversity through time at the fine taxonomic resolution (family, genus, species) of interest to ecologists. In a series of landmark papers, Niklas, Tiffney, and Knoll analyzed richness compiled from the paleobotanical literature and uncertainties therein (Knoll *et al*., 1979; Niklas *et al*., 1983, 1988; Niklas & Tiffney, 1994), highlighting several difficult problems in resolving

plant diversity through time. In my view, the major issues, most of which could be corrected eventually, are (i) the low number of species known from any particular time period, such that a single diverse flora can greatly distort the pattern; (ii) mixing of floras within time periods from diverse paleolatitudes, paleoenvironments, and paleoclimates, combined with a high degree of spatial patchiness and geographic disparity in the record from time interval to time interval (Rees, 2002); (iii) lost stratigraphic resolution from binning into long time intervals, or inaccurate stratigraphy in poorly studied areas, both blunting the potential to detect extinctions and short-term climate responses; (iv) general lack of information in the literature about sampling intensity or abundance data that would allow sampling standardization; and (v) inconsistent and obsolete taxonomy. In passing, I note that many of the same problems, coupled with an even more patchy, episodic, and unevenly sampled record, affect empirical measures of insect body-fossil diversity through time (Labandeira & Sepkoski, 1993; Labandeira, 2007a).

For our purposes, a far more productive alternative to global data is regional studies from areas with well-developed stratigraphic context and well-documented, consistent sampling procedures, allowing comparisons of relative diversity through time and space. Unbiased, bulk collections, known as censuses, have proved especially valuable because they provide relative abundance data amenable to statistical analyses, including adjustment of samples to uniform sizes via rarefaction and related techniques. After a representative voucher suite has been collected, censusing also allows many specimens to be identified, tallied and left in the field, a major practical advantage when dealing with hundreds to thousands of rocks. Censusing is a standard tool in paleontology and ecology alike, and it has a long history in paleobotany (e.g. Chaney & Sanborn, 1933; McElwain *et al.*, 2007), where the technique is especially amenable to the large sample sizes obtainable from fossil leaves. Further, litter trap work in extant forests validates the technique by analogy. For example, the ranked cumulative leaf area per species correlates well to the ranked stem basal area in local forest (Burnham *et al.*, 1992), and a significant percentage of local forest diversity is represented in a litter sample (Burnham, 1993).

Censuses are demonstrably most effective when combined with simplistic but critical and insufficiently practised techniques, including bench quarrying down to a fossiliferous horizon in an outcrop (rather than chipping from the side) to remove overburden and access less weathered and larger material; field labeling of specimens; and field and laboratory trimming, gluing, and airscribing (dégaging) to reveal the full potential of a leaf specimen. These rules are followed by many different researchers, and a large body of comparable census data has accumulated in the literature. Each census from a single bed represents a restricted spatial and temporal scale, and by iteration this information can be integrated horizontally (through space) and vertically (through time). A leaf census,

at a site with highly resolved stratigraphic context, is the ideal platform for also censusing insect damage on the leaves. Large museum collections (typically 400 or more leaves), if known not to be biased against insect damage or particular host plants, can be substituted for a field census with obvious time savings.

3. Sampling fossil insect-damage diversity

Insect ecologists do not work under the constraints and filters imposed by the fossil record. For good reason, they prefer to tally the diversity of live insects (including rearing them on the plants they are found on, to confirm that they are not merely visiting) rather than ignore the animals in favor of the leaf damage (Basset *et al.*, 1996; Basset, 1999; Barrios, 2003). Quantification of insect damage is almost always in amount or frequency rather than in diversity, usually taking the form of amount of leaf area removed per unit time (Coley, 1983; Lowman, 1984; Basset *et al.*, 1992). Certain major feeding categories, such as galls and mines, are often tallied separately (Basset, 1991). For obvious reasons, rates of herbivory are not retrievable from fossil plants, although the amount and frequency of damage are available. It is possible, but extremely labor-intensive, to approximate the amount of leaf area removed in fossils (Beck & Labandeira, 1998; Labandeira & Allen, 2007; Royer *et al.*, 2007a); although useful, this does not reveal feeding diversity directly and is not informative about leaves that were chewed beyond the point where original area estimation is possible.

Faced with the need to quantify insect-damage diversity in fossils, Wilf & Labandeira (1999) inspected a set of $> 10^4$ compressed plant fossils from the late Paleocene and early Eocene of southwestern Wyoming (Wilf, 2000) and delineated 41 reproducible, countable, discrete morphologies of insect damage, termed damage types (DTs; Fig. 1). The DTs were assigned to functional feeding group categories and also assigned to a crude index of host specificity, as known from the extant insects that generally make the DT, with values of 1 for polyphagous, 3 for monophagous or oligophagous, and 2 for intermediate. As many more fossil floras were studied, the number of DTs recognized, still only a small fraction of those present in nature today, rose rapidly to more than 150 to date. The DTs have been illustrated in a series of publications, most notably Labandeira (2002) and Labandeira *et al.* (2002a), and recently exemplary voucher specimens of each DT, along with descriptions, have been compiled in an illustrated guide that is available and continuously updated on the Web (Labandeira *et al.*, 2007b). An earlier damage type system restricted to fossil galls was presented by Scott *et al.* (1995). Reliable criteria for distinguishing insect damage from mechanical abrasion and other types of degradation are summarized elsewhere (Labandeira, 2006).

The DT system, coupled to stratigraphically controlled, often censused paleobotanical collections of well-preserved,

nonfragmentary, identified leaves bearing the DTs, is the bedrock approach that allows quantitative analysis of both plant and insect-damage diversity through time. Thus, the fossil leaf is the source of both categories of information.

III. Hypotheses and case studies

The fossil floras discussed below are referenced in Table 1, and summary data from the most comparable, fluvially deposited bulk floras (i.e. not including the taphonomically dissimilar lake floras) are shown in Fig. 2 along with estimated mean annual paleotemperatures derived from leaf-margin analysis (details in caption). Many of the most interesting patterns are revealed at the level of individual host plant species, not shown in Fig. 2 because of space limitations but discussed below. As described in detail in the cited literature, most are from field census collections of 400 to several thousand specimens; a few derive from museum censuses of collections with at least 400 specimens.

The Laguna del Hunco, Republic, and Bonanza samples are preserved in fossil lakes, representing accumulations on the order of 10^2 to 10^4 yr (Wing & DiMichele, 1995). The rest are derived from a suite of lowland floodplain environments, including channels, oxbows, ponds, and swamps, thought to accumulate generally in less than 100 yr (Wing & DiMichele, 1995). Most of the samples derive from humid, warm-temperate to subtropical climates; however, the Castle Rock flora represents tropical rainforest conditions. The Republic flora comes from an Eocene volcanic upland with a humid temperate climate, and the Bonanza assemblage was deposited in a markedly more seasonally dry climate than the other samples. For taphonomic consistency, all of the data in Fig. 2 are restricted to leaves (or leaflets in the case of compound leaves) of angiosperms, excluding monocots. All comparative analyses of diversity used standard statistical adjustments for sample size, such as rarefaction or random resampling (Fig. 2, caption).

Hypothesis 1. Insect-feeding diversity and frequency correlate with temperature

There are three major bodies of evidence relevant to this hypothesis: latitudinal gradients in herbivory, experimental data, and the fossil record emphasized here. First, despite greatly elevated plant defenses, insect diversity and attack rates on host plants both tend to increase with decreasing latitude (Erwin, 1982; Coley & Aide, 1991; Coley et al., 1996). Although there is no consensus on the cause, these observations are in accord with primary temperature effects on metabolic rate and thus on much biological activity including both feeding and speciation (Brown et al., 2004; Allen et al., 2006). Galler diversity and abundance are notable exceptions, apparently because moisture disproportionately increases the vulnerability of gallers to predators and pathogens

(Fernandes & Price, 1991, 1992; Godfray, 1994; Price et al., 1998). The latitudinal gradient in herbivory is due for a rigorous re-examination with standardized sampling across latitudes (Novotny et al., 2006; A. T. Moles World Herbivory Project, www.vuw.ac.nz/staff/angela_moles/herbivory.htm).

Secondly, there is a vast literature of modern experimental data on temperature and pCO_2 (the principal cause of temperature change throughout the record: Royer et al., 2007b) effects that tends, for reasons of time and cost, to focus on limited species pairs of plants and herbivores over relatively short time periods of a few months to years (e.g. Zvereva & Kozlov, 2006). In general, effects of increased pCO_2 alone are to lower foliar nitrogen (N) concentration and raise the carbon:nitrogen (C:N) ratio, forcing insects to eat more; however, elevated temperature increases insect growth rates and other performance indices. Much experimental work does not show an increase in herbivore abundance or feeding intensity (Zvereva & Kozlov, 2006; Adler et al., 2007), and the data are not predictive regarding insect diversity. Moreover, in nature, temperature and pCO_2 rise and fall together, and their combined effects on herbivory rates and related plant traits are highly complex and difficult to scale up from experimental to ecosystem level, especially over long time periods (Fajer et al., 1989; Bazzaz, 1990; Lincoln et al., 1993; Cannon, 1998; Coley, 1998; Bale et al., 2002; Zvereva & Kozlov, 2006).

Thirdly, the paleobiological approach reviewed here uniquely shows the integrated sum of changes in a local ecosystem over time, both at whole flora and at host species levels. By analogy to the latitudinal gradient, we can use the fossil record to ask whether herbivore pressure increases with rising temperature, or decreases with falling temperature, at constant latitude and under relatively uniform moisture conditions.

Wilf & Labandeira (1999) quantified insect damage on a latest Paleocene and a middle early Eocene flora from southwestern Wyoming (Table 1, Clarkforkian and Sourdough; Fig. 2). These samples represent a gradual, global warming trend from the late Paleocene to a sustained Cenozoic maximum during the middle early Eocene (Zachos et al., 2001). Locally, the floras represent warming on the order of 3–7°C (depending on which starting point is chosen) and floral diversification over a 3-Myr interval in a humid wetland environment, without significant drying (Wilf, 2000). Results showed a significant increase in attack frequency on bulk floras and host species and in damage type diversity on host species but not bulk floras (Wilf & Labandeira, 1999; Fig. 2). The most abundant plant clade in both samples, Betulaceae, was the most heavily attacked and also showed a significant herbivory increase. Later work in this area added older late Paleocene floras (Table 1, Kevin's Jerky, Haz-Mat, and *Persites* Paradise). These assemblages had significantly lower damage type diversity than the subsequent latest Paleocene floras, correlating to gradual warming during this time period also (Fig. 2; Wilf et al., 2006).

More recently, working in the Bighorn Basin of northern Wyoming, Wing *et al.* (2005) discovered the first macrofloras reliably constrained to the Paleocene–Eocene Thermal Maximum (PETM). Subsequent to the Wing *et al.* (2005) paper, a new, diverse PETM flora was discovered with outstanding preservation (Table 1, Hubble Bubble; Wing & Lovelock, 2007). The PETM was a transient spike in global temperatures, with an onset on the order of 10^4 yr and total duration of *c.* 10^5 yr. It is intensively studied because of its association with massive faunal turnover in both marine and continental settings and because its intensity and rapidity of onset approximate modern anthropogenic warming (e.g. Gingerich, 2006; Sluijs *et al.*, 2006). Locally, the PETM temperature increase was on the order of 4–5°C (Wing & Lovelock, 2007; Currano *et al.*, 2008). Thus, the new PETM floras offered the first opportunity to examine insect–herbivore response to warming at a much finer time resolution than that used by Wilf & Labandeira (1999), through comparison to an outstanding suite of floras available in the Bighorn Basin from before and shortly after the PETM (Table 1).

Currano *et al.* (2008) examined this floral sequence (Table 1) and found a significant increase in both amount and diversity of insect damage during the PETM, both on bulk floras and on host species, including a significant increase in specialized damage such as galls and mines (Fig. 2). A provocative auxiliary result was that the reconstructed leaf mass per area of plant species did not change during the PETM, suggesting that the nutritional nature of the local food source remained constant despite the presumed increased $p\mathrm{CO_2}$ (see detailed discussion of leaf mass per area and its correlated traits in the next section). Thus, part of the herbivory increase was apparently related to increased insect performance (including growth rate and population density) attributable to increased temperature, rather than any major decrease in food quality resulting from increased $p\mathrm{CO_2}$ (i.e. N concentration, C:N ratio, etc.). Also, the significant increase in feeding diversity is best explained by a temperature response. Alternatively, leaf nutritional attributes may have responded to elevated $p\mathrm{CO_2}$ without linkage to leaf mass per area.

Of equal interest to the increase with warming shown by Currano *et al.* (2008), herbivory declined shortly after the PETM with cooling (Fig. 2), showing that the PETM feeding intensification was not derived from a coincidental evolutionary radiation unrelated to warming (Currano *et al.*, 2008). Also, herbivory increased within the late Paleocene gradual warming that preceded the PETM, as in southwestern Wyoming (Fig. 2; Wilf *et al.*, 2006).

In addition to these examples, which represent more than one time scale and two basins of Wyoming, warming during the latest Cretaceous of North Dakota also correlated with increased herbivory, within a time frame of < 1 Myr (Fig. 2; Labandeira *et al.*, 2002b). However, the low herbivory in the extremely warm, wet, and diverse Castle Rock rainforest flora from the early Paleocene of Colorado (Fig. 2) is a major exception which is addressed below.

In summary, the paleobiological results are strongly consistent with correlations of insect-feeding diversity and frequency with temperature. The fossil evidence, when combined with the modern latitudinal diversity and herbivory gradient (which is also the observable result of evolutionary response to climate variation over long time intervals), now provides the most holistic framework for predicting effects of future climate change. However, short-term experimental work will continue to reveal the processes and mechanisms affecting particular interacting groups.

Hypothesis 2. Insect-feeding diversity and frequency increase in variance with decreased rainfall and associated changes in leaf traits

Available moisture has significant effects on leaf properties that impact herbivores. Starting with leaf properties, the global correlations of a large suite of leaf-trait variables have been identified in leaf economic studies (e.g. Small, 1972; Reich *et al.*, 1997; Wright *et al.*, 2004). These include leaf lifespan, leaf mass per area, and area- and mass-based N, phosphorus (P), photosynthesis, and respiration. Decreased moisture has long been strongly associated with decreased leaf size and increased leaf thickness (Webb, 1959; Givnish, 1987). More recently, Wright *et al.* (2005) quantified several moderate but significant climatic effects on leaf economic traits in a global compilation. Of particular interest to herbivores, leaf mass per area increases with increasing vapor pressure deficit and potential evapotranspiration, and with decreasing rainfall among evergreen but not deciduous species. Also, mass-based leaf N decreases with increasing vapor pressure deficit and potential evapotranspiration. Higher leaf mass per area (which associates with thicker, tougher, better defended, lower-nutrient, longer lived leaves) and decreased N, the most important nutrient for herbivores, each negatively correlate with herbivory (Mattson, 1980; Coley, 1983; Poorter *et al.*, 2004; Coley in Royer *et al.*, 2007a), as does leaf lifespan (Stanton, 1975; Coley, 1983, 1988; Basset, 1994).

The combined evidence above suggests that decreased moisture availability in the fossil record should be associated with increased leaf mass per area, lower foliar N (not measurable in fossils), and decreased herbivory, particularly on host species with long leaf lifespans. However, host species occupying relatively wet, riparian areas of the landscape, or with a dry deciduous habit, may be able to continue a 'fast' growth strategy with short leaf lifespans and associated leaf traits (or alternatively riparian vegetation may toughen to repel attack: Stanton, 1975). The likely cost is that herbivores shift to and intensify feeding on the 'fast' plants, as seen on riparian sycamores and poplars (*Platanus* and *Populus* spp.) from dry environments in the southwestern USA and northwestern Mexico (Smith, 1944; Brown & Eads, 1965),

and more generally in elevated herbivory on dry deciduous Neotropical vegetation (Stanton, 1975; Filip *et al.*, 1995; Coley *et al.*, 1996). Thus, variance in herbivory should increase as different plants in a community adopt more extreme defensive or accommodationist strategies.

The early and middle Eocene Green River floras of Wyoming, Utah, and Colorado comprise a classic example of subtropical, seasonally dry vegetation in the fossil record (MacGinitie, 1969), following the more humid interval represented by regional Paleocene and early Eocene floras (Table 1). Increased development of adjacent mountain ranges altered drainage patterns and created significant rain shadows for the area (Roehler, 1993a,b; Smith *et al.*, 2008). Thick-textured, tiny-leaved species are abundant and diverse in the Green River floras, with an admixture of large- and apparently thin-leaved, riparian taxa with presumed short leaf lifespans. The latter include an iconic, extinct sycamore species, *Macginitiea wyomingensis*, and several extinct poplars (e.g. Manchester *et al.*, 2006). Insect fossils are locally abundant in the Green River lake beds, and their richness has been only partly described since Scudder's pioneering efforts (e.g. Scudder, 1872, 1878; Cockerell, 1925).

Wilf *et al.* (2001) assigned all abundant host species in a middle Eocene Green River flora from Bonanza, Utah (Table 1), and in the preceding late Paleocene and early Eocene floras from adjacent southwestern Wyoming studied earlier by Wilf & Labandeira (1999), into categories of presumed short, long, and unassigned lifespan. Assignments were based on combined evidence from nearest living relatives, reproductive strategy known from associated fossil fruits and seeds, whether leaves were thick-textured, and leaf shape. Variance in both frequency and diversity of insect damage, on bulk floras and on individual host species, was significantly higher in the Bonanza flora than in the preceding floras from a more humid climate. Significantly, the species assigned *a priori* to short and long leaf lifespans tended to have high and low herbivory, respectively (following predictions from ecological data), and the maximum herbivory in all three floras was on the Bonanza sycamores and poplars. Galling increased, supporting modern data showing galler preference for dry habitats cited above, and mining decreased, although sample sizes of these rare damage categories were low.

The recently developed, easily applied proxy for fossil leaf mass per area, requiring only petiole width and leaf area measurements from fossils (Royer *et al.*, 2007a), allows a more quantitative approach to hypothesis 2. Royer *et al.* (2007a) took these measurements to estimate leaf mass per area on the Bonanza flora (discussed above) and on the 2-Myr-older Republic flora, which comes from a more humid, temperate, volcanic upland environment in Washington (Table 1). As predicted, estimated leaf mass per area had a much greater range and higher maximum at Bonanza, the drier site (70–157 vs 57–87 g m^{-2}). Herbivory on single plant host species in both floras (whether measured as damage type

diversity, frequency of attack, or amount of leaf area removed) showed a broad range at low leaf mass per area, including very high values in both floras, but was nearly uniformly lowest in the five species at Bonanza with the highest leaf mass per area.

The above results show predicted effects of leaf traits, modulated by climate, on herbivory in the Bonanza flora: the middle Eocene drying climate increased the defensive properties of some lineages, while others became targets of intensive feeding. However, only the Bonanza flora, derived from a single stratigraphic horizon, has been investigated under this framework, and testing on other floras is needed. There may be a strong local effect of legumes at Bonanza, which dominate the species inferred to have high leaf(let) mass per area.

Hypothesis 3. Insect-feeding diversity tracks plant diversity

With some exceptions, there is a general consensus in ecology that the diversity of insect herbivores is strongly related to the diversity of host plants (Murdoch *et al.*, 1972; Siemann *et al.*, 1998; Wright & Samways, 1998; Leigh, 1999; Knops *et al.*, 1999; Haddad *et al.*, 2001; Hawkins & Porter, 2003; Novotny *et al.*, 2006, 2007; Dyer *et al.*, 2007). Using the time dimension of the fossil record, we can extend this hypothesis to fluctuations in plant diversity that far exceed modern observations in magnitude. We can ask whether insect extinctions are linked to plant extinction and, if they are, whether insects recover in or out of step with plants.

Insect herbivores should be especially vulnerable to extinctions that affect plants because nearly three-quarters of their species consume only single or a few closely related plant species or genera (Bernays & Chapman, 1994; Novotny *et al.*, 2002; Schoonhoven *et al.*, 2005). Yet, detecting insect extinctions from the body-fossil record is extremely difficult (Labandeira, 2005). In Labandeira & Sepkoski's (1993) literature compilation of fossil insect orders and families, the only major drop in insect diversity is at the time of the largest mass extinction in the fossil record, across the Permian–Triassic boundary (251 Ma). No extinction of insect families is associated with the more recent, end-Cretaceous (known as the 'K-T') mass extinction, famous for the demise of dinosaurs and ~70% of species on Earth, and caused by an extraterrestrial impact at 65.5 Ma (Alvarez *et al.*, 1980; Bottke *et al.*, 2007). However, a closer look at the insect record across the K-T shows an absence of well-sampled, informative insect fossils any closer than *c.* 10 Myr on either side (Labandeira *et al.*, 2002b). Presumably, like insect family diversity (Labandeira & Sepkoski, 1993), insect species and genetic diversity were much lower during the Permian than the Late Cretaceous, making unlikely the global elimination of entire Cretaceous families containing extremely high numbers of insect genera, species, and individuals, similar to the situation today. Thus, insect extinction at the K-T must be sought regionally or below the family level.

Fortunately, the macrofloral record spanning the K-T in the vicinity of Marmarth, southwestern North Dakota made by Johnson (Johnson *et al.*, 1989; Johnson, 1992, 2002) is unique for this time period for its density of sampling and stratigraphic precision, including more than 350 species from more than 22 000 specimens, 160 plant localities, and 125 stratigraphic levels (Wilf & Johnson, 2004). Some of the best-sampled levels are indicated (Table 1, Fig. 2). A recent quantitative analysis of this data set showed dynamic turnover of plant communities with warming, cooling, and local facies changes through *c.* 1.4 Myr preceding the K-T, and a major extinction pulse precisely at the K-T that is significantly distinct from the preceding turnover; the most conservative estimate of plant species extinction is 57%, and plant diversity did not recover in the ensuing ~0.8 Myr represented by local Paleocene strata (Wilf *et al.*, 2003b; Wilf & Johnson, 2004). A vast regional extent for the K-T plant extinction and a prolonged period of low plant diversity throughout western North America are further supported by numerous high-resolution palynological studies (Tschudy *et al.*, 1984; Nichols *et al.*, 1986; Johnson *et al.*, 1989; Sweet & Braman, 1992; Hotton, 2002; Nichols & Johnson, 2002; Nichols, 2007) as well as macrofloral data (Wolfe & Upchurch, 1986, 1987; Johnson & Hickey, 1990; Barclay *et al.*, 2003).

Of interest here, the North Dakota floras bear a full suite of abundant and diverse insect damage (Labandeira *et al.*, 2002a; only a handful of fragmentary insect fossils are present), offering a unique opportunity to evaluate K-T insect extinction by proxy, at high resolution. Labandeira *et al.* (2002b) analyzed 13 441 of Johnson's museum voucher specimens for presence–absence of 51 DTs in the North Dakota floras. Results showed a drastic 70% loss of specialized associations, such as mines and galls, at the K-T boundary, and a significant drop in frequency and overall diversity of damage (42% loss of all damage types). There was no evidence for recovery except possibly for generalized associations at the top of the section. Generalized damage, on a presence–absence basis, did not decline across the K-T, but this is not surprising because by definition it can be made by many different groups of insects and may represent a low diversity of surviving, mostly externally feeding groups (for the most part hole feeders, margin feeders, and skeletonizers). The loss of specialized damage more closely maps the loss of biological insect species and genera, and Labandeira *et al.* (2002b) suggested that host-specialized herbivores suffered both from the primary impact effects that killed the plants, and secondarily from the loss of their food supply. Although regional climate cooled immediately before the K-T boundary (Wilf *et al.*, 2003b), climate alone cannot explain the dramatic and sustained loss of specialized feeding, coupled to a major plant extinction. Presumably, extinctions of herbivores cascaded to their closely linked, and typically very diverse, parasites and parasitoids (e.g. Lewis *et al.*, 2002).

The Labandeira *et al.* (2002b) study resolved only the first ~0.8 Myr of the 10-Myr Paleocene that are available locally in North Dakota, whereas Wilf & Labandeira's (1999) work included the last 1 Myr of the 10-Myr Paleocene in southern Wyoming (Table 1). Thus, there was a major, 8-Myr gap in knowledge about the timing of the Paleocene recovery of the plant–insect system. Wilf *et al.* (2006) addressed this with insect-damage analysis using a suite of newly collected early and early late Paleocene floras from southwestern Wyoming, southeastern Montana, and the Denver Basin, combined with the most productive Cretaceous levels from North Dakota (Table 1, Fig. 2; suitable middle Paleocene floras for insect-damage analysis have yet to be identified in the region). Although nearly all of the Paleocene samples (Table 1) contain a familiar, low-diversity succession of species found throughout Western Interior North America (Brown, 1962), the major exception is the 63.8-Ma Castle Rock tropical rainforest flora from the Denver Basin (Johnson & Ellis, 2002; Ellis *et al.*, 2003, 2004). This assemblage represents a previously unsampled premontane environment with a mean annual temperature of over 20°C and annual rainfall of over 2 m; it has well over 100 species, an order of magnitude more than are found at thousands of typical Paleocene localities (Brown, 1962), and has raised many new questions about how Paleocene plant recovery varied environmentally (Johnson & Ellis, 2002). Thus, the ideal test for correlated plant and insect diversity was presented: there should be high insect-feeding diversity at Castle Rock, and low insect-feeding diversity at other Paleocene sites.

Although in the majority of cases plant and insect-feeding diversity were comparably high during the Cretaceous and low during the Paleocene, the exceptions are striking and unexpected (Wilf *et al.*, 2006; Fig. 2). First, Castle Rock's insect-damage diversity was extremely low, as at typical Paleocene sites, even though its floral diversity exceeded even that at the Late Cretaceous sites (Fig. 2). Only two mines were found on 2309 leaves of 130 species. Secondly, in sharp contrast to Castle Rock, the nearly coeval Mexican Hat site (64.4 Ma; Montana), with a typical Paleocene angiosperm leaf flora of 16 species, was as intensely consumed as Late Cretaceous sites with up to four times more diverse floras (Fig. 2). Most strikingly, Mexican Hat exceeded all sites in the prevalence of diverse insect mines among host plants (Wilf *et al.*, 2006): mines, first noted at Mexican Hat by Lang (1996), occurred at double the frequency (2.6% of leaves mined) of those at other Paleocene sites, including representatives of at least three insect orders (Diptera, Hymenoptera and Lepidoptera) on one sycamore host, and more than two mine DTs occurred on each of the four dominant host plants. The presence of more than one mine DT on a host plant was only observed elsewhere in the Cretaceous and latest Paleocene samples, and on fewer host species per site. Only one mine DT at Mexican Hat was also known from the Cretaceous. Thirdly, within the end of the Paleocene in southern Wyoming, there was a modest uptick in insect-feeding diversity and a significant increase in mining diversity,

even though plant diversity showed a negligible increase (Fig. 2). This was recently corroborated in the Bighorn Basin (Currano *et al.*, 2008; Fig. 2). At no time during the Paleocene in this region was there a diverse flora with diverse insect damage (Currano *et al.*, 2008), but the three other combinations are recorded (Fig. 2).

The results of the recovery study (Wilf *et al.*, 2006) indicate that plant and insect diversity, although strongly linked today, can decouple during ecological recovery from extinction, which severs trophic links by destroying loci in food webs. This results in drastically simplified ecological landscapes, ripe for opportunistic development of unbalanced food webs not seen today. Castle Rock is a case of runaway floral diversification without an accompanying insect radiation, apparently made possible by a short interval of highly favorable climate. The Castle Rock flora, with its large, thick-textured, presumably long-lived and unpalatable leaves typical of modern rainforest vegetation, apparently was too difficult a venue for the re-establishment of insect herbivores. The Castle Rock example contrasts with modern rainforests, where herbivores may be involved in the maintenance or promotion of plant diversity (Janzen, 1970; Connell, 1971; Wills *et al.*, 2006).

The other, typical Paleocene floras were dominated by a handful of thin-textured species, mostly from deciduous lineages such as Platanaceae, Cornales, Juglandaceae, Trochodendraceae, and Cercidiphyllaceae (e.g. Brown, 1962; Hickey, 1977; Crane *et al.*, 1991; Manchester & Hickey, 2007), that were presumably poorly defended against rare insect attacks. Mexican Hat appears to offer a rare glimpse of a localized and ephemeral, but massive, Paleocene opportunistic invasion onto vulnerable hosts from an unknown, possibly distant source. None of the Paleocene samples represents a true ecosystem recovery because there is no example of diverse floras and feeding in the same sample. Contrary to expectations, true recovery appears to have been led by insects, not by plants, during latest Paleocene warming preceding the PETM (Wilf *et al.*, 2006; Currano *et al.*, 2008; Fig. 2).

Although the first K-T insect-damage investigation (Labandeira *et al.*, 2002a,b) was from a single basin in North Dakota, the recovery study and ongoing work in the Cretaceous and early Paleocene of the Denver Basin (Wilf *et al.*, 2006; Labandeira *et al.*, 2007a), 700 km south of the North Dakota floras, strongly corroborate the evidence for a major K-T extinction of plants and insects throughout the Western Interior USA. All results clearly indicate high Late Cretaceous herbivory followed by severe depression in insect-feeding diversity and intensity lasting through most of the Paleocene. However, this overall pattern is made more interesting by the unbalanced food webs seen ephemerally at Mexican Hat and Castle Rock.

The fact that nearly all insect families present in the Late Cretaceous are still with us today (Labandeira & Sepkoski, 1993) is used to argue that insects did not suffer a significant K-T extinction (Grimaldi & Engel, 2005). Although this is true in a strict phylogenetic context, the family-level, global body-fossil data are incapable of revealing the profound and long-lasting ecological crisis revealed in the insect-damage record, which leaves no doubt that plants and their insect herbivores over a large area of North America were strongly affected for millions of years. This included severe losses of population density and presumably species and generic diversity in host-specialized herbivore lineages; in addition, many families may have been lost regionally.

Example from Patagonia I briefly note a completely different test of correlated plant and insect diversity, from southern South America. Extremely diverse fossil floras are known from the Eocene of Patagonia, Argentina, including an early Eocene fossil lake site known as Laguna del Hunco (Berry, 1925, 1938; Wilf *et al.*, 2005a and references therein; Zamaloa *et al.*, 2006). Relatively rare but informative insect body-fossils also come from the Laguna del Hunco site (Petrulevičius & Nel, 2005). The Laguna del Hunco flora was located at a similar absolute paleolatitude (~47°) to many North American Eocene floras. It has recently been sampled using the same field census and damage typing methods described here and dated precisely to 51.91 ± 0.22 Ma, using new Ar-Ar data (Wilf *et al.*, 2003a, 2005a,b). Thus, both plant and insect-damage diversity can be compared between continents, statistically adjusted for sample size.

Results show the Laguna del Hunco flora, with ~186 plant organ species, to be at least as speciose as any North American Eocene flora known, the closest comparison being to Republic (Wilf *et al.*, 2003a, 2005a). For example, the most speciose quarry at Laguna del Hunco yields approx. 57 dicot leaf species at a rarefied sample size of 500 specimens, versus 37 at Republic (Wilf *et al.*, 2005a). Insect damage at all four different quarry sites at Laguna del Hunco is extremely diverse, richer than any known Eocene example whether measured on bulk samples or individual host species (Wilf *et al.*, 2005b). For example, when the abundant plant host species from Laguna del Hunco, Republic, Bonanza, and Sourdough (see Table 1) are ranked by damage type and feeding group diversity, hosts from Laguna del Hunco represent 11 of the top 15 in both cases, and five and four of the top five, respectively (Wilf *et al.*, 2005b). Because very little is known about the deep-time diversity of plants and insects in South America (Petrulevičius & Martins-Neto, 2000; Jaramillo *et al.*, 2006), these results reveal a deep historical context for the extraordinary diversity of the continent today, and they amply demonstrate that a major radiation of insect herbivores occurred on one of the richest paleofloras in the world.

IV. Extant calibrations needed

Insect-damaged fossil leaves have much potential to add a deep historical dimension to ecological observations of living

floras and faunas. Many of the paleontological results described here are in line with predictions from modern ecology, whereas others, such as the ephemeral Paleocene diversifications of plants or herbivory, but not both concurrently, reveal novel ecological patterns out of the reach of modern observation. Although confirmation and clarification require the usual – many more fossils from many more times and places – I focus here on three issues that divide the ecological and paleoecological realms of observation and caution against oversimplified comparisons, as discussed in part earlier (Wilf & Labandeira, 1999; Wilf *et al.*, 2001).

The first, and self-explanatory, issue is that paleobiology and ecology use very different techniques and time scales of observation. Perhaps the most pressing example is the damage typing system, which has moved ahead quickly in paleobiology without extant calibrations needed to constrain diversity interpretations, such as how many insect taxa can be represented by a single damage type. Even the fundamental sample is different: paleobiologists must measure, nearly exclusively, mature leaves bearing the cumulative damage of their lifespans, whereas ecologists routinely measure time series of damage on living leaves, especially young, expanding foliage that bears the highest attack rates (Coley *et al.*, 1996; Moles & Westoby, 2000).

Secondly, variation in herbivory is typically immense in extant communities, by season, from tree to tree, and within a tree (e.g. Feeny, 1970; Basset, 1991, 1992; Lowman, 1995; Filip *et al.*, 1995; Barrios, 2003). In fossil leaf deposits, even small amounts of spatial and time averaging probably smooth the variation to reveal meaningful trends, but this hypothesis needs to be tested and any degradation of signal mapped along the route to preservation. This can be done using straightforward comparisons of seasonally timed and three-dimensionally mapped live material (of mature canopy leaves, to best match the fossil record), fresh leaf litter, and transported leaf litter, by analogy to plant taphonomy studies. I note that host plant identifications, at whatever resolution is achievable (or to morphotypes when taxonomy is ambiguous), are essential to all informative interpretations of modern or fossil insect damage, as shown throughout the literature. Unfortunately, host identification was not included in one of the only studies of insect damage in modern leaf litter (Smith & Nufio, 2004).

Taphonomic investigations could also address a third issue, the frequent, but not uniform observation that fossil herbivory is lower than modern herbivory (Beck & Labandeira, 1998; Smith & Nufio, 2004). Although part of this signal could genuinely reflect increasing herbivory through time, it is more likely attributable to a suite of taphonomic factors that all tend to bias significantly downward the observation of fossil herbivory (Wilf & Labandeira, 1999). Nearly all fossil leaves are incompletely preserved, making it more likely that insect damage originally present will be missed; damaged leaves have lost structural integrity and are more likely to be mechanically destroyed before being fossilized; heavily chewed leaves are

usually not identifiable, making them unusable; and completely chewed leaves cannot preserve. Work to date has assumed these biases to be relatively uniform across the fossil record, allowing comparisons through time as discussed here, but a stronger quantitative framework from taphonomy would be a major improvement.

Most of all, more workers are needed to advance this promising area of research. Fossil leaves with insect damage remain a mostly untapped, unique source of information about food web evolution on time scales short enough to be linked to neoecological observations. Nearly all temporally fine data come from a single region of one continent, from a 20-Myr window out of the more than 400-Myr history of plants on land with leaves. I hope this article has stimulated some readers to consider their potential contributions.

Acknowledgements

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