The Fossil Record of Plant-Insect Dynamics

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Keywords
damage type, end-Cretaceous event, functional feeding group, herbivory, Paleocene-Eocene Thermal Maximum, pollination

Abstract
Progress toward understanding the dynamics of ancient plant-insect associations has addressed major patterns in the ecology and evolution of herbivory and pollination. This advancement involves development of more analytical ways of describing plant-insect associational patterns in time and space and an assessment of the role that the environment and internal biological processes have in their control. Current issues include the deep origins of terrestrial herbivory, the spread of herbivory across late Paleozoic landscapes, recoveries from sudden major crises, reaction to and accommodation of protracted environmental perturbations, and the nature of herbivory and pollination before the appearance of angiosperms during the mid-Mesozoic. These and other exploratory research themes provide a more complete account of a great nexus of ecological activity that has been wedged between the two most diverse organismic groups on land for the past 410 million years.
Mimicry: the resemblance of an insect to another organism in its environment, or to another unpalatable insect through camouflage

Damage type (DT): the basic defined and diagnosable unit of a plant-insect association in the fossil record

INTRODUCTION

Continental arthropods and vascular plants unarguably are the most diverse multicellular organisms on the planet. If one conservatively tallies the average number of ecological associations or interactions of insects and mites found on a single host-plant species, then the number of interactions present today is a tenfold to a hundredfold multiple of the number of host plants (Strauss & Irwin 2004, Zheng & Dicke 2008). These figures result in tens to hundreds of millions of associations that presently occur, on the basis of a minimal estimate of one million described and known insect herbivore species (Schoonhoven et al. 2005). Throughout geologic time, this figure would be a vast number. Almost all of these associations are categorized into two types: herbivory and pollination. Herbivory, or the consumption of live plant tissue, has been the overwhelmingly dominant association through time, in part attributable to the variable but overall elevated host specificity of herbivores (Novotny & Basset 2005), whereas pollination has an opposite tendency of pollinating many typically unrelated host plants (Waser et al. 1996). Other associations include plants and insects exhibiting general to intimate connections with a variety of microscopic and macroscopic fungi (Vega & Blackwell 2004, Janson et al. 2008), physical and chemical defenses of plants to ward off insect herbivores (Krings et al. 2002, Royer et al. 2007, Futuyma & Agrawal 2009, Pott et al. 2012), and various types of deceptive camouflage and other categories of mimicry between plants and insects (Wedmann et al. 2007, Wang et al. 2012).

This multitude of associations in time and space has resulted from processes that occur at a broader environmental scale and also in the local habitat. These processes include (a) competition among species and (b) historical causes, such as the particular evolutionary trajectories of plant hosts and associated insect lineages (Pellmyr & Leebens-Mack 1999, Lopez-Vaamonde et al. 2006, McKenna et al. 2009, Winkler & Mitter 2009). For some time, it has been acknowledged that the mechanisms of how insects and plants come to be associated with each other involve responses to sudden and prolonged events of the global environment (Labandeira et al. 2002, Currano et al. 2010), as well as local ecological and evolutionary effects (Wappler & Denk 2011). For herbivory, detection of these patterns requires the examination of bulk floral data for determining community-wide and habitat-level patterns, as well as the examination of plant-host species data for specific lineages of the plant hosts and their herbivores, such as tracking the component community of herbivore species successively on a particular plant lineage through time. [The component community described by Root (1973) consists of all organisms trophically dependent on a plant-host species.] One goal of such studies is to establish the effects of major physical and biological events, such as mass extinctions or rapid diversification events. An equally important goal is the examination of associational changes in specific plant and insect lineages, such as shifts in insect herbivore and pollinating taxa accompanied by short-term turnovers of their plant hosts. One recently developed, utilitarian system for documenting such changes of herbivore taxa through time is the damage-type system, which provides definitions, comparative diagnoses, and related information about distinctive, categorizable types of insect damage, termed damage types (DT’s) (Labandeira et al. 2007b).

In this review, we present new, emerging ways of examining and analyzing the fossil record of plants, insects, and their interactions through quantitative and qualitative analysis of the local communities and regional ecosystems in which they occur. Studies involving such a perspective extend to approximately the past 15 years and involve instrumental and especially analytical techniques for examining the plant-insect associational record. We discuss recent case studies and hope that similar approaches will be extended to the relevant, unexplored dynamics of the plant-insect associational record.
SOLVING EVOLUTIONARY AND ECOLOGICAL PUZZLES

Plants and insects record their effects on each other in intricate ways. For the fossil record, the most widespread example is insect herbivore damage on plant leaves, but also on other organs such as stems (Sarzetti et al. 2009, Petrulevičius et al. 2011, Moisan et al. 2012); seeds (Labandeira 2006a, Naugolnykh 2008); and, rarely, roots (Labandeira 1998). One recently examined system involves the evolution and origin of cynipid (gallwasp) galls on oak leaves in the Neogene of western North America, where distinctive gall shapes, host associations, and body-fossil records provide insights into the evolutionary biology of a fascinating relationship (Waggoner & Poteet 1996, Erwin & Schick 2007, Stone et al. 2009). More difficult to detect are plant reproductive structures that have been modified for the reception of insect mouthparts in pollination (Labandeira et al. 2007a). Mouthpart modifications, such as elongate proboscides, have an interlocking function as a hand-and-glove device for receiving plant reproductive structures (Labandeira 2010). Another consequence of pollinated plants is tissue consumption typically by larvae whose life cycle involves pollination as an adult (Klavins et al. 2005). The most intractable association to ascertain is mimicry, whereby wings or even entire insects uncannily resemble, respectively, smooth-margined leaflets or leaves (Wang et al. 2010), or entire highly lobed leaves (Wang et al. 2012) of coexisting plants in the same habitat.

The detective process begins with data collection. A fossil leaf assemblage for an herbivory study, and ideally for a pollination study, is retrieved from a methodically quarried pit. Adequately preserved to well-preserved specimens are collected in an unbiased way and constitute a sufficiently abundant sample, typically from several hundred to a few thousand specimens, to accurately represent the originally preserved flora. The specimens are identified for their plant-host morphotypes and insect DTs and are frequently analyzed in the context of other relevant data sets for trends based on time, biogeography, habitat, climate, plant host, or other variables of interest (Labandeira et al. 2007b). A battery of analytic techniques and instrumentation has been assembled to ferret out correlations and other patterns between plant hosts and their insect herbivores and pollinators (e.g., Currano et al. 2010, Labandeira 2010, Wappler et al. 2012).

Four case studies demonstrate the puzzle-solving nature of understanding the ecology and evolutionary biology of ancient plant-insect associations (Figure 1). These examples spotlight the eclectic uses of plant-insect associational data from the fossil record that may not be evident from an initial survey of the field. The first example comes from leaf mining (Figure 1a), specifically recognition of a stereotyped serpentine leaf mine (DT104) that has a distinctive frass trail alternating between either side of the mine and that is associated with a field of miniscule ovipositor probe marks surrounding the mine origin (Winkler et al. 2010). These and other features of the mine restrict its identity to the lineage Agromyzidae (leafmining flies), whose earliest body-fossil occurrence previously was in much younger strata but now is extended significantly earlier in time. Consequently, the earliest Agromyzidae now occur in the Early Paleocene of North America, and the origin of the larger fly clade to which the Agromyzidae family belongs, the Schizophora, is similarly extended earlier, with a probable latest Cretaceous origin. In addition, Paleocene Agromyzidae mines occur on an extinct woody species of sycamore, whereas the clade currently consists of miners that are almost exclusively on herbaceous plants, particularly grasses (Winkler et al. 2010), indicating a major host shift sometime during the mid-Cenozoic.

A second example is from external foliage feeding and involves the assessment of the highly stereotyped DT28 (Labandeira et al. 2007a), found on the ginger Zingiberopsis in Late Cretaceous and Paleogene deposits from the western interior of North America (Wilf et al. 2000). The distinctive surface-abrasion feeding mark of DT28 displays a suite of micromorphological modifications of host-plant tissues by mandible chew marks (Figure 1b) that exactly match the adult hispine
Figure 1

Plant-insect interactions that are important for solving evolutionary and ecological puzzles. (a) The leaf mine (DT104) on an early Paleocene sycamore host was made by an agromyzid fly, providing the earliest fossil date for not only the Agromyzidae but also its broader, encompassing lineage, the Schizophora, indicating a Late Cretaceous origin (Winkler et al. 2010). (b) Latest Cretaceous surface-feeding damage (DT28) on the ginger Zingiberopsis, showing the antiquity of a stereotyped association currently occurring in the Neotropics (Wilf et al. 2000). (c,d) Death-grip marks (DT212) astride the midrib of a middle Eocene dicot leaf from Messel, Germany, revealing the existence of a modern plant–ant–parasitoid fungus association that induced zombification of ants (Hughes et al. 2010). (e) A Middle Jurassic specimen of a long-proboscid scorpionfly (order Mecoptera) that exhibited specialized tubular mouthparts for fluid feeding on gymnosperms and associated pollination (Ren et al. 2009). Scale bars: solid, 1cm; striped, 1 mm. Panels b and e are reproduced with permission from the American Association for the Advancement of Science; panels c and d are reproduced with permission from the Royal Society. Abbreviation: DT, damage type.

beetle damage of the modern neotropical taxon Cephaloleiini (Strong 1977). In addition, closely associated slot-hole feeding between two adjacent minor veins, typical of DT08 (Labandeira et al. 2007a), is an exact match for the larval stages of the same adult Cephaloleiini found on modern gingers and closely related heliconias. Because the match of two types of co-occurring damage, one larval and the other adult, on the same host-plant family (Zingiberaceae) has been found as
a set in the Late Cretaceous–Paleogene of the western interior and also in modern Mesoamerica, an extension of the association was made. This association subsequently was challenged on the grounds that certain beetle and moth larvae could produce a similar DT (Garcia-Robledo & Staines 2008), but the adult damage of the beetle larvae does not match that of the moth larvae; they differ in the pattern of chewed edges and lack any conspecific, early-instar moth larvae that would produce the associated slot-feeding damage. The fossil occurrence of the moth lineage, the more likely of the remote possibilities, does not occur earlier than mid-Cenozoic, on the basis of molecular phylogenetic grounds (Regier et al. 2012) and the fossil record (Sohn et al. 2012).

In the third example, a unique system of tritrophic interactions was investigated, involving the preserved chew marks on a leaf, an ant that made the foliar damage, and a parasitoid fungus that eventually killed the ant. This is the case of the zombie ants. The evidence begins with a distinctive “death grip” DT212 on a fossil leaf from the Middle Eocene lake deposit at Messel, Germany (Figure 1c,d), that matches the same damage produced by particular ant species in a modern Thai forest understory (Hughes et al. 2010). After the modern ant’s brain has been invaded by a parasitoid fungus, zombification ensues and induces a final death grip on the midvein of an accessible dicot leaf. Simultaneously, the ant dies and releases spores from a fungal fruiting body emerging from its head capsule, thus continuing the parasitoid fungus life cycle. This tritrophic leaf–ant–parasitoid fungus association consequently has been extended geographically and temporally to the middle Eocene of Germany.

The fourth case study involves discovery of the long-proboscid pollination mode, now known to occur from the late Middle Jurassic (165 Mya) to the later Early Cretaceous (~100 Mya). For some time, paleobotanists mentioned in passing that some gymnosperm female (ovulate) reproductive organs possessed interesting surface orifices leading to internal channels, tubes, funnels, micropylar siphons, and other tubular structures that connected with an ovule or group of ovules (Harris 1940, 1951; Axsmit & Jacobs 2005; Crane & Herendeen 2009; Osborn & Taylor 2010). This suggested a unique but unspecified reproductive system. Also discussed were apparent rewards, such as glandular structures placed in orifices or near pollen sacs (Harris 1973, Kvaček 2000). Meanwhile, paleontomologists were mostly concerned with the better and more consistently preserved wings for characters for systematic studies and paid less attention to often difficult-to-interpret, poorly preserved heads and mouthparts. Later, an interest in the relationship between the tubular structures of the receiving plant structures and the projecting long proboscides with food tubes of various insects (Figure 1e) led to the proposal of the mid-Mesozoic long-proboscid mode of gymnosperm pollination (Ren et al. 2009, Labandeira 2010).

**INSECT HERBIVORY**

Studies of plant hosts and their insect herbivores have concentrated sporadically on intervals spanning the Early Devonian to the Recent. Comparatively unstudied times involve the Early Devonian to Early Carboniferous (Mississippian) when herbivory initially was launched; the Early Triassic immediately after the end-Permian (P-Tr, Permo-Triassic) extinction; the mid–Late Triassic to the end of the Jurassic; and, surprisingly, the middle Miocene to Pleistocene, with a notable exception being Opler’s (1973) seminal demonstration of the significant antiquity of several modern leaf-miner associations. Almost all of the quantitative examinations to date have been confined to the Permian (Beck & Labandeira 1998, Adami-Rodrigues et al. 2004, Labandeira & Allen 2007, Prevec et al. 2009, Pinheiro et al. 2012), the latest Cretaceous to early Miocene (see Supplemental Table 1; follow the Supplemental Materials link from the Annual Reviews home page at [http://www.annualreviews.org](http://www.annualreviews.org)), and relevant modern studies (Smith & Nuño 2004; Adams et al. 2010, 2011). Examinations of other crucial episodes such as the radiation of...
Piercing and sucking: the penetrative puncturing of plant and other tissues by insects that bear mouthparts modified into piercing stylets

Galling: a parasitic interaction typically by a subadult animal that invades host-plant tissue and exerts hormonal control for production of tissues used in its nutrition and protection

Holometabolism: the complete developmental transformation in which an insect egg hatches a larva, which is transformed into a pupa, from which the adult emerges

plant-host and insect-herbivore diversity during the Late Triassic (Scott et al. 2004, Labandeira 2006a) and the expansion of the mid-Cenozoic grassland biome (Strömberg 2005) are noteworthy but are just beginning. Given this context, we discuss five of the more-studied episodes.

The Initial Launch of Herbivory

Detritivory (the consumption of dead tissues) has been proposed as the exclusive mode of plant feeding during the time interval between the earliest compelling evidence for well-established terrestrial biotas—mostly of macroscopic plants, fungi, and arthropods of the Early Devonian—and the major development of coal-swamp and adjacent habitats during the Late Carboniferous (Pennsylvanian) (Shear & Kukalová-Peck 1990). The few studies of continental plant-arthropod associations during this interval documented the near or total exclusion of herbivory in a variety of settings within the paralic to the more inland deposits of Euramerica (Shear & Kukalová-Peck 1990, Edwards & Selden 1992). Although a few studies (Kevan et al. 1975, Banks & Colthart 1993) have demonstrated herbivore piercing and sucking and surface abrasion on stems, only recently have diverse associations such as hole feeding, margin feeding, surface abrasion, piercing and sucking, and galling been demonstrated on Middle Devonian liverworts, a land plant with photosynthetic, leaf-like equivalents (C.C. Labandeira, S. Tremblay, K. Bartowski & L. Hernick, submitted). For external foliage feeding, the next earliest occurrence is much later and on anatomically true leaves of an early seed fern from the late Mississippian of Australia (Iannuzzi & Labandeira 2008). This evidence, although sporadic, indicates that Devonian and Mississippian herbivory is more frequent than previously considered and perhaps was modulated by highly varying levels of the partial pressure of oxygen ($\text{pO}_2$) (Berner 2009), which affected arthropod respiration and thus herbivore metabolic activity (Ward et al. 2006). The $\text{pO}_2$ highs during this interval are approximately coincident with two pulses of arthropod herbivory. An earlier event corresponds to the initial consumption of sporangia and stem tissues in the Early Devonian. After a long lag, a second event unfolded in which leaves, seeds, true roots, and wood were consumed during the Late Mississippian and ensuing Pennsylvanian (Labandeira 2007).

How Did Herbivory Expand on Vegetated Landscapes?

During this second pulse of herbivory, there was initial consumption of anatomically true leaves, seeds, true roots, and wood—organs that earlier were present but not herbivorized (Scott & Taylor 1983, Labandeira et al. 1997). The second, more extensive pulse is coincident with the first occurrences of 12 ordinal-level insect lineages, including mayflies, archaic “dragonflies,” piercing-and-sucking paleodictyopteroids, grasshopper-like orthopteroids, and the earliest holometabolous insects (Grimaldi & Engel 2005, Labandeira 2011). Ecological components of this diversification were herbivorous insects and mites that were external foliage feeders, piercers and suckers, gallers, pith borers, spore and pollen feeders, and root consumers. The partitioning of plant taxa by these herbivore guilds represents the first extensive and diverse component communities, as documented by histologically preserved permineralized compressions (Scott & Taylor 1983; Lesnikowska 1990; Labandeira & Phillips 1996, 2002; Labandeira et al. 1997). The apparently rapid clado-genetic and ecological events are associated with significantly increasing $\text{pO}_2$ levels (Clapham & Karr 2012). The distinctive plant-herbivore associations of the Pennsylvanian and Early Permian wetlands were extirpated in Euramerica but were spatiotemporally displaced to similar, later Permian, peat-dominated habitats in Cathaysia (Glasspool et al. 2003, D’Rozario et al. 2011).

During the latest Pennsylvanian, various regions of Gondwana emerged from a glaciated regime as the supercontinent moved northward (Césari 2007). The first documented glossopterid
Figure 2
Middle Permian leaf specimens of a glossopterid seed-fern species showing the predominance of oviposition (DT100). The specimens are from the Paraná Basin, in Santa Catarina State, southeastern Brazil, and are part of the White collection (White 1908) at the National Museum of Natural History in Washington, DC. (a) A shale slab containing glossopterid foliage with individual leaves magnified in panels b and c. (b) Eight oviposition scars with reaction rims of callus tissue oriented parallel to venation. (c) Two ellipsoidal oviposition marks with an enveloping rim of scar tissue, one of which shows a protruding egg. (d) A magnified oviposition scar showing an insertion slit at the bottom and an upward-trending lesion with a surrounding scar. (e) Two oviposition scars showing inner and outer reaction rims. Scale bars indicate millimeter increments; the scale in panel d is approximately twice that in panels e and e.

seed-plant forests occurred during the earliest Permian (McLoughlin 2012), and by the end of the Early Permian, a diverse spectrum of associations occurred at one site, Hammanskraal in the Karoo Basin of South Africa, which displays a rich assortment of plant-insect associations, especially ovipositional damage (C.C. Labandeira & R. Prevec, personal observation). This predominance of ovipositional damage continues in Karoo floras of the Middle Permian (Figure 2) and intensifies with a broader spectrum of DTs during the Late Permian. By this time, varied glossopterid-dominated floras and their insect herbivores were well established in several swamp, lacustrine, and especially fluvial environments (Banerji 2004; Gastaldo et al. 2005; Prevec et al. 2009; McLoughlin 2011; C.C. Labandeira & R. Prevec, unpublished data).
**Oviposition**: the insertion by a female of insect eggs into host-plant tissues, resulting in scarring and callus formation

**Damage diversity (or damage richness)**: the number of damage types on a leaf, plant host, or bulk flora

**Damage intensity**: the frequency of occurrence of damage types on a leaf, plant host, or bulk flora

**Specialization**: the feeding of insect herbivores on a single or perhaps a few phylogenetically related plant hosts

By contrast, studies of north-central Texas show significant differences from the Karoo Basin of Gondwana throughout the same Permian interval (Beck & Labandeira 1998; Labandeira & Allen 2007; S. Schachat & C.C. Labandeira, unpublished data). These studies document a much greater spectrum of major host-plant lineages, the dominance of external foliage feeding over oviposition, the earliest occurrence of insect outbreak-like phenomena, and a significantly different composition of insect herbivore component communities between the two supercontinents (Labandeira & Allen 2007; Labandeira 2012; S. Schachat & C.C. Labandeira, unpublished data). As insect herbivore colonization advanced toward more arid landscapes of continental interiors and away from wetland basins, it appears that plant-host xeromorphy in both southern Gondwana and southwestern Euramerica played an important role in the spectrum of insect damage.

### What Were the Effects of Ecosystem Change on Landscapes?

The dynamics and tempo of plant-insect interactions in the geological record are profoundly influenced by biotic and abiotic environmental perturbations. The Parasitoid Revolution and the Angiosperm Revolution are two examples of biotic events that restructured plant-insect food webs. The Parasitoid Revolution represented the emergence of a new feeding guild consisting principally of members of the Hymenoptera (small wasps) but also Diptera (brachyceran flies), which are parasitoids that feed largely on larval herbivorous insects (Labandeira 2002a). The diversification of major parasitoid lineages during the Jurassic introduced a major top-down regulator of insect herbivores that, together with existing predators, forever changed the trophic structure of insect herbivore communities and their associated food webs. With the addition of parasitoids, resource-driven bottom-up regulation became proportionately less effective, as modern studies show that parasitoids are more effective than predators, particularly those that target endophytic herbivores that feed within plant tissues (Memmot et al. 1994). In contrast to the Parasitoid Revolution, the Angiosperm Revolution, another biotic perturbation, was a mid-Cretaceous resource-driven enhancement of plant-insect associational diversity that resulted in the creation of new opportunities for insect herbivores and pollinators (Grimaldi 1999, Krassilov & Shuklina 2008). Abiotic environmental perturbations include the P-Tr and Cretaceous-Paleogene (K-Pg) crises and climate change, discussed in detail below.

### Permo-Triassic event

Preliminary work on plant-insect interactions from glossopterid-dominated floras of the Karoo Basin in South Africa indicates that moderately diverse and modest levels of damage occurred in a variety of habitats prior to the P-Tr event (Prevec et al. 2009; C.C. Labandeira & R. Prevec, unpublished data). Poorly preserved, fragmentary Karoo floras in Early Triassic deposits immediately after the P-Tr crisis suggest a profound downturn in plant and insect diversity and the near absence of plant-insect associations (Labandeira 2005, 2006a), although the Eurasian data are richer (Krassilov & Karasev 2008, Shcherbakov 2008). This dramatic fall in Karoo associational diversity was reversed sometime during the Middle Triassic, when plant diversity was relatively low, but as new plant lineages appeared, the latter became speciose during the Late Triassic. Similarly, Middle Triassic damage diversity and damage intensity were low but very generalized, and the insect herbivores responsible for the damage experienced a rebound before the Late Triassic, seemingly in synchrony with their plant hosts (R. Prevec, C.C. Labandeira, E.D. Curran, J.M. Anderson, H.M. Anderson, unpublished data). Upon diversification of horsetails, ferns, and several major seed-plant lineages during the early Late Triassic, plant-insect associations became significantly diverse in the total number of DTs, exhibited greater host specialization, and emphasized internal feeding over external feeding (Scott et al. 2004, Labandeira 2006a). The Late Triassic radiation of plant hosts and their herbivores may have reached a level...
REGIONAL PATTERNS OF THE CRETACEOUS-PALEOGENE EXTINCTION?

The significant extinction and prolonged recovery interval in the western interior of the United States (Figure 3) is commonly considered the baseline for our understanding of terrestrial ecosystem response to the Cretaceous-Paleogene (K-Pg) impact. However, recent data from other continents suggest that the net effects of the bolide impact decrease with increasing distance from the Chicxulub crater in Mexico. Both floral and insect damage diversity at the 58-Ma-old Cerrejón site in Colombia (8 Ma postimpact; 2,100 km modern distance from Chicxulub) are notably low for a tropical forest (Wing et al. 2009). By contrast, the middle Paleocene Menat site in France (5–6 Ma; 8,500 km) (Wappler et al. 2009) and the late early to middle Paleocene Firkanten flora from Spitsbergen (age poorly constrained to 2.9–6.8 Ma post-K-Pg boundary; 8,000 km) (Wappler & Denk 2011) show the combinations of high floral, total damage type, and mining diversity that suggest balanced and fully functional ecosystems completely unlike those in Cerrejón or the United States [e.g., southwestern North Dakota (10 Ma; 3,100 km)]. These results are consistent with paleobotanical studies showing high Paleocene plant diversity in Chubut, Argentina (4.3 Ma; 7,700 km) (Iglesias et al. 2007) and rapid postimpact ecosystem recovery in New Zealand (a few thousand years; 12,300 km) (Vajda et al. 2001). We emphasize that more data, particularly from the late Cretaceous, are needed to test this pattern.

of intensity and diversity of interactions similar to that of the angiosperm radiation (Labandeira 2006b). After the Late Triassic increase in herbivory, little is known about global trends and other patterns in Jurassic floras. Current research is under way (Vasilenko 2005, 2006; Pott et al. 2008; C.C. Labandeira & J.A. Santiago-Blay, unpublished data), and preliminary results indicate that bennettitaleans may be the most herbivorized group of plants during this interval (Pott et al. 2008, 2012; Popa & Zaharia 2011; Meller et al. 2011; Q. Ding & C.C. Labandeira, unpublished data).

Cretaceous-Paleogene event. Compared with the P-Tr event, much more is known about the effects of the K-Pg event, particularly in North America (Labandeira et al. 2002). Current evidence suggests that floras from the Williston Basin in North America underwent a significant decline in plant taxa and plant-insect associations, especially a decline in host-specialized DTs (Labandeira et al. 2002). Quantitative insect damage data from Early Paleogene sites in Montana, Wyoming, and Colorado demonstrate that terrestrial ecosystems remained depauperate and ecologically unstable for 10 million years (see Figure 3 and Supplemental Table 1). An imbalance in specialized associational diversity is illustrated by leaf-mine DT diversity in two contrasting floras. One diverse flora from the Denver Basin of central Colorado exhibits the virtual absence of leaf mining, whereas a depauperate flora of similar age from the Williston Basin of eastern Montana displays an unusually rich spectrum of leaf mining (Wilf et al. 2006). Stable terrestrial ecosystems, as evidenced by moderately diverse floras with total and leaf-mine DT diversity at Late Cretaceous preimpact levels, do not occur in the western interior until the latest Paleocene (see sidebar, Regional Patterns of the Cretaceous-Paleogene Extinction?). As currently known, both the K-Pg and P-Tr crises resulted in geochronologically sudden ecological rearrangements concomitant with mass extinction and major turnovers in plant-insect associations (Labandeira et al. 2002). The major comparative difference is condensation of the recovery interval from 65.5 to 55.8 Ma (~10 million years for the K-Pg interval, compared to from 252 Ma to ~228 Ma (~24 million years) for the P-Tr interval, which was two-and-a-half times longer (Labandeira 2006a, Wilf et al. 2006)).
Plant diversity (number of species) vs. Age (Ma)

Plant diversity (number of species) vs. Percent damage

Damage type diversity (number of DTs) vs. Mine diversity (number of mine DTs)

Herbivory metric vs. Plant diversity (number of species)

Herbivory metric vs. MAT (°C)

Legend:
- Paleocene, South America
- Paleocene, high latitudes
- Paleocene, Europe
- Paleocene, North America
- Cretaceous, North America
- Eocene, South America
- Eocene, high latitudes
- Eocene, Europe
- Eocene, North America
- Bighorn Basin damage census site
- Castle Rock
- Other damage census site

Equations:
- $R^2 = 0.07, p = 0.15$
- $R^2 = 0.38, p = 0.08$
- $R^2 = 0.08, p = 0.09$
- $R^2 = 0.57, p = 0.02$
- $R^2 = 0.30, p < 0.01$
- $R^2 = 0.89, p < 0.01$
- $R^2 = 0.13, p < 0.05$
- $R^2 = 0.78, p < 0.01$
**Hothouse earth conditions.** Unlike the P-Tr and K-Pg events, the Paleocene-Eocene Thermal Maximum (PETM) is a longer event (10^5 years) embedded in a protracted period of elevated temperatures from the latest Paleocene to the middle Eocene. An influx of 13C-depleted carbon into the atmosphere during the onset of the PETM caused the partial pressure of carbon dioxide (pCO2) to approximately double and global temperatures to increase by at least 5°C (Kennett & Stott 1991, Koch et al. 1992, Zachos et al. 2003). In a study from 59 to 52.7 Mya in the Bighorn Basin of Wyoming, insect damage diversity and abundance were sampled from nine floras before, during, and after the PETM (Currano et al. 2008, 2010). The results indicate that increased levels of insect-mediated damage diversity and to a lesser extent damage frequency are correlated with the short-lived PETM, in particular with increased temperature but not with changes in floral diversity, as shown in Figure 4 (Currano et al. 2008, 2010).

The only other Bighorn Basin flora with comparable damage diversity, frequency, and specialization is from the Early Eocene Climatic Optimum (EECO, 53–51 Mya), when the mean annual temperature (MAT) was approximately 2°C warmer than during the PETM (Wing et al. 2000). The high damage diversity, particularly specialized damage diversity, suggests that PETM forests were balanced, fully functional ecosystems, in contrast to those of the Early Triassic or early Paleocene. Thus, either the rate of temperature change was slow enough to allow plants and insects to migrate or adapt or the temporal resolution of the fossil record is too low to distinguish stressed ecosystems at the onset of the PETM. However, elevated damage intensity during the PETM may indicate ecosystem stress owing to elevated pCO2, which often leads to decreased leaf nitrogen concentrations (Bazzaz 1990, Lincoln et al. 1993) and higher insect feeding rates (Watt et al. 1995). Dwarfing in terrestrial vertebrates (Clyde & Gingerich 1998, Secord et al. 2012) and soil-dwelling invertebrates (Smith et al. 2009) also supports a decrease in food quality.

The best archive of southern neotropical plant-insect associational diversity during the EECO occurs at Laguna del Hunco (52 Mya) (Wilf et al. 2005). Four separate sites from Laguna del Hunco were sampled and compared with sites of a similar age in western North America (sites from Washington, Utah, and Wyoming). Significantly more damage was found at the South American sites, regardless of whether functional feeding groups or DTs were analyzed. In addition, a rank order of insect functional feeding group and DT diversity showed a disproportionate representation of Laguna del Hunco plant hosts exhibiting greater feeding diversity than hosts from the three sites in North America. These data indicate that an early Cenozoic history of elevated herbivore damage intensity and a high level of specialized associations were present on diverse plant hosts during a warm interval of the early Eocene. This ancient pattern may explain the high diversity levels of plants and their insect associates today in neotropical South America (Gentry 1988, Price et al. 1995).
The sustained warmth of the EECO continued throughout the early Eocene. Two maar lake sites in Germany, at 47.8 Mya (Messel) and 44.3 Mya (Eckfeld), capture the initial decline from hothouse conditions. These sites document an elevated level of plant-insect associations compared with sites of similar age in western North America and southern South America (Wappler et al. 2012). However, in Germany, elevated temperature and pCO2 produced disproportionate herbivory on evergreen over deciduous angiosperms, a trend opposite to that seen in penecontemporaneous sites of the Green River flora in Wyoming (Wilf & Labandeira 1999, Wilf et al. 2001). This trend is explained by historical enrichment of evergreen taxa in western Europe, also borne out by diverse and apparently long-standing trophic links among herbivores and evergreen source plants at Messel (Labandeira et al. 2011, Wappler et al. 2012). The Messel food web (Figure 5) represents a highly integrated, continental ecosystem of 700 taxonomically highly resolved, trophically unique taxa, dominated by plants and arthropods (71% of the total); the latter are overwhelmingly herbivores and pollinators (Labandeira et al. 2011). Plant-insect associational links and their trophic cascades form the majority of the web links, providing a realistic capture of ecosystem structure that has historically been neglected in almost all modern and fossil food webs analyzed to date (but see Pocock et al. 2012). The ameliorated paleoclimate and decreased diversity and abundance of plant-insect interactions of the later Eocene and Oligocene (Wappler 2010, Currano et al. 2011) contrasted dramatically with those of middle Eocene Messel and Eckfeld.

The specific examples above demonstrate that warming and elevated pCO2 affect plant-insect interactions. Insect damage diversity and frequency strongly, significantly, and positively correlate with the MAT over six million years within the Bighorn Basin (Currano et al. 2010). Furthermore, there are weak but significant positive correlations between DT diversity and MAT when data from all of the latest Cretaceous and Paleogene insect damage censuses are compiled (Figure 3). That these weak correlations exist at all is surprising given the number of other factors affecting plant-insect herbivore interactions, including but not limited to latitude, continent, geologic age, phylogeny, nutrient availability, and climate factors other than temperature. Additionally, multiple scientists collected the insect damage data, and a variety of methods were used to reconstruct the MAT at each site. The fossil record makes it clear that elevated insect herbivory in natural and managed ecosystems will be a consequence of current anthropogenic increases in temperature and pCO2.

**How Are Modern and Fossil Herbivory Connected?**

One approach to understanding the importance of insect damage on fossil leaves is to analyze modern floras using the same research protocol used for fossil material. Several modern studies have established herbivory patterns analogous to those within fossil associational data, such as...
Trophic level

Plants, algae, and diatoms
Bacteria, fungi, and detritus
Invertebrates
Vertebrates

Figure 5
Visualization of the Messel forest food web. Spheres represent taxa and lines represent feeding links. Links that loop refer to cannibalism. The vertical axis corresponds to trophic level. Plants, algae, and diatoms are shown in green; bacteria, fungi, and detritus in blue; invertebrates in yellow; and vertebrates in red (although the colors of the links are not easily distinguished at this scale). Feeding links are tied up disproportionately among the land plants (green) and primary consumers (yellow), overwhelmingly herbivores and pollinators and their consumers (Labandeira et al. 2011).

spatiotemporal variation in diversity and intensity of feeding guilds among sites (Smith & Nuñio 2004), effects of leaf toughness and predation between monocot and dicot angiosperms (Grubb et al. 2008), diversity and intensity of latitudinal gradients (Adams et al. 2010), and differences in temperate versus tropical specialization (Adams et al. 2011). One fundamental issue involves how accurately associational data retrieved from fossil sites match analogous modern data when the latter are appropriately standardized. One study (Carvalho et al. 2011) tested the correlation between the leaf-chewing DT diversity made by mandibulate insects and the diversity of the mandibulate insects (at various developmental stages) responsible for the leaf damage on 24 plant-host species from two different Panamanian forests. This correlation was found to be robust in modern forests across a range of hosts and their herbivores, regardless of mouthpart and behavioral convergences across insect groups or their developmental stages. As an alternative to the study of Smith & Nuñio (2004), this study validates the assumptions of paleobiological studies that rely on DT diversity as a means of comparing herbivory through time. Additionally, it provides an actualistic example that supports use of bulk herbivory values in assessing the evolution of fossil herbivore assemblages through time.

INSECT POLLINATION
Herbivory affects the development and efficiency of a plant’s photosynthetic organs, representing a cost to a plant. By contrast, insect pollination is advantageous to plants through enhancement
of reproductive fitness. However, insect pollination comes with a cost, resulting in a cost-benefit resonance with herbivory and an ecological tension between these two dominant insect-related parts of a plant’s life.

How Ancient Is Pollination?

The origins of active insect pollination lie in the earlier consumption of pollen and prepollen in wind-pollinated plants with incidental and passive insect-vectored pollination. This process undoubtedly occurred during the early Mesozoic, and more remotely during the late Paleozoic (Labandeira et al. 2007a), but except for the angiosperms, it never resulted in pollinated plant lineages that underwent any significant diversification (Gorelick 2001). Although pollen and its developmental precursors constitute the rewards of accessible solid grains, parallel rewards also existed in seed plants that typically produced pollen-related fluids such as pollen drops (gymnosperms) and later nectars (angiosperms). Insects with specialized mandibulate (chewing) and long-proboscid (siphoning) mouthparts are known from the Permian of Russia (Rasnitsyn 1977, Labandeira 2010), indicating that both pollen and pollination drop rewards, respectively, were being actively consumed. For plants, large-size pollen from the Pennsylvanian would be inefficient as an abiotic dispersal mode (Schwendemann et al. 2007). In addition, Permian pollinate and ovulate reproductive organs consistent with insect pollination are known (Archangelsky & Cúneo 1987).

Which Groups Were Responsible for Mid-Mesozoic Pollination?

We mentioned above the match of some peculiar elongate, tubular structures in gymnosperm ovulate organs with contemporaneous long-proboscid insect mouthparts (Labandeira 2010). Several studies indicate that multiple lineages of mid-Mesozoic insects developed siphonate proboscides of different lengths, diameters, and aspect ratios (Figure 6) for imbibing fluids such as pollen drops from a wide variety of gymnospermous hosts (Ren et al. 2009, Labandeira 2010). These matches depended on the fit of the proboscis to the receiving tube-like structure of the ovulate organ (Ren et al. 2009; Labandeira 2010; C.C. Labandeira, Q. Yang, J.A. Santiago-Blay, W. Wu, C.L. Hotton, A. Monteiro, Y. Wang, C. Shih, T. Rose, D. Dilcher & D. Ren, submitted) and occasionally the pollinate organ (Labandeira 2010) and may have been aided by colorful displays (Briscoe & Chittka 2001). These structural specializations were present by the late Middle Jurassic (165 Mya), which is the current date for the oldest definitive pollinating insects (Ren et al. 2009, Labandeira 2010). Relevant mid-Mesozoic insect clades included several lineages of true flies (Ren 1998); three lineages of scorpionflies belonging to the Aneuretopsychina clade (Ren et al. 2009); and the nonsophogrammatine Kaligrammatidae, representing four subfamilies of large butterfly-like lacewings (C.C. Labandeira, Q. Yang, J.A. Santiago-Blay, W. Wu, C.L. Hotton, A. Monteiro, Y. Wang, C. Shih, T. Rose, D. Dilcher & D. Ren, submitted). Collectively, these insect taxa represent at least 85 described and known species across the Eurasian mid-Mesozoic. Proposed pollinated plants possessing features consistent with long-proboscid insects were members of corystospermalean and caytonialean seed ferns, ginkgophytes (e.g., czekanowskialeans), cheirolepidiaceous conifers, gnetaleans, and bennettitaleans (Harris 1940, 1973; Retallack & Dilcher 1988; Stockey & Rothwell 2003; Labandeira et al. 2007a, 2012b; Crane & Herendeen 2009; Ren et al. 2009; Labandeira 2010; Rydin & Friis 2010). Other possible modes of insect pollination on gymnosperms were pollen-feeding mandibulate insects, such as beetles and katydid-like orthopteroids for cheirolepidiaceous conifers, cycads, and bennettitaleans.
Proboscis
Head and mouthpart regions
- Proboscis
- Palps
- Labrum/clypeus
- Antennae
- Compound eyes

All specimens shown at the same scale
1 mm
How Did the Angiosperm Revolution Affect Pollination?

The emergence of major angiosperm clades during an interval from 120 to 100 Mya replaced older pollination modes involving gymnosperms with new associations of angiosperms. Three patterns express this transformation (Labandeira 2010): (a) the extinction of most gymnosperms and their pollinators (some melanthripid thrips, many beetles, orthopteroids, scorpionflies, kalligrammatid lacewings); (b) the lateral transfer of some lineages of brachyceran flies to angiosperms (tanglevein flies, flower-loving flies, pangionine horse flies); and (c) the origination of new lineages associated with the pollination of early angiosperms (thripid thrips, moths, bees). Early in angiosperm evolution, initial pollinator associations included flowers with special fly traps (Gandolfo et al. 2004); small bowl-shaped flowers that were muted in color and mostly lacking nectarial rewards and that were pollinated by small thrips, nematocerous flies, moths, wasps, and probably bees (Luo & Li 1999; Thien et al. 2000, 2009; Hu et al. 2008; Danforth & Poinar 2011; Hartkopf-Fröder et al. 2011); and flowers with structures for advanced bee pollination (Crepet & Nixon 1998). Later, during the mid–Late Cretaceous, heath-like flowers with modestly deep throated floral tubes signal the earliest occurrence of an abbreviated long-proboscid mode that would accommodate short to modestly elongate, probing mouthparts, such as those of larger wasps, smaller bees, or moths with short siphonate proboscides (Nixon & Crepet 1993, Schönberger & Friis 2001). Further structural elaborations of flowers continued into the Paleogene, such as more-differentiated nectarial tissue and bilaterally symmetrical flowers for specialized pollination (Crepet 1979, Taylor & Crepet 1987). More recent, Late Paleogene–Early Neogene occurrences include the familiar fig-fig wasp (Peñalver et al. 2006, Compton et al. 2010), yucca-yucca moth (Pellmyr & Leebens-Mack 1999), and orchid-bee pollination mutualisms, the latter involving pseudocopulatory deceit, wherein a male pollinating insect attempts to mate with a modified floral structure that closely resembles the species’ female (Ramírez et al. 2007).
SUMMARY POINTS

1. Examination of the fossil record of plant-insect dynamics is a fruitful way to understand deep-time terrestrial ecology at the local habitat level. This fossil archive offers an important opportunity for understanding broader, community-level patterns in time and space, providing an ecologic component to major evolutionary trends.

2. Deciphering plant-insect dynamics of the past requires assembling a case using a detective-like approach based on a variety of direct, indirect, and circumstantial evidence. Such an inquiry also requires a battery of analytical tools for robustly demonstrating associational patterns.

3. Arthropod herbivory was initiated during the Early Devonian within early detritivore-based terrestrial ecosystems. This early herbivory is characterized by two pulses: one during the Early Devonian and a second, more extensive one commencing at the Mississippian–Pennsylvanian boundary.

4. Continuation of the second herbivory pulse into the Permian resulted in the spread of plant-insect interactions across vegetated landscapes in a variety of habitats, including those with xeromorphic vegetation.

5. The P-Tr and K-Pg ecological crises had a devastating effect on plant-insect associations, resulting in major lags in plant-host recovery and their subsequent colonization by insect herbivores.

6. The PETM expressed a transient, short-lived increase in temperature and $pCO_2$ levels within a longer term, several-million-year Eocene warm interval. Both are associated with increases in insect herbivory.

7. Although pollination is an ancient association with roots in the late Paleozoic, there was establishment of distinctive mid-Mesozoic modes of feeding on pollen and the pollen drops in some gymnosperm reproductive organs, including the long-proboscid pollination mode.

8. Early angiosperms and their repertoire of insects extinguished mid-Mesozoic modes of pollination and reinvented pollination during the mid-Cretaceous, initially with generalist associations and later with specialist associations during the Late Cretaceous and Paleogene.

FUTURE ISSUES

1. The ecological change of insect herbivore component communities in well-preserved, recurring, and geologically long-lived plant hosts needs to be investigated. Candidates include (a) the Pennsylvanian–Early Permian medullosan seed fern Macroneuropteris scheuchzeri, (b) the Jurassic bennettitalean Anomozamites-Williamsonia-Welrichia-Bucklandia plant, and (c) the Late Cretaceous–Recent sycamore lineage of Sapindopsis-Platantes-Platanus.

2. The radiation of plant hosts and their insect herbivores following the P-Tr crisis in the Karoo Basin of South Africa must be explored in greater detail.
3. The number of worldwide K-Pg data sets for understanding the global patterns of the end-Cretaceous crisis for early Paleogene plant-insect associations needs to be expanded. Possibilities include the Denver Basin in Colorado and the Raton Basin in Colorado and New Mexico.

4. The Eocene–Miocene plant-insect associations in northeastern Africa should be examined, and their links to a known ecological and paleoclimatological history of the region need to be established.

5. The past trophic role of plant-insect associations in establishing highly resolved food webs in well-preserved, deep-time deposits should be evaluated. Possibilities include extensive lake deposits in western Eurasia of Jurassic and Early Cretaceous age.

6. The fidelity at which the fossil record captures insect damage on the basis of modern damage-spectra studies should be ascertained in more detail.

7. Jurassic floras need to be evaluated for insect damage and evidence of pollination. In addition, a relationship between bennettitalean herbivory levels and their possible pollination needs to be explored.

8. Knowledge is needed of the complete spectrum of pollination modes during the pteridophyte and seed-plant radiation of early Mesozoic compressions. One focus is the timing of origin of the siphonate proboscis in early insect lineages.

DISCLOSURE STATEMENT
The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS
We thank the editorial board of Annual Review of Earth and Planetary Sciences for inviting us to contribute this review. We thank our numerous colleagues who have worked with us and influenced our thoughts on plant-insect interactions. Finnegan Marsh produced Figures 1, 2, 5, and 6. This is contribution 250 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History in Washington, DC.

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Contents

On Escalation
Geerat J. Vermeij

The Meaning of Stromatolites
Tanja Bosak, Andrew H. Knoll, and Alexander P. Petroff

The Anthropocene
William F. Ruddiman

Global Cooling by Grassland Soils of the Geological Past and Near Future
Gregory J. Retallack

Psychrophiles
Khawar S. Siddiqui, Timothy J. Williams, David Wilkins, Sheree Yau, Michelle A. Allen, Mark V. Brown, Federico M. Lauro, and Ricardo Cavicchioli

Initiation and Evolution of Plate Tectonics on Earth: Theories and Observations
Jun Korenaga

Experimental Dynamos and the Dynamics of Planetary Cores
Peter Olson

Extracting Earth’s Elastic Wave Response from Noise Measurements
Roel Snieder and Eric Larose

Miller-Urey and Beyond: What Have We Learned About Prebiotic Organic Synthesis Reactions in the Past 60 Years?
Thomas M. McCollom

The Science of Geoengineering
Ken Caldeira, Govindasamy Bala, and Long Cao

Philippe Gillet and Ahmed El Goresy

The Fossil Record of Plant-Insect Dynamics
Conrad C. Labandeira and Ellen D. Currano
The Betic-Rif Arc and Its Orogenic Hinterland: A Review
John P. Platt, Whitney M. Behr, Katherine Johanesen, and Jason R. Williams ............................................................... 313

Assessing the Use of Archaeal Lipids as Marine Environmental Proxies
Ann Pearson and Anitra E. Ingalls .......................................................... 359

Kevin P. Furlong and David S. Chapman .................................................. 385

The Isotopic Anatomies of Molecules and Minerals
John M. Eiler .......................................................................................... 411

The Behavior of the Lithosphere on Seismic to Geologic Timescales
A.B. Watts, S.J. Zbong, and J. Hunter ....................................................... 443

The Formation and Dynamics of Super-Earth Planets
Nader Haghighipour ............................................................................. 469

 Kimberlite Volcanism
R.S.J. Sparks .......................................................................................... 497

Differentiated Planetesimals and the Parent Bodies of Chondrites
Benjamin P. Weiss and Linda T. Elkins-Tanton ........................................ 529

Splendid and Seldom Isolated: The Paleobiogeography of Patagonia
Peter Wilf, N. Rubén Cúneo, Ignacio H. Escapa, Diego Pol, and Michael O. Woodburne ......................................................... 561

Electrical Conductivity of Mantle Minerals: Role of Water in Conductivity Anomalies
Takashi Yoshino and Tomoo Katsura ...................................................... 605

The Late Paleozoic Ice Age: An Evolving Paradigm
Isabel P. Montañez and Christopher J. Poulsen .......................................... 629

Composition and State of the Core
Kei Hirose, Stéphane Labrosse, and John Hernlund .................................... 657

Enceladus: An Active Ice World in the Saturn System
John R. Spencer and Francis Nimmo ......................................................... 693

Earth’s Background Free Oscillations
Kiwamu Nishida .................................................................................... 719

Global Warming and Neotropical Rainforests: A Historical Perspective
Carlos Jaramillo and Andrés Cárdenas .................................................... 741

The Scotia Arc: Genesis, Evolution, Global Significance
Ian W.D. Dalziel, Lawrence A. Lawver, Ian O. Norton, and Lisa M. Gahagan .......................................................... 767