Ozone loss increases

Starlab

Also see the archival list of *Science*'s Compass: Enhanced Perspectives

Similar articles found in:
SCIENCE Online

Search Medline for articles by:
Coley, P. D.

Search for citing articles in:
ISI Web of Science (1)

Alert me when:
new articles cite this article

Collections under which this article appears:
Ecology
Enhanced Content

PALEOECOLOGY:

Enhanced: Hungry Herbivores Seek a Warmer World

Phyllis D. Coley [HN14] *

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) [HN1]. The short explanation is that populations of herbivores [HN2] are kept in check by plant defenses as well as by predators. Plants have evolved a formidable arsenal of chemical and physical defenses [HN3], 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).

A katydid mimicking a dead leaf with herbivore damage.

Research into the interactions between plants and herbivores [HN4] has included inquiries into how these

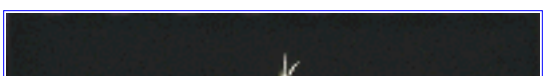
relationships evolved and how they affect species diversity and population dynamics in present-day communities (see the photographs of tropical leaf-chewing herbivores). Current concerns over global climate change [HN5] have also focused attention on how climate might influence these crucial interactions. 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.

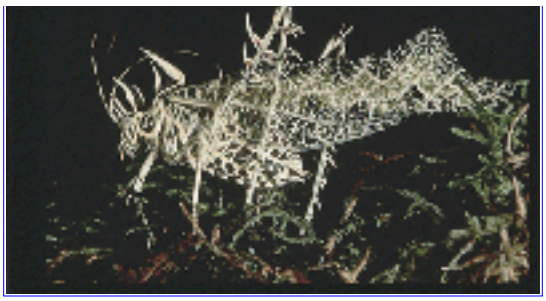
On page 2153 of this week's issue, Wilf and Labandeira [HN6] present one of the first attempts to test the universality of ecological trends by careful analysis of fossil evidence [HN7]. They examined fossils of leaves with insect damage from the period of global warming between the late Paleocene and early Eocene epochs [HN8] (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 [HN9] 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 [HN10] (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 [HN11]), before and after a large thermal event, greatly extending the robustness of modern-day latitudinal observations.





A tropical rainforest grasshopper.

What do these observations reveal about the effects of latitude [HN12]? 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 [HN13], 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, 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 detoxification mechanisms or defenses against predators), or both, is not yet fully established.

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 7ºC, 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).

A Lepidopteran caterpillar with warning eyespots.

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

1. N. Hairston, F. Smith, L. Slobodkin, *Am. Nat.* **94**, 421 (1960).
2. G. Rosenthal and M. Berenbaum, *Herbivores: Their Interactions with Secondary Metabolites* (Academic Press, San Diego, CA, 1991).
3. B. Hawkins, H. Cornell, M. Hochberg, *Ecology* **78**, 2145 (1997); J. Rosenheim, *Annu. Rev. Entomol.* **43**, 421 (1998).
4. D. Strong, J. Lawton, R. Southwood, *Insects on Plants* (Blackwell Scientific, Oxford, 1984). According to *Science Watch* (April 1995), the study of plant herbivory is currently one of the most important topics in the disciplines of ecology and environmental sciences.
5. P. Wilf and C. C. Labandeira, *Science* **284**, 2153 (1999).
6. C. Mitter, B. Farrell, B. Wiegmann, *Am. Nat.* **132**, 107 (1988); B. Farrell, D. Dussourd, C. Mitter, *ibid.* **138**, 881 (1991); D. Funk, D. Futuyma, G. Orti, A. Meyer, *Evolution* **49**, 1008 (1995); J. Becerra, *Science* **276**, 253 (1997); B. Farrell, *ibid.* **281**, 555 (1998); S. Kelley and B. Farrell, *Evolution* **52**, 1731 (1998).
7. P. Opler, *Science* **179**, 1321 (1973); D. Smith, *Phytophaga* **6**, 35 (1994); C. Labandeira, D Dilcher, D. Davis, D. Wagner, *Proc. Natl. Acad. Sci. U.S.A.* **91**, 12278 (1994); C. Labandeira, *Annu. Rev. Earth Planet. Sci.* **26**, 329 (1998).
8. A. Wallace, *Tropical Nature and Other Essays* (Macmillan, London, 1878); T. Dobzhansky, *Am. Sci.* **38**, 209 (1950); E. Pianka, *Am. Nat.* **100**, 33 (1966); D. Schluter and R. Ricklefs, *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Univ. of Chicago Press, Chicago, 1993) [publisher's information]; M. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995) [publisher's information].
9. P. Coley and T. Aide, in *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, P. Price, T. Lewinsohn, W. Fernandes, W. Benson, Eds. (Wiley, New York, 1991), pp. 25-49 [publisher's information]; P. Coley and J. Barone, *Annu. Rev. Ecol. Syst.* **27**, 305 (1996).

10. R. Root, *Ecol. Monogr.* **43**, 95 (1973); P. Opler, *Am. Sci.* **62**, 67 (1974); J. Lawton and D. Schroeder, *Nature* **265**, 137 (1977).
11. M. Ayres, in *Biotic Interactions and Global Change*, P. Kareiva, J. Kingsolver, R. Huey, Eds. (Sinauer, Sunderland, MA, 1993), pp. 75-94 [publisher's information]; D. Lincoln, E. Fajer, R. Johnson, *Trends Ecol. Evol.* **8**, 64 (1993); P. Coley, *Clim. Change* **39**, 455 (1998).

The author is in the Department of Biology, University of Utah, Salt Lake City, UT 84112, USA. E-mail: coley@biology.utah.edu

HyperNotes

Related Resources on the World Wide Web

General Hypernotes

The Ecology WWW Page, maintained by A. Brach, is a searchable list of ecology resources on the Internet.

The PaleoNet Pages, maintained by N. MacLeod, Department of Palaeontology, Natural History Museum, London, is a collection of Internet resources designed to enhance electronic communication among paleontologists.

K.-P. Kelber, Mineralogisches Institut, Universität Würzburg, Germany, maintains a Web page with annotated Internet links for paleobotanists.

The Internet Resource Guide for Zoology from the *Zoological Record* includes sections of links to Web resources on phylogeny and evolution, biodiversity, ecology, and palaeontology.

Links to Great Earth-Science Resources, maintained by E. Fookes and C. Nussbaumer, Department of Geology, University of Geneva, Switzerland, includes links to paleontology and fossil information on the Web.

The University of California Museum of Paleontology (UCMP) presents extensive Web exhibits about the phylogeny of living and fossil organisms, geology and geologic time, and evolutionary theory.

The online Funk and Wagnalls Encyclopedia has an article on paleontology.

S. Leslie, Department of Earth Sciences, University of Arkansas, Little Rock, provides lecture notes for a paleobiology course. A lecture on paleoecology is included.

M. Weissburg, School of Biology, Georgia Institute of Technology, presents lecture notes for a general ecology course.

D. Bogler, Division of Biological Sciences, University of Texas at Austin, maintains a Web site with lecture notes and Internet links for a course on ecology and evolutionary biology.

D. Rand, Department of Biology, Brown University, Providence, RI, provides extensive lecture notes for a course on evolutionary biology.

J. Holmes, Division of Life Sciences, University of Toronto at Scarborough, provides lecture notes

for a course on advanced community ecology.

D. Walters, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, provides extensive lecture notes for a course on evolution. A presentation on the coevolution of species is included.

In its report titled *Botany for the Next Millennium*, the Botanical Society of America includes a chapter on evolution, development, and ecosystems research.

The International Organisation of Palaeobotany maintains the Plant Fossil Record Database.

Numbered Hypernotes

1. In lecture notes for an advanced community ecology course, J. Holmes discusses theories of why plants are relatively abundant and herbivores relatively rare.
2. J. Holmes provides lecture notes on herbivory for a course on advanced community ecology. B. Smith, Department of Science, Black Hills State University, SD, provides lecture notes on herbivory for an ecology course. J. Braatne and R. del Moral, Department of Botany, University of Washington, offer lecture notes on herbivory for a course on plant ecology. A paper titled "Herbivory, a continuum from antagonistic to mutualistic relationships" by J. Gowda is provided in the course materials for the animal ecology course offered by the Swedish University of Agricultural Sciences.
3. A. Davison, Department of Agricultural and Environmental Science, University of Newcastle upon Tyne, UK, discusses plant defenses against animals in lecture notes on plants and environment. L. Blumer, Department of Biology, Morehouse College, Atlanta, GA, discusses plant defenses against herbivores, herbivore responses, and examples of the effects of plant-herbivore interactions in lecture notes for a Web course on the fundamentals of ecology, which is hosted by Northern Arizona University and sponsored by the U.S. Department of Energy, Albuquerque Operations Office, in support of the Technical Qualification Program. PEST CABWeb provides in its "Spotlight on --" section an introductory overview to insect-plant interactions and induced plant defense; abstracts of journal articles about the subject are provided. A student review article titled "Evolutionary plant defense strategies: Life histories and contributions to future generations," prepared for a chemical ecology course by B. Kimball, is available from the Department of Entomology, Colorado State University.
4. The Swedish University of Agricultural Sciences, Umeå, offers an online course on animal ecology that includes a section on plant-herbivore interactions; a tutorial on the evolution of plant-animal interactions is also available. D. Rand discusses coevolution of plants and animals in lecture notes for a course on evolutionary biology.
5. The Paleoclimatology Program of the U.S. National Oceanic and Atmospheric Administration provides an introduction to climate change and a presentation on global warming. J. D. Allen, School of Natural Resources and Environment, University of Michigan, offers lecture notes on climate change as a threat to biodiversity for a course on conserving biological diversity. The U.S. Global Change Research Information Office offers a presentation on Global Warming and Climate

Change; more detailed information about the possible impact of global warming is also provided. The Environmental Pollution/Climate Change Section of the UK Institute of Terrestrial Ecology's Bangor Research Unit, University College of North Wales, offers a presentation on the impacts of climate change that includes a discussion of the possible effect of climate change on interactions between plants and associated herbivores. *Climate Change and Biodiversity Conservation*, a report issued in 1996 by the World Wide Fund for Nature, includes a chapter titled "The ecological impacts of climate change."

6. P. Wilf is in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, until August 1999; thereafter he will be at the Museum of Paleontology, University of Michigan. C. C. Labandeira is in the Department of Paleobiology, National Museum of Natural History, and the Department of Entomology, University of Maryland, College Park. The 3 April 1998 issue of *Science* had an Enhanced Perspective by Labandeira titled "How old is the flower and the fly?"
7. P. Gore, Georgia Perimeter College, Clarkston, provides an introduction to the fossil record for a course on historical geology; links to fossil resources on the Internet are provided. The UCMP offers a presentation titled "Learning from the fossil record."
8. The Department of Geology and Geophysics, University of Alaska, Fairbanks, presents a geologic time scale. The UCMP presents a geological time scale that links to information on the periods. The Infoplease encyclopedia has entries briefly describing the Paleocene and Eocene epochs of the Tertiary period, Cenozoic era. P. Gore provides an illustrated presentation on the Cenozoic era in lecture notes for a course on historical geology. The Global Earth History Web site presents a brief introduction to the Eocene and Paleocene with links to maps. The 28 February 1997 issue of *Science* had a Research News article by Richard Kerr titled "Did a blast of sea-floor gas usher in a new age?" about a possible cause of the late Paleocene warming.
9. The UCMP offers a Web exhibit about phylogenetic systematics. Phylogenetic analysis is discussed in the section on evolution and diversity of the Botanical Society of America's report *Botany for the Next Millennium*. The Tree of Life is a project under the direction of D. Maddison, University of Arizona, that provides information about the phylogenetic relationships and characteristics of organisms.
10. R. Richardson presents lecture notes on evolutionary mechanisms and methods of speciation for a general biology course at Bellevue Community College, WA.
11. An article by B. Spice titled "Global warming 55 million years ago caused migration to North America" in the 8 February 1999 edition of the online Pittsburgh Post-Gazette described paleontological research in southwestern Wyoming. Science Notes, a Web publication of the Science Communication Program, University of California, Santa Cruz, has an article by L. Guterman titled "A warming argument" about scientists combining the analysis of fossils with paleoclimate modeling in an effort to understand Wyoming's warm winters of 55 million years ago.
12. M. Weissburg discusses latitudinal diversity gradients in lecture notes on diversity for an ecology course. A seminar paper by M. Putze and S. Rinkevich titled "Biodiversity patterns (latitudinal

gradients)" is available from the Seminar in Ecological Complexity Web page, Department of Biology, University of New Mexico.

13. Exploring the Tropics is a Web exhibit presented by the Missouri Botanical Garden; it includes a section on plant and animal interactions. "Rainforest structure and diversity," a chapter in *A Neotropical Companion* by J. Kricher, is made available on the Web by the publisher Princeton University Press. For a course on global change, J. D. Allen provides lecture notes on the tropical rain forest and its biodiversity. A discussion of species richness in the tropics is included in lecture notes for an ecology course taught by T. Sherry and J. Whitbeck, Department of Ecology, Evolution, and Organismal Biology, Tulane University, New Orleans. The World Resources Institute provides an introduction to tropical species diversity with links to other resources.
14. P. D. Coley is in the Department of Biology, University of Utah, Salt Lake City.

- Similar articles found in:
  SCIENCE Online
- Search Medline for articles by:
  Coley, P. D.
- Search for citing articles in:
  ISI Web of Science (1)
- Alert me when:
  new articles cite this article

- Collections under which this article appears:
  Ecology
  Enhanced Content

Volume 284, Number 5423 Issue of 25 Jun 1999, pp. 2098 - 2099
©1999 by The American Association for the Advancement of Science.

Copyright © 1999 by the American Association for the Advancement of Science.