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Decoupled Plant and Insect Diversity After the End-Cretaceous Extinction

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

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

Insect damage on compressed fossil leaves provides abundant information about terrestrial food webs, because the diversity of plants and their insect feeding associations can be directly compared using the same fossils, at high sample sizes and in fine stratigraphic context (*5–7*). Modern ecological observations generally show positive correlations between insect herbivore diversity and plant diversity (*8–10*), and the evaluation of fossil insect damage can test whether past extinctions disrupted this linkage. In southwestern North Dakota, for example, the K-T event caused a significant floral extinction (*11*) accompanied by a major extirpation of insect feeding morphotypes (*6*). These included diverse and abundant leaf mines and galls, whose extant analogs are typically made by host-specialized insects (*12, 13*). No significant recovery of specialized feeding was found in 80 m of local section representing the first ~0.8 million years of the 10-million-year Paleocene (*6*), prompting us to examine the geographic and temporal extent of the Paleocene ecological dead zone.

We investigated the recovery of plant-insect associations in the western interior United States, with emphasis on the Paleocene. We focused on insect mines (hereafter "mines") because they are a specialized feeding category commonly preserved in fine morphological detail (Fig. 1) (*14, 15*). We compared four latest Cretaceous, nine early and late Paleocene, and one early Eocene megafloral sites (Table 1, table S1, and fig. S1) from warm temperate and subtropical fluvial paleoenvironments, selected to optimize preservation and diversity, sample size, stratigraphic control, and temporal and geographic coverage. The sites are located in several basins, forming a composite regional data set. Nearly all the Paleocene samples have similar taxonomic composition and the low floral diversity that is typical of the time period and region (Fig. 2 and tables S2 and S3). The major exception is the Castle Rock flora from the Denver Basin: a highly diverse and compositionally distinct early Paleocene assemblage with tropical rainforest characteristics, located in a warm and humid, apparently geographically restricted, belt on the eastern margin of the Laramide Front Range (*16–20*).

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

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

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

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

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

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

Fig. 1. Representative leaf mines on the botanically depauperate Mexican Hat [(A) to (H)] flora and the diverse Castle Rock [(I) and (J)] flora, both early Paleocene (Table 1). Scale bars, 1 mm in (C) and (E), 1 cm in the other panels. (**A**) Elongate, serpentine, agromyzid dipteran mine (DT104) characterized by a hairline trail of fluid-ized frass and occurring only on *Platanus raynoldsi* (Platanaceae) [USNM specimen 498154 (National Museum of Natural History)]. (**B**) Blotch mine on *P. raynoldsi* with small ellipsoidal frass pellets (DT36), probably made by a tenthredinid hymenopteran, USNM 498155. A similar mine also occurs on a rare unidentified host at Mexican Hat (not shown in the figure). (**C**) Moderately sinusoidal to linear lepidopteran mine on *P. raynoldsi* with pelleted frass trail of variable width and undulate mine margins (DT91, USNM 498156). (**D**) Sinusoidal mine, probably lepidopteran, on *Juglandiphyllites glabra* (Juglandaceae; fragment, not included in analyses) with frass trail of dispersed rounded pellets oscillating across the full mine width (DT92, USNM 498157). (**E**) Mine on "*Populus*" *nebrascensis* (Trochodendrales) with distinct pelleted frass trail occupying the median 80% of the mine width (DT91, USNM 498158). (**F**) Curvilinear aborted mine lacking frass (DT105) on *J. glabra*, USNM 498159. (**G**) Serpentine lepidopteran mine with thick, initially intestiniform but subsequently looser frass trail (DT41), common throughout the Paleocene in the western interior United States and shown here on *Zizyphoides flabella* (Trochodendraceae), USNM 498160. (**H**) Serpentine lepidopteran mine (DT91) displaying frass detail of early instar stages at bottom, on *Cercidiphyllum genetrix* (Cercidiphyllaceae), USNM 498161. (**I**) Aborted mine on host morphotype CR9, showing confined, linear, median frass trail with lateral reaction rim [DT43, DMNH specimen 26060 (Denver Museum of Nature and Science)]. (**J**) Complete, serpentine, straight-margined mine lacking frass (DT45) on host morphotype CR59, DMNH 26039.
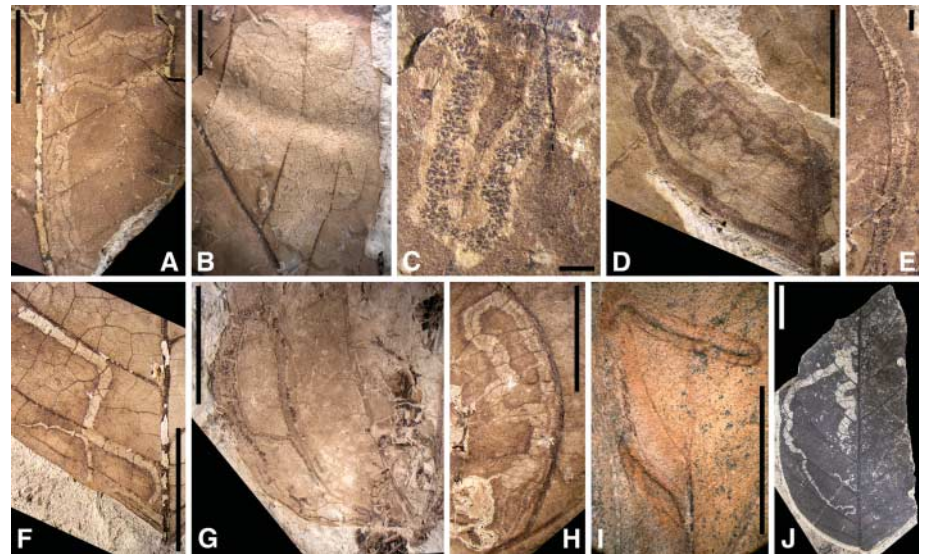
Table 1. Sampling summary. All insect-damage data are new between Mexican Hat and Lur'd Leaves, inclusive. The Cretaceous and Pyramid Butte samples were reanalyzed from our K-T data set (6), with the addition of >700 newly analyzed leaf specimens. Data are not adjusted for sample size as in Fig. 2 (see also fig. S1 and table S1).

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

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

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

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

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

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

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

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

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

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

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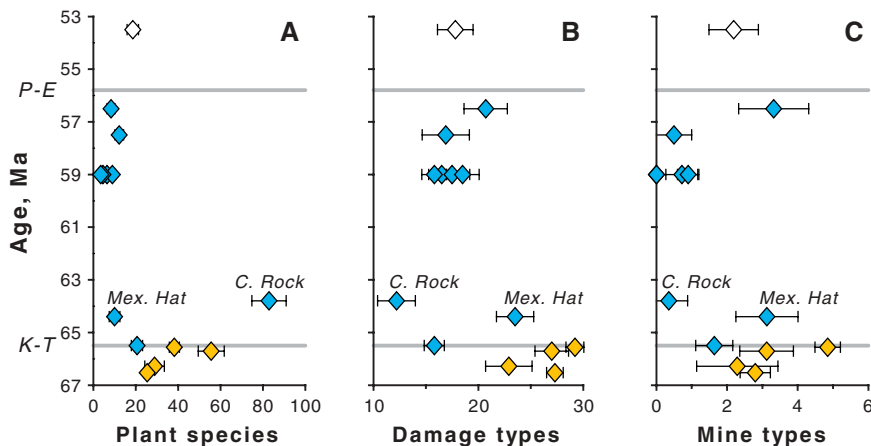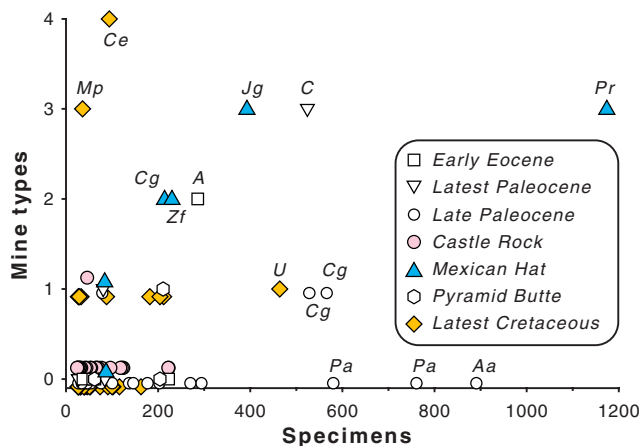
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Why Are There So Many Species of Herbivorous Insects in Tropical Rainforests?

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

Large numbers of herbivore species in the Tropics relative to temperate communities might reflect differences in (i) host plant species diversity, (ii) numbers of herbivore species per host, and/or (iii) host specificity, the number of plant species hosting each insect species. The tropical maximum in plant species richness is well documented. For instance, there are 5 to 10 times as many plant species per 10,000 km² in tropical than in temperate areas (1), and woody plant species richness per hectare in the Tropics is on average six times as high as that in temperate forests (156.8 ± 63.6 and 25.2 ± 19.7 species with diameter at breast height ≥10 cm; fig. S1). However, latitudinal differences in host specificity and numbers of insect species per host plant species are more difficult to assess (2, 3).

A recent proliferation of quantitative studies on tropical insect herbivores that include feeding and rearing experiments (4–9) have not been matched by comparable activity in temperate forests (10, 11), perhaps because patterns of host use are believed to be well documented for temperate herbivores. Much qualitative data on host associations of herbivores accumulated during the past two centuries, particularly in Great Britain and Central Europe, are not directly comparable to recent, quantitative studies in the Tropics (12). A temperate-tropical comparison of herbivore communities is further complicated by differences in the phylogenetic diversity of the vegetation. Temperate forests are dominated by a relatively small number of woody plant lineages as compared to tropical forests (13).

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

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It has been known for more than 40 years that a moon whose orbit is tidally evolving away from a planet can trap a more distant moon in an orbital resonance, pushing the exterior moon outward ahead of itself (5). As the inner orbit expands due to tidal forces, the satellites thereby maintain the commensurate mean motions and move outward together (6).

The ratio of energy to angular momentum required to expand an orbit without changing its eccentricity is just the orbital frequency. So if energy is transferred outward to a moon with a longer orbital period, not enough angular momentum is available to maintain the circularity of the orbits, and the eccentricity of one or both moons increases (7). In the case of Jupiter's large inner moons Io, Europa, and Ganymede, which are locked in a 4:2:1 resonance identified by Pierre-Simon Laplace two centuries ago, tides raised by Jupiter on the satellites damp this eccentricity, producing persistent volcanic activity on Io and a liquid ocean below Europa's thin ice crust. Pluto itself was pushed hundreds of millions of kilometers away from the Sun by Neptune, as this giant planet migrated outward (as a back reaction from throwing solid bodies sunward, however, not solar tides) (8). Pluto is still locked in a 3:2 resonance with Neptune, and its high eccentricity is evidence of this migration.

But what of Nix and Hydra, which travel on circular orbits and are too small and distant to have their orbital eccentricities tidally damped? The answer is that the resonances in which Pluto's tiny moons were trapped, both were maintained by and acted to enhance (albeit not by much) the eccentricity of Charon. Charon, being much larger as well as closer to Pluto, has its eccentricity damped in a time that is much less than the age of the solar system. Indeed, for this mechanism to work, Charon must have initially been on a highly eccentric orbit, which would be expected if it was captured nearly intact after an inelastic collision (3), rather than having accreted from a giant impact–produced disk (the preferred mechanism for the formation of Earth's Moon).

Ward and Canup have offered a model that explains the origin of the orbital configuration of Pluto's three known satellites via tidal expansion from a compact system that was produced by a giant impact. Their model requires the impact origin of an intact Charon, which previous models (3) suggest is likely only if the Pluto impactor was a homogeneous mixture of ice and rock. Hence, the model of Ward and Canup also predicts that Nix and Hydra are made of ice-rock mixtures. Pluto is by far the brightest and best known of the Trans-Neptunian Objects (TNOs). Once believed to be a planet-sized body, it is now viewed as one of the larger members of a populous class of distant solar system bodies. Many other TNOs are known to have moons. Observations of the orbital characteristics of additional, smaller moons of such minor planets could indicate whether their observed large moons were formed by giant impacts or purely gravitational capture (9).

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ECOLOGY

Crafting the Pieces of the Diversity Jigsaw Puzzle

R. L. Kitching

Herbivorous insect species are more numerous in tropical than in temperate forests. Studies of present-day forests and fossil leaf patterns show how plant diversity controls insect diversity.

After his encounter with the Atlantic rainforest of Brazil, Charles Darwin observed that "the land is one great, wild, untidy, luxuriant hothouse, made by Nature for herself" (1). Increasing knowledge of the forest fauna over the past 30 years has only underscored Darwin's point: 978 species of beetles from six trees in Venezuela, 160 species of grasshoppers in 60 trees in Amazonia, 218 species of ants from 19 trees in Sabah—the list goes on (2). Dobzhansky, with characteristic prescience, asked "why?" as early as 1950 (3). He suggested that the animals of the Tropics were fundamentally different from those of temperate regions: In general, tropical species were more specialized, with niche limits defined by interactions among species rather than by physical or chemical factors. This has proved very difficult to test; indeed, it moved surreptitiously from hypothesis to dogma without any very critical evaluation. This difficulty is nowhere more acute than in the case of tropical herbivores. Two reports in this issue, one by Novotny et al. (4) on page 1115 and the other by Wilf et al. (5) on page 1112 shed light on both old and new aspects of these issues.

The relationships between the diversity of tropical trees and that of the associated arthropods have been central in the exciting if somewhat circular debates on global species richness. It is relatively easy to count the number of tree species in a forest and to extrapolate this count to a region, continent, or even planet. If each tree species supports a certain number of herbivorous insects, then we can extrapolate to a global estimate of herbivore richness. With a few further assumptions, we can obtain an overall number of all arthropod species. That the estimates range from 5 to 100 million (6) suggests that this is not an exact science.

The Novotny/Basset group based in Papua New Guinea has been one of only two or three groups that have measured tropical host specificity empirically by field collecting, larval rearing, and choice experiments. Based on

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thousands of rearing records from almost 60 tree species, they have constructed a database that promises answers to many fundamental questions on herbivory and diversity. They showed previously (*7*) that host plant phylogeny plays a key role in determining levels of specialization in dominant groups of insect herbivores. But how to use this information to say something general about insect herbivory in tropical as opposed to temperate ecosystems?

The problem is the perennial one of just what is a legitimate comparison: how to line up insect responses to ecosystems that, on the one hand, exhibit a tree diversity of perhaps 200 per hectare with one with perhaps 20? This is compounded when host plant records from temperate forests have been accumulated by centuries of anecdotal observation rather than by the intense, controlled observation of the best current tropical studies. In a masterful piece of interdisciplinary work, Novotny and his colleagues have overcome these problems and come up with an utterly unexpected answer. First, they applied their "tropical" methods to a mature forest in central Europe. They then used the power of GenBank to produce a phylogeny for the 14 tree species studied in Moravia. In a stroke of remarkable originality they then extracted from their database from New Guinea the 14 tree species that presented a phylogeny most closely congruent with the central European data set. So they were able to make a legitimate quantitative comparison of herbivore host specificity in temperate and tropical forests. There was no difference in the distribution of host specificities between the two regions. The huge richness of herbivorous insects in tropical rainforests is driven by the phylogenetic diversity of the plant assemblage in those forests and not by any fundamental differences in the nature of the niches of the herbivores.

The Novotny *et al.* result supports the general idea of a post-Pleistocene equilibrium (setting aside the anthropogenic clearing of trees on a vast scale) and an explanation of the herbivore diversity that we observe in nature. Simply stated, the Novotny law becomes: "Herbivore richness in forests is related positively to the phylogenetic breadth of its supporting tree assemblage."

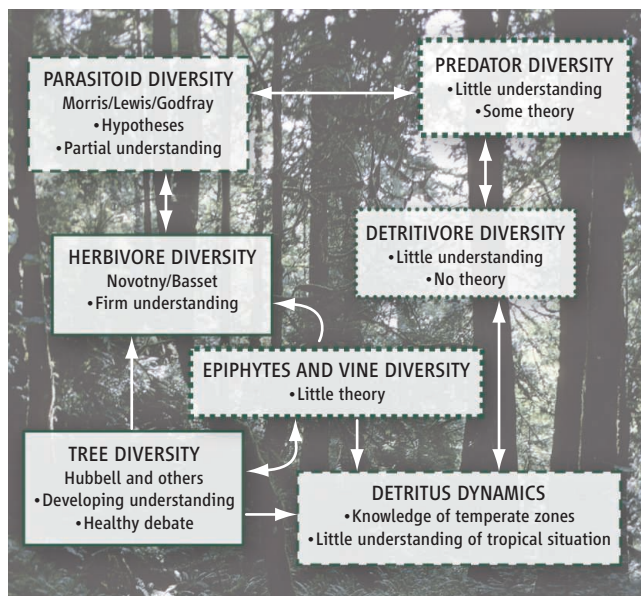In a fascinating contrast, Wilf *et al.* have used the vast deposits of leaves from Cretaceous and Tertiary beds in North America to demonstrate that an equilibrium world is, geologically speaking, but a temporary end point rather than a constant property of ecosystems. Leaves carry with them species-specific patterns of herbivore activity. They show clearly that after the Cretaceous-Tertiary (K-T) mass extinction about 65 million years ago, recovery of herbivore richness was both slow and,

Components of biodiversity in the forest. The diagram depicts a highly simplified rainforest food web. Dashed or dotted boxes indicate areas for which general explanations of diversity are either incomplete (dashed) or lacking (dotted) altogether.

more important, patchy. The rainforest-like faunas of the Castle Rock site in Colorado show a Paleocene herbivore signal more diverse than anything from the Cretaceous. In contrast, most other more temperate floras from the Paleocene show a dramatic reduction in herbivore signal. Bringing the two results together, Cretaceous assemblages should obey the Novotny law, whereas post–K-T ones may deviate from it significantly. With only a modestly richer database than the currently available one, this contention could be tested and so combine paleoecology and its modern counterpart in a productive way.

The firm basis of understanding as to just why herbivores are so diverse in tropical forests is part of a recent and welcome transition in tropical ecology. Over the past few decades, we have built up an impressive body of data that identifies biodiversity patterns in tropical rainforests. There remains much to be done, but there is enough information that we can look for general mechanistic explanations of the patterns. A recent flurry of activity followed Hubbell's work (*8*), resulting in an active, firmly based debate on the generation

of rainforest tree diversity. The initial proposition of equivalence across all trees of whatever species, melded with essentially random replacement processes (the "neutral" theory), produced results that mimicked well some commonly used species/abundance relationships. That such relationships could be generated with patently unrealistic assumptions has refocused attention on how we look at and interpret diversity data. The heated debate that followed points now to a more deterministic theory focusing on the idea of rare species advantage. The generalizations that emerge from the work of Novotny *et al.* mean that we can extend our understanding of biodiversity-generating processes to the next trophic level—the herbivores. Their results make clear the "bottom-up" effects of plant diversity on the herbivore assemblage. There are undoubtedly "top-down" effects as well. Here the work of Lewis and Godfray (*9*) and Morris *et al.* (*10*) shows that apparent competition among host species is mediated through their assemblage of parasitoids—larval insects that prey on their hosts from the inside, so to speak.

In a simplified, general, rainforest food web (see the figure), the consensus (or at least the basis for a healthy debate) that we may now expect on tree diversity and the associated herbivores leaves several components requiring explanation: the third trophic level comprising the parasitoids and predators, and the externally maintained food chains based on decomposition processes (plus, incidentally, a general understanding of the interaction between herbivores and the epiphytes and vines so characteristic of tropical forests).

Processes determining the diversity of predators await their champions. Parasitoid assemblages are better understood as modifiers of herbivore diversity than as community-level objects in themselves. There has long been work on the top-down role of predators and parasitoids as modifiers of the assemblages of potential prey items, notably the idea that key predators can be the forces that flip whole food webs among different equilibria. We also have some controversial evidence of invariant or at least constrained predator-prey statistics within simple food webs (*11*), but mechanistic explanations are lacking. Finally, there are the chewers of rubbish—the "garbos" (if I may be permitted an Australianism). Arthropods that feed either on fungi or directly on detritus and its associated

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microorganisms make up as much as 30 to 40% of the rainforest fauna. General patterns for these components are few, and diversity-generating mechanisms are entirely conjectural at this time (*12*). There remains much to do, but this is an exciting time for rainforest ecologists. Encouraging progress toward a general theory has been made, and the field, laboratory, and statistical tools surely exist to maintain this drive.

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PHYSICS

Surface Transfer Doping of Semiconductors

The local conductivity of semiconductors can be changed by incorporating various atoms into the semiconductor material. New work shows that manipulation of the surface can produce the same effect.

Jürgen Ristein

"Doping" of semiconductors—that is, the local manipulation of their conductivity—is a key technology for electronic devices. Without doping, for example, a gallium nitride sample larger than the White House would be needed to host a single mobile charge at room temperature; for diamond, not even the volume of the globe would be sufficient. It is only through doping that semiconductors become useful electronic materials. Recent studies have revealed an unconventional way to achieve doping through surface engineering.

Doping of semiconductors is usually achieved by incorporating atoms of appropriate elements into the host lattice of the semiconductor. The dopants either release an excess electron as a free negative charge carrier to the semiconductor (n-type doping) or they consume one more electron for chemical bonding than they brought with them (p-type doping). In the latter case, the "stolen" electron behaves like a positive charge carrier—a hole—in the semiconductor.

The electrons or holes remain weakly bound to the dopants that carry their respective counter charge, and it takes a characteristic activation energy Δ to release them as free charge carriers. For effective dopants, this energy is rather small. At room temperature, it is easily supplied by the vibrations of the semiconductor atoms, and one ends up with free charge carriers of one sign and fixed ionized dopants with opposite charge. This situation is sketched for p-type doping in the figure (left panel).

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If the dopants are distributed homogeneously in the semiconductor lattice, then so will be the mobile charge carriers. Positive and negative charge cancel, and on average, no electric field acts on the mobile charge carriers. For electronic devices to function, the doping must therefore be inhomogeneous. Inhomogeneous doping results in local variations of electron and hole concentrations, which tend to equalize by diffusion. The result is a delicate equilibrium between charge separation and electric field that determines the electrical response of a device to externally applied voltages. The simplest such device is the p-n junction, which consists of a p-type and an n-type doped layer of the same semiconductor.
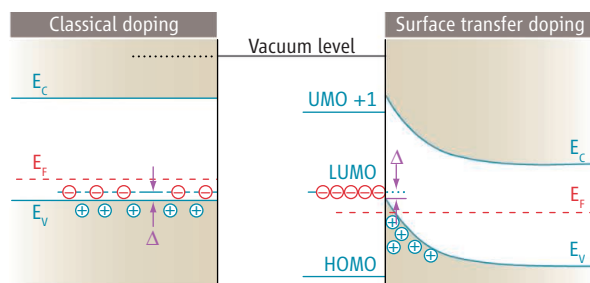
In all classical devices, the dopants are impurity atoms introduced into the bulk of the semiconductor. But doping can also be achieved by an electron exchange between a semiconductor and dopants situated at its surface. The surface dopants—below, we will use acceptors for illustration—possess unoccupied molecular orbitals for electrons (UMOs). If the energetically lowest of these orbitals (called LUMO) is close to the valence band maximum of the semiconductor, it will steal an electron from the semiconductor, just as classical acceptors do (see the figure, right panel). As a result, holes will form in the semiconductor, and negative charge will be localized on the surface acceptors (*1*). This charge separation will automatically establish an electrostatic potential that con-

fines the holes in a perpendicular direction but leaves them free to move parallel to the surface.

This kind of p-type surface transfer doping has recently been demonstrated for fullerene (*2*) and fluorofullerene molecules (*3*) serving as surface acceptors on hydrogen-terminated diamond. The hydrogen termination leads to an exceptionally low ionization energy for the diamond; the fullerenes were chosen for their high electron affinities. For $C_{60}F_{48}$ (*4*), the activation energy Δ is even negative, and each molecule brought onto the diamond surface creates a hole (*1*).

The electronic states at the surface are not necessarily associated with molecular adsorbates. In fact, the first observation of p-type surface transfer doping of diamond involved a complex electrochemical system, in which hydrated ions acted as surface acceptors (*5*). These ions were usually created unintention-

Beyond conventional doping. This band diagram illustrates classical p-type doping (**left**) and p-type surface transfer doping (**right**), using the energy of an electron in free space as a reference (vacuum level). E_c and E_v are the energies of the conduction band minimum and the valence band maximum, respectively. The balance between electrons localized in acceptor states and free holes in the valence band is expressed by the constant Fermi energy E_F. The closer E_F is to E_v, the higher the local density of holes. LUMO and HOMO are the lowest unoccupied and highest occupied molecular orbitals of the surface acceptors, respectively.