PERSPECTIVES: PALEOECOLOGY

Hungry Herbivores Seek a Warmer World

Phyllis D. Coley

Most people take it for granted that when they are hiking in the country, the landscape will be dominated by plants—and, probably, few hikers bother to question why all the plants have not been eaten by animals. Ecologists and evolutionary biologists have long pondered why the world is green (*1*). The short explanation is that populations of herbivores are kept in check by plant defenses as well as by predators. Plants have evolved a formidable arsenal of chemical and physical defenses, making them at best unpalatable and at worst inedible (*2*). Moreover, predators and parasites have united to prevent herbivores from becoming too populous (*3*). More comprehensive explanations for a green world are complicated by the fact that the balance of interactions between animals and plants depends on the ecological context and the evolutionary history of the players. But, as 50% of Earth's extant organisms are either plants or the herbivores that eat them, understanding the interactions between these two groups is fundamental for understanding life on Earth (*4*).

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A katydid mimicking a dead leaf with herbivore damage.

Research into the interactions between plants and herbivores has included inquiries into how these relationships evolved and how they affect species diversity and population dynamics in present-day communities (see the photographs of tropical leaf-chewing herbivores). Current concerns over global climate change have also focused attention on how climate might influence these crucial interactions. Most of our knowledge about plant-herbivore interactions comes from studies of living organisms rather than from the fossil record, partly because of the difficulty of reconstructing interactions that occurred millions of years ago.

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On page 2153 of this week's issue, Wilf and Labandeira present one of the first attempts to test the universality of ecological trends by careful analysis of fossil evidence. They examined fossils of leaves with insect damage from the period of global warming between the late Paleocene and early Eocene epochs (*5*). In support of the popular view that the intensity of herbivory increases with an increase in temperature (or decrease in latitude), the investigators found that early Eocene plant fossils had sustained a greater variety of insect damage and higher frequencies of attack than their counterparts from the cooler Paleocene. The success of this study suggests that analysis of fossil evidence has much to teach us about the dynamics of plant-herbivore associations long ago.

Just how abundant, how damaging, how diverse, and how specialized were the herbivores of millions of years ago? At least two approaches to the investigation of these questions are shedding light on ancient associations between plants and their animal predators. One approach reconstructs past associations on the basis of host preferences seen among modern taxa. The creation of phylogenetic trees allows inferences about whether a particular ancestral herbivore was generalized or specialized, and what its preferred plant foods may have been. This powerful technique has shown that many plant-herbivore associations are very ancient, whereas others are labile; that innovations in plant defenses have led to diversity within a plant lineage; and that the herbivorous habit has promoted speciation (*6*). Despite the obvious value of these findings, phylogenetic analysis is limited to inferences rather than observations of past events.

A second, direct approach for determining ancient associations between plants and herbivores is to look at the fossils themselves (*7*). Scrutiny of fossils not only allows the identification of plants, but also makes it possible to relate a type of leaf damage to an attack by a particular herbivore. This is most reliable for insects that mine leaves or make galls at sites of attack, but valuable information about leaf-chewers can also be gathered.

The images obtained by Wilf and Labandeira demonstrate the extraordinary detail that can be seen in their well-preserved specimens. Until now, analysis of fossil evidence of herbivory has primarily focused on descriptions of the species involved and host-plant associations. But Wilf and Labandeira push the fossil evidence farther than ever before by quantitatively testing ecological hypotheses. Instead of just asking who ate whom, they also quantified the amount of damage and the diversity and specialization of herbivores. Using these data, they were able to test the effect of climate on plant-herbivore interactions. To date, ecologists have examined climate effects by comparing ecosystems in different latitudes that are warmer or cooler. In contrast, Wilf and Labandeira examined ancient plant-herbivore interactions in a single research area (southwestern Wyoming), before and after a large thermal event, greatly extending the robustness of modern-day latitudinal observations.

What do these observations reveal about the effects of latitude? One of the best established truths in ecology is that most groups of organisms are more diverse in tropical than in temperate ecosystems (*8*). Given the greater species diversity in the tropics, one might suppose that there are also more opportunities for biotic interactions. Indeed, a compilation of many independent studies supports the supposition that there are greater opportunities for plants and herbivores to interact in the tropics (*9*). On average, tropical plants invest more in chemical and physical defenses, suggesting that, over evolutionary time,

A tropical rainforest grasshopper.

herbivores have exerted more selective pressure in tropical regions. However, despite their greater defenses, tropical plants suffer higher rates of damage. Whether this reflects the greater number of herbivorous species or the larger populations of herbivores (which have thrived because of better

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detoxification mechanisms or defenses against predators), or both, is not yet fully established.

A Lepidopteran caterpillar with warning eyespots.

This latitudinal trend of greater diversity, more numerous plant defenses, and increased herbivore pressure in the tropics suggests that climate is important. Wilf and Labandeira tested this hypothesis by examining floras from the late Paleocene (~56 million years ago) and the early Eocene (~53 million years ago). During this 3-million-year interval, temperatures in their study area warmed by about 7°C, changing the climate from humid temperate to humid subtropical. Consistent with the latitudinal data, they found that plant diversity increased, the amount of herbivore damage to leaves increased, and the diversity of herbivores per plant species increased. In addition, more abundant species suffered higher damage rates, again consistent with data from modern communities (*10*).

It is perhaps tempting to extrapolate from these patterns to predict changes in plant-animal interactions caused by the current global warming trend. Such extrapolations may be misguided, however, because the rates of climate change today are several orders of magnitude faster than before. This rapidity may not permit significant evolutionary change or plant dispersal, and is more likely to disrupt existing plant-herbivore associations (*11*).

Although Wilf and Labandeira's study may not be able to directly predict future changes in plant-herbivore interactions, it goes a long way toward explaining present and past communities. These data are exciting because they suggest that the greater capacity for plant-herbivore interactions in tropical as compared to temperate climates may have been the case throughout the last 100 million years in which angiosperms (flowering plants) have been diverse. Thus, climate may lead to different evolutionary histories, with herbivores and plants exerting stronger selective pressure on each other in Earth's warmer zones. Climate may also influence the dynamics of herbivore and plant populations, with herbivores being more abundant, more diverse, and more damaging in tropical climates. Their work also suggests that fossil evidence can be used productively to test ecological theories, and this should encourage more dialogue between neo- and paleoecologists.

References and Notes

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PERSPECTIVES: MAGNETISM

Shining Soft X-rays on Magnetic Structures

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The study of magnetic materials with x-rays is developing at a breathtaking pace. The methods used in these studies extend magneto-optics—the response of a material to optical excitation as a function of the relative orientation of magnetization and light polarization—to the x-ray regime. One of the key advantages of these techniques is that they are element specific, because the photon wavelength (or energy) in the x-ray regime can be tuned to match the excitation energy of a discrete core electronic level. Also, layer thicknesses of magnetic multilayers and lateral structures in novel magnetic devices that are presently being developed are comparable to soft x-ray wavelengths. Therefore, detailed insight into the magnetic properties of these technologically important magnetic structures can be obtained by use of soft x-rays. The soft x-ray regime is of importance because all technically relevant magnetic materials contain 3d transition metals, for which the 2p excitation that shows the highest sensitivity to the magnetic state lies between 500 and 1000 eV.

Synchrotron radiation is a particularly powerful tool for soft x-ray magneto-optics, offering tunability to virtually any core level resonance, high intensity and brilliance, good collimation, and complete control over polarization. Recently developed polarizers and wave retarders allow us to analyze and modify the state of polarization for soft x-rays (*1*), further increasing the scope of these magneto-optic studies. On page 2166 of this issue, Dürr *et al.* (*2*) demonstrate the power of x-ray magneto-optics in a synchroton study of single crystalline FePd layers, which provides detailed insights into their complex magnetic domain structure.

In a classical picture, magneto-optic effects occur when the magnetic field associated with a magnetic material acts on the electron currents induced by an incident electromagnetic wave. A charge moving in a magnetic field experiences the so-called Lorentz force, the direction of which is normal to the velocity of the charge and the magnetic field (see top figure on page 2100). The Lorentz force leads to light with polarization perpendicular to the incident light in the reflected beam. Microscopic theories (*3*) show that this magneto-optic effect is connected to excitations from the core shell to spin-polarized unoccupied electronic states and the interaction of magnetic moments due to the spin of the electrons and their orbital motion.

The change of polarization when light is passed through a magnetic material, known as the Faraday effect, is in principle

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