



PLANT–ANIMAL INTERACTIONS

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GLOSSARY

Allee effect For population size to be regulated, it must exhibit a negative density dependence. That is, the population growth rate must decline as the population gets larger. However, under certain circumstances, some populations exhibit positive density dependence. This phenomenon, in which population growth rate increases as the population gets larger, is called an Allee effect. An Allee effect may generate a critical minimum population size, below which extinction will occur.

angiosperm Flowering plant. A lineage characterized by flowers, seeds enclosed in carpels, specialized conducting elements in the phloem (sieve tube members) and xylem (vessels), presence of endosperm, double fertilization, and tectate pollen.

diaspore A plant part distributed by dispersal, regardless of its developmental and morphological origins. A diaspore may be a naked seed, a seed enclosed in a fruit, or many seeds enclosed in a fruit. It may also mean bulbs or lengths of rhizomes. A good synonym is propagule.

fitness Relative contribution of offspring to the next generation. An individual, genotype, or phenotype

whose progeny constitutes a large proportion of the succeeding generation has high fitness.

granivores Animals that eat seeds or achenes (grass fruits).

herbivores Animals that eat plants. Usually excludes instances when a single animal eats an entire plant, which is categorized as predation.

phylogeny The evolutionary relationships among taxa (groups of related organisms), often portrayed with some kind of branching diagram, with branches representing speciation events. Typically, the true phylogeny of a group is hidden deep in the past and evolutionary biologists must infer relationships. Various types of data and methods of analysis are used in this effort and there is considerable contention among groups of scientists as to which are most likely to estimate the true phylogeny.

symbiosis Interaction in which two organisms live in close proximity. Symbiosis can be antagonistic or mutualistic. Often, the larger individual is called the *host*, and its inhabitant is called the *guest*.

trophic level Position of a species in the food web (Fig. 1). Plants—autotrophs that convert solar energy to chemical energy and utilize mineral nutrients—constitute the first trophic level. Primary consumers—animals that feed on living plants—constitute the second trophic level. The third trophic level is composed of secondary consumers—animals that feed on primary consumers. Predation, parasitism, grazing, and herbivory are intertrophic level interactions; competition occurs among species in the same trophic level.

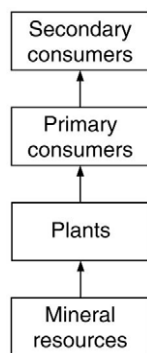


FIGURE 1 Trophic levels within a food web. Each trophic level is comprised of one or more species that consume individuals or resources at the next lower trophic level and are, in turn, consumed by species in the next higher trophic level. Arrows indicate the direction of flow of energy and resources in the food web.

BECAUSE PLANTS CAN OBTAIN nourishment and energy from inorganic sources, they are the foundation of most biotic communities. Animal consumption of plants is the primary conduit by which energy and resources enter the food web. However, the wide-ranging effects of plant-animal interactions on biotic diversity extend far beyond simple trophic links. This article will summarize the various types of plant-animal interactions and use a multidisciplinary approach to examine their implications for biotic diversity.

I. TYPES OF INTERACTIONS

Biotic interactions can be categorized by their effects on the interacting parties (Table I). An interaction may not affect a species, or may be beneficial or detrimental. Antagonistic interactions negatively influence one or both species. Some interactions are clearly antagonistic: When a vole consumes an oak seedling, the rodent benefits while the plant dies. In other cases, it seems clear that both parties are benefiting, as when a hummingbird obtains nectar while transporting pollen from one plant to another. These interactions are termed mutualistic. The implications of other interactions may be more ambiguous. For example, Clark's nutcrackers consume pine nuts but are also important agents of seed dispersal, and it is unclear whether the interaction is mutually beneficial to both species or whether one species is benefiting at the expense of the other. The fitness costs and benefits to the parties involved in such an interaction may be conditional on the current environment. For example, during years of heavy seed production, birds may provide plants with a net benefit,

TABLE I
Pairwise Ecological Interactions between Plants and Animals
Categorized by Their Effects on the Fitness of Each Party

	Plant effect on animal	Animal effect on plant
Antagonisms		
Herbivory	+	-/0
Carnivory	-	+
Mutualisms	+	+

whereas during poor seed years, the net effect of birds on the plant may be negative.

Ecologists seek to categorize interactions because they have distinct ecological and evolutionary implications. Within biotic communities, certain kinds of interactions increase species diversity whereas others reduce it. Similarly, the nature of interactions determines their impact on genetic diversity within populations.

II. ANTAGONISTIC INTERACTIONS

A. Plant Consumers—Herbivores and Granivores

1. Types of Plant Consumers

Animals consume plants in all kinds of habitats, including marine, terrestrial, and freshwater, and do so in wildly diverse ways. For some plants, there is at least one animal species devoted to consuming each type of organ. Some animals remove tissues by chewing; others suck plant sap. Grazing individuals feed from many different individual plants. Some animals live within plants, literally surrounded by food. These include borers, gallers, and leaf miners.

Many animals chew on plants, just as we do. However, another important mode of consumption is to use strawlike mouthparts to pierce and suck fluids from vascular structures such as xylem and phloem, which transport water, minerals, and other compounds throughout the plant. Aphids are common sap feeders. Spider mites are another type of plant-sucking arthropod that may be familiar to unhappy owners of house plants. The origin of this feeding mode probably extends back to the Carboniferous with the Paleodictyopteroidea, an assemblage of insects with sucking mouthparts.

Sap feeders share an interesting problem in common with many blood feeders: Neither blood nor plant sap provides a balanced or complete supply of vitamins

and amino acids. One solution to this problem among aphids has been to host intracellular microbial symbionts with the enzymes necessary to convert common nonessential amino acids into essential rare ones, much as *Midas* converted base metals to gold (Douglas, 1994). These intracellular guests inhabit special cells near the gut and oviducts and are transmitted by the mother to her eggs.

Perhaps the best known mode of plant consumption is grazing. All of us are familiar with picturesque scenes of cows grazing or deer browsing in verdant pastures. Far from peaceful, these are scenes of graphic violence. Hundreds, perhaps thousands, of plants are being eaten alive! Each grazer is eating photosynthetic organs from numerous living plant individuals. However, because the aboveground parts of most plants are constructed of repeating, renewable modules called shoots, a single episode of grazing or browsing rarely kills a plant.

Less well-known grazers include parrot fish, which maintain well-mown lawns of algae on coral reefs. When portions of the reef are protected from parrot fish, luxuriant algal growth can smother the coral. Sea urchins graze kelp forests and, when their natural predators are eliminated, may create vast barrens on the ocean floor. On land, many plant-eating insects, such as grasshoppers, katydids, and some beetles, are grazers. Some grazers feed on roots. These include tiny soil insects called springtails, relatives to silverfish, which move around in the air spaces between soil particles, nibbling on roots. Microscopic crustaceans in the water column of oceans and freshwater lakes and ponds graze on tiny photosynthetic single-celled organisms called phytoplankton. In this case, however, the animals function more like predators because they must kill their prey to eat it.

In contrast to grazers, which move from plant to plant and eat only a portion of each plant, some animals feed entirely on one plant during their lifetime. In some cases, many generations of the consumer will occupy the same tree, evolving greater and greater specialization to that one individual. The rate of evolutionary change in a lineage is a negative function of generation time. Organisms such as long-lived trees, which have very long generation times, are at a distinct evolutionary disadvantage relative to their short-lived pests, which may be able to evolve very quickly because they go through multiple generations every year. Indeed, an important unanswered question in evolutionary biology is how long-lived plants such as trees avoid being destroyed by rapidly evolving pests.

Some consumers live inside their food. Perhaps the most intriguing are gall-forming arthropods—wasps, flies, and mites that induce plants to form elaborate

structures within which the animal munches away on the host. Galls occur in many forms, including small red swellings on leaf blades, large globular swellings on branches, or bristly structures in odd places. In most cases, the female insect induces the gall when she injects her eggs into the plant tissues. Her young hatch and feed inside the gall, where they are relatively protected from enemies and the rigors of the physical environment. The relative frequency of gall-forming herbivores increases with increasing aridity of the environment, presumably because insects in galls are less vulnerable to desiccation. Plant-feeding nematodes, called vinegar eels, often live in galls on roots. The earliest known gall was produced by an insect feeding on tree fern fronds in the late Carboniferous.

Experiments show that the same species of galling insect produces very different looking galls on different plant species, suggesting that the plant determines gall form. Detailed work on the goldenrod ball galler, however, indicates that both insect and plant genes interact to determine gall size (Abrahamson and Weis, 1997). Although these insects appear to successfully manipulate plant development, which is a goal of many biotechnologists, relatively little research has been devoted to understanding the molecular mechanisms of this fascinating interaction.

Another group of consumers that lives inside plants are leaf miners. As their name suggests, the larvae of these flies and moths burrow within a leaf like a miner, eating the tissue they excavate and leaving behind their waste material, called frass. Some leaf miners snake along, leaving a long serpentine mine in their wake. Others remain in one place, creating a large blotch in the leaf. In many cases, leaf miners can be identified to species on the basis of host plant and the appearance of the mine. This has also made leaf miners easy to detect in the fossil record. Because they must live between the top and bottom surfaces of leaves, leaf miner larvae are very flattened from top to bottom. Some leaf miners pupate within the mine; others exit the mine and pupate in the soil beneath the host plant. In addition to leaf miners, some other insects mine plant stems, burrowing just beneath the stem surface and leaving similar-looking feeding galleries.

Bark beetles are economically very important plant consumers (Paine *et al.*, 1997). Adults attempt to bore into tree trunks, but healthy trees generally can “pitch” them out, literally flooding the bore holes with sap. However, the sap attracts more adults of these gregarious beetles and an ailing tree’s defenses can be quickly overcome. Female beetles then excavate extensive galleries just beneath the bark and lay their eggs in the termini of the tunnels. The larvae feed on both the host

wood and tree-feeding fungi that adults transport in special structures called mycangia. Often, bark beetles do not kill their host but are indirectly responsible for its death because they introduce deadly fungal pathogens.

2. Evolutionary Responses by Plants

Plants have evolved numerous responses to their consumers. Primary among these is resistance. Plants resist consumers in three main ways. They may defend themselves chemically or mechanically, or they may escape damage by being difficult for consumers to discover.

a. Chemical Defenses

Plants are highly proficient chemists. There has been ongoing controversy as to why plants produce such a startlingly diverse array of chemicals, which, because they had no known function in primary metabolism, became known as secondary compounds. Early theories proposed that these compounds were waste products from "pathological overproduction of carbon." But this explanation begged the question, "Why so many ways of throwing out the trash?"

By the 1950s phytochemists had begun speculating that secondary chemicals were important in plant defense, and this theory has dominated the latter half of the twentieth century. Nevertheless, competing hypotheses have held their own—notably that secondary chemicals are important in protecting plants from physical dangers such as ultraviolet light. Undoubtedly some plant chemicals do perform such functions, but it is certainly not clear why plants should have so many kinds of sun screen. Perhaps the most defensible alternative hypothesis is that secondary compounds are important in defense against microbial enemies such as fungal, bacterial, and viral pathogens. It is quite likely, in fact, that many compounds defend plants against both these agents and animal consumers.

Chemical defenses are divided into three categories: digestibility reducers, toxins, and repellents. Many plants produce digestibility reducers such as tannins, which are high molecular weight carbon-rich compounds that bind proteins and make them difficult to digest. Thus, these compounds do not directly kill the consumer, but make the plant less nutritious to eat. This indirect mechanism of defense leads to important questions about the selection pressures that might have led to their evolution. In particular, it is not always clear that individual consumers know the nutritional value of their host. Moreover, in many cases the individual that chooses the plant is not the one destined to feed on it. For example, when choosing among a population of the same plant species, female butterflies do

not necessarily lay their eggs on the individuals on which their larvae can develop best. Another question is, "If the chemical does not kill the consumer, why would it be evolutionarily advantageous to plants possessing it?" This question becomes even more vexing in light of considerable evidence that, when protected from other causes of mortality, consumers can compensate for poor food quality by consuming more (not less!) plant tissue. The leading hypothesis to explain this paradox is that consumers feeding on a plant with a digestibility-reducing compound will grow more slowly, making them more vulnerable to enemies, such as predators, parasites, or diseases, and therefore die before consuming much plant tissue.

Toxins, as their name implies, are poisons that have direct negative effects on animals that consume them. Some plants are so toxic that apparently no animals will eat them. However, in many cases certain animals have evolved mechanisms that detoxify extremely potent poisons. Often, these animals are specialists on that host plant. There may be strong evolutionary benefits to feeding on such a previously unexploited resource. The most obvious benefit is that no one else is using the plant, which reduces competition for food. However, because a toxic plant harbors so few consumers, it may also provide "enemy-free space" in which consumers are less likely to be discovered by predators or parasites. Enemy-free space could also arise by a slightly different mechanism, which is nicely illustrated by small consumers on seaweeds. Small crustaceans called amphipods live on the algae they eat. Parrot fish also eat algae, but when they discover an amphipod, they snap it up like candy. Thus, amphipods that feed on very toxic species of algae are less likely to be consumed by herbivorous fish that are opportunistically omnivorous.

Perhaps because of these kinds of benefits, many animals that have evolved the ability to consume a toxic plant have also evolved specialization to that host. For example, specialist herbivores may use the toxic compound as a cue to find their host. Additionally, the compounds may stimulate feeding or egg laying. This level of specialization sets up an important evolutionary trade-off for toxic plants. A compound that previously killed all consumers has become an attractant to at least one consumer. Any individuals that have higher levels of the compound may be better defended against most consumers but may be more attractive to the specialist. Conversely, individuals with lower toxin concentrations will be less attractive to the specialist but may become vulnerable to other generalist consumers. This type of situation may create stabilizing selection and cause the plant population to evolve an intermediate

concentration of the compound (Simms, 1992). Alternatively, the specialist could become a major cause of death and seriously reduce abundance of the host. Indeed, when plants introduced into new habitats become noxious weeds, specialist consumers are sometimes imported as biocontrol agents.

A final class of chemical defenses are repellents, which, as their name suggests, repel animals from laying eggs on or eating plants that possess them. Some evolutionary biologists have argued that herbivores will not quickly evolve mechanisms that overcome repellents. This argument is based on the understanding that the rate of evolution depends in part on the strength of selection. Toxins impose strong selection for detoxification mechanisms because they kill animals. Repellents simply cause animals to look elsewhere for food, which might impose weaker selection. The strength of selection imposed by repellents on consumers will, however, depend critically on the fitness cost to the animal of finding an acceptable alternate host.

i. Animal Uses of Plant Defensive Compounds

Whatever the evolutionary reasons for these compounds, plant secondary chemicals have enormous value to humans. For example, synthetic pyrethroids, which were originally extracted from a species of chrysanthemum, are valuable insecticides because they are effective but degrade quickly and so do not accumulate in the environment. Plant secondary chemicals are the source of virtually all of the herbs and spices that make food interesting to eat. In many cases, these compounds were first important in preserving foods and keeping them safe to eat. Finally, plant secondary compounds are an important source of pharmaceuticals. In fact, 25% of the modern medical drug prescriptions (119 different chemical substances) written between 1959 and 1980 in the United States were pharmaceuticals derived from 90 different plant species (Farnsworth *et al.*, 1985).

Other animals also use plant secondary compounds in interesting ways. Many consumers sequester plant compounds from their food and use them for their own defense, the best known example being the monarch butterfly, which harbors cardiac glycosides from its milkweed hosts. Some animals even self-medicate with secondary compounds (Rodríguez and Wrangham, 1993). For example, healthy woolly bear caterpillars avoid poison hemlock, the plant used to execute Socrates. But woolly bears infested with a lethal parasitoid will preferentially consume poison hemlock (*Conium maculatum*), which can kill the parasite and allow the caterpillar to survive to adulthood. European starlings

may protect their nestlings by lining their nests with fresh plant materials that inhibit arthropod hatching and bacterial growth. Animals may also use plant secondary compounds to preserve their food. Pikas, relatives of rabbits, live in burrows in talus slopes. To survive the winter in their alpine homes, they harvest and store enormous quantities of vegetation, which they store in haypiles. Pikas prefer to eat grass hay, but they often will harvest toxic herbs as well. Haypiles with these herbs are less likely to become moldy than those without them.

b. Mechanical Defenses

Mechanical resistance to consumers may be obvious, as in the case of spiny cacti and thorny shrubs, or more subtle, as in the case of silica bodies that render grass leaves less palatable to many consumers. Some plants combine both chemical and mechanical defenses. For example, Wright's datura possesses both toxic alkaloids and leaf hairs, called trichomes. Moreover, some genotypes possess simple hairs (mechanical defense), whereas others have a sticky surface provided by glandular hairs that excrete a sticky exudate (mechanical and chemical defense). The sticky hairs defend plants against whiteflies but not mirid bugs; plants with simple hairs are better defended against the latter pests. It is generally supposed that mechanical defenses are more difficult for consumers to overcome.

When animals consume other animals, they eat tissue that has a composition similar to their own. However, plant tissues are generally richer in carbon and poorer in nitrogen than animal tissues. In part because of mechanical defenses, a high proportion of the carbon in terrestrial plants is devoted to structural molecules such as cellulose and lignins. Animals lack the enzymes necessary to digest these compounds. Microbes do have such enzymes, however, and herbivores sometimes have elaborate modifications of their guts that house microbial symbionts that can digest the fibrous fare.

c. Escape

In addition to defending tissues, plants may also escape consumers in time or space. Ephemeral plants, especially those with annual life cycles, may obtain temporal escape with a life cycle that does not sustain consumers long enough for them to complete their life cycles. Even if short-lived plants do not starve out their consumers, they may limit them to only a single generation. This constraint prevents the buildup of dense pest populations which short-lived consumers can attain on long-lived plants. Escape may also be achieved by appearing only during seasons when consumers are rare. For ex-

ample, many cool-season plants are relatively unaffected by insect consumers, which are far more abundant during warm weather.

Highly dispersed plants may also escape consumption if the distances between them are greater than the average distance traveled by their consumers. This mechanism may be in part responsible for the astonishing diversity of certain tropical forests, in which only one individual of each tree species will be found in a large area. This concept is also embodied in the “resource-concentration hypothesis,” which states that dense concentrations of host plants will harbor the highest densities of consumers. If a plant species is both short-lived and rare, it may be so difficult to find that it can complete its life cycle before being found by consumers.

d. Tolerance and Compensatory Growth

Even if plants are damaged by consumers, they may evolve mechanisms that allow them to maintain fitness in the face of damage. Plants may tolerate damage through various compensatory mechanisms, including reallocating resources from undamaged plant parts to replace damaged tissues. Resources are usually allocated among plant parts in response to gradients between points of production (sources) and points of use (sinks). Thus, leaves, which produce photosynthate, typically function as sources, sending resources to meristematic sinks where new growth is occurring. However, if consumers damage actively photosynthesizing leaves, the area around the damaged leaves may shift from source to sink, thereby attracting resources for compensatory growth. Tolerance of consumers may be especially important among fast-growing plants living in resource-rich environments.

3. Coevolution of Plants and Herbivores

In 1964, Ehrlich and Raven conceived a coevolutionary hypothesis to explain the magnificent diversity of plant chemistry. They postulated that herbivorous insects are a strong mortality agent for plants and that if any trait arose that protected a plant from its herbivorous insects, that trait would quickly spread in the plant population. Further, they argued that escaping its herbivores would create for the plant the opportunity for a period of rapid speciation, called an adaptive radiation. They postulated a similar process for the insects. For the herbivores, the newly evolved plant species represent unused resources. Any insect trait that allowed an insect to exploit these plants would likewise result in an adaptive radiation of herbivores. As Janzen later argued, the crucial characteristic of this process that distinguishes it from

ordinary evolution by natural selection is its reciprocal nature. The plant evolves resistance to the herbivore, the herbivore then evolves a mechanism that negates the resistance, after which the plant evolves resistance to the herbivore, and so on, *ad infinitum*. With every crank of the coevolutionary process, new species arise through adaptive radiation.

This hypothesis has excited considerable controversy. Some authors argue that reciprocal coevolution is rare or nonexistent because insect herbivores do not impose sufficiently strong selection pressures on plants. Others argue that herbivores experience more selection from their natural enemies than from plants and that moving to new plants is driven by the adaptive advantage of enemy-free space. Further, Labandeira and Sepkoski have pointed out fossil evidence that indicates that the great radiation of modern insects began 245 million years ago and was not accelerated by the expansion of angiosperms during the Cretaceous period. However, neither insects nor plants have stopped evolving, and currently evolving systems provide the best tests of the coevolutionary hypothesis.

One way that scientists have tried to test the coevolutionary hypothesis is to compare the evolutionary lineages (phylogenies) of host plants and insect consumers that narrowly specialize on that group of hosts. Coevolution can lead to a pattern called cospeciation, in which the two phylogenies match, much like your fingers do when you place your palms together, fingers up. One hand represents the plant lineages, the other the insects. At the base of your palm is the ancestral species; the fingers represent various derivative lineages. An alternative phylogenetic pattern, in which lineages do not match, is produced by host switching. Host switching is the phenomenon whereby specialist consumers shift host species and then speciate on that new species, without any speciation by the host plant.

The alliance of Hawaiian silverswords and the plant hoppers that live and feed on them provides a particularly exciting pair of phylogenies with which to test the coevolutionary hypothesis. The Hawaiian silverswords are derived from a pair of ancestral species in the rather prosaic group of California plants called the tarweeds. Over the past 5 million years the Hawaiian descendents have rapidly radiated into a stunningly diverse array of species. Some of these Hawaiian descendents are magnificent rosette plants with life histories much like century plants—they live long lives terminating in the production of giant flowering stalks. Others are multi-branched perennial shrubs. Most are attacked by members of the plant hopper genus, *Nesosydne*, in the family Delphacidae. The plant hoppers are highly host specific;

each species feeds on one or a few closely related plant species. Phylogenetic analysis of molecular data from the plant hoppers and their hosts reveals a pattern of cospeciation: Each plant hopper species is most likely to use the host species that is most closely related to the host of its most close relative. This pattern is exciting, because it is expected to arise from reciprocal coevolution.

However, other mechanisms could produce the same pattern. For example, the plants could be evolving in response to some other selective pressure, with the insects following along behind. Matching phylogenies can also arise when both an insect and its host plant might speciate simultaneously in response to some external event as, for example, when they become geographically isolated from their main populations by a geologic event such as mountain building. Thus, phylogenetic comparisons alone cannot deduce whether coevolution has occurred. Other types of data must be examined. Careful observation of host use across hybrid zones suggests that the most likely explanation of the match between silversword and plant hopper phylogenies is that plant hosts are speciating in response to some external pressure and plant hoppers are tagging along behind plant host speciation.

4. Community and Ecosystem Effects of Plant–Consumer Interactions

Considerable evidence suggests that consumers can reduce the fitness of individual plants and thereby impose selection pressures that produce evolutionary changes in plant traits. However, it is less clear whether consumers influence plant abundance in the landscape. This issue is at the heart of a controversy that has raged among community ecologists for the past two decades over the relative importance to community structure of top-down control by consumers of their resource populations versus bottom-up control of consumer populations by resources at the base of the food web. The current view is that both types of forces interact in complex ways to structure biotic communities. However, several competing hypotheses aim to explain how these forces interact. Three of the major models are summarized here.

Donor control models predict that while plants are food to their consumers, consumers have little effect on plant abundance. Thus, biomass of organisms at one trophic level is a function of the productivity of their resource base at lower trophic levels. This means that adding resources to the base of a food web will trickle up the web, increasing biomass at all trophic levels. In

contrast, consumer control models predict that each trophic level can be controlled by either its resources or its consumers, but not by both. They further predict that the direction control moves depends on the trophic level being examined and the number of trophic levels in the ecosystem. In particular, plants, at the base of the food web, are expected to dominate in ecosystems with odd numbers of trophic levels whereas herbivores will dominate in ecosystems with even numbers of trophic levels. Thus, increasing abundance in a particular trophic level will cascade up and down the food web, alternately expanding or shrinking trophic levels. Finally, keystone predation models predict that the species composition at each trophic level modifies the relative effects of resources and consumers.

The last model is more complex than the previous two, incorporating aspects of each. It is of particular interest here because it incorporates information about the relative vulnerability to consumers (i.e., resistance) of different resource (e.g., plant) species. The keystone model predicts that species diversity in resource populations can be maintained if resource species exhibit trade-offs between their relative competitive abilities and their relative resistance to consumers. Further, the model predicts that when resources are scarce, consumer populations will be small and the plant community will be dominated by a few fast-growing, strong competitors that are highly vulnerable to consumers, which are therefore consumer controlled. Under nutrient-rich conditions, consumer populations will be large and the plant community will consist primarily of a few slow-growing, well-defended species that are resource controlled because of their heavy investment in resistance. At intermediate levels of nutrient availability, both types of plants can coexist because of the trade-off between competitive ability and resistance to consumption (Leibold *et al.*, 1997). Consequently, species diversity will be greatest at intermediate levels of productivity. Other factors will determine whether these diverse communities are controlled by consumers (top down) or by resources (bottom up).

Leibold examined this prediction in planktonic communities of fishless ponds that varied in their level of mineral nutrient availability. These communities consist of photosynthetic planktonic algae (phytoplankton: single-celled green plants) that are grazed by herbivorous microarthropod zooplankton. Leibold found that algae in low-nutrient ponds consisted primarily of small, unprotected forms thought to be fast-growing but susceptible to grazing. Algae from more eutrophic (nutrient rich) ponds were larger and often sheathed

or gelatinous forms thought to be slow-growing but resistant to grazers.

In another recent analysis, Chase and colleagues reviewed studies of temperate terrestrial grasslands to determine whether the effects of consumers on plant biomass fit the keystone herbivore model, which predicts that consumer control should be strongest at high levels of resource availability and decline with declining productivity. They reviewed the results of experiments that manipulated the presence or absence of large grazers. Because most temperate grasslands are water-limited, they sought evidence for a correlation between consumer effect and precipitation. As predicted, the proportional effect of consumers on plant biomass declined significantly with increasing precipitation. Schmitz found a similar relationship between plant productivity and the effect of insect herbivores on plant biomass. Further, Chase and colleagues found a turnover in species composition among plants along the precipitation gradient, as predicted by the keystone model.

B. Plants as Consumers— Carnivorous Plants

The most ubiquitous interaction between plants and animals is the use by animals of plants as sources of material resources and energy. However, there are a few plants that turn the tables. In a world of plant-eating animals, carnivorous plants eat animals. To be considered carnivorous, a plant must have some mechanism to attract, capture, and/or digest prey and must be able to absorb nutrients from those prey (Givnish, 1989). Over 500 species in nine plant families have evolved the carnivorous habit.

1. Mechanisms of Prey Capture

Carnivorous plants capture prey in several remarkable ways (Table II). The evolutionarily independent origin of carnivory is demonstrated by the many ontogenetic origins of the traps. A pitfall trap is a tubular structure, often containing liquid, which prey can enter but have difficulty leaving. Although five different plant families capture prey in some kind of pitfall trap, called tanks or pitchers, these traps may be comprised of leaf rosettes (e.g., *Brocchinia*), modified leaves (e.g., *Sarracenia*), or modified leaf tips (e.g., *Nepenthes*). Some plants have active mechanisms to trap prey. For example, the leaves of the Venus flytrap (*Dionea muscipula*) function like a

TABLE II
Presence (+) or Absence (–) of Adaptations for Active Prey Attraction, Capture, and Digestion in Carnivorous Plant Genera and Species^a

Genera (no. of species)	Attraction	Digestion	Type of trap
Bromeliaceae			
<i>Catopsis</i> (1)	+	–	Pitfall
<i>Brocchinia</i> (2)	+	–	Pitfall
Eriocaulaceae			
<i>Paepalanthus</i> (1)	+	–	Pitfall
Sarraceniaceae			
<i>Heliamphora</i> (6)	Chemical and visual	–/+	Pitfall
<i>Darlingtonia</i> (1)	+	–	Pitfall
<i>Sarracenia</i> (9)	+	+/-	Pitfall
Nepenthaceae			
<i>Nepenthes</i> (82)	+	+	Pitfall
Cephalotaceae			
<i>Cephalotus</i> (1)	+	+	Pitfall
Droseraceae			
<i>Drosera</i> (90)	–	+	Active flypaper
<i>Aldrovanda</i> (1)	–	+	Steel trap
<i>Dionaea</i> (1)	+	+	Steel trap
Dioncophyllaceae			
<i>Triphyophyllum</i> (1)	–	+	Passive flypaper
<i>Drosophyllum</i> (1)	+	+	Passive flypaper
Roridulaceae			
<i>Roridula</i> (2)	+	+	Passive flypaper ^b
Lentibulariaceae			
<i>Pinguicula</i> (35)	–	+	Active flypaper
<i>Utricularia</i> (280)	+/-	+	Bladder trap
<i>Genlisea</i> (35)	–	+	Lobster pot
<i>Biovularia</i> (1)	–	+	Bladder trap
<i>Polypompholyx</i> (2)	–	+	Bladder trap
Byblidaceae			
<i>Byblis</i> (2)	–	+	Passive flypaper

^a Modified from Givnish *et al.*, 1984 (Givnish, 1989).

^b Nutrient uptake apparently assisted by exudations of the kleptoparasitic bug *Pameridea roridulae*.

miniature steel-jawed trap when tripped by the hapless prey. There are even aquatic plants (e.g., *Utricularia*) with sophisticated underwater traps that slurp up prey unlucky enough to trip them.

2. Costs of Carnivory

Carnivorous plants are usually restricted to sunny, moist, nutrient-poor habitats, such as bogs and fens. Their slow growth and restricted distribution suggest

that there are fitness costs associated with carnivory. For example, it has been argued that leaves morphologically specialized for prey capture have compromised photosynthetic abilities, making carnivorous plants poor competitors. This hypothesis is supported by studies of the pitcher plant, *Sarracenia alata*, which produces two kinds of leaves, a “regular” leaf and one that is modified into a pitcher. The plant responds to competition from neighboring vegetation by diverting resource allocation from pitchers to regular leaves. Small stature and slow growth also make many carnivorous plants (e.g., *Pinguicula* and *Utricularia*) vulnerable to being buried by litter fall. Because of their compromised competitive ability, carnivorous plants generally respond poorly to addition of nutrients to their habitat, being easily outcompeted by plants that thrive under richer conditions. This characteristic creates important conservation concerns in the many parts of the world where atmospheric input of anthropogenic nitrogen is significantly increasing nitrogen availability in previously nitrogen-poor bogs and fens.

Another fitness cost of carnivory was identified by Zamora, who found that *Pinguicula vallisneriifolia* tends to trap its own pollinators. He also found that reproduction in the plant is limited by pollen availability, indicating that feeding on its pollinators reduces plant fitness.

3. Benefits of Carnivory

As with so many plant novelties, these were noticed by the inquiring mind of Charles Darwin (1874), who demonstrated that the sticky traps of *Drosera rotundifolia* do indeed capture and digest animals. Darwin's son, Francis (1878), first demonstrated experimentally that prey capture enhances the growth and reproduction of this species. Similar studies have subsequently found that in most circumstances, growth of carnivorous plants benefits from prey capture.

In many cases, the majority of a carnivorous plant's nitrogen and phosphorus is obtained from prey. However, carnivorous plants appear to obtain only a small proportion of other necessary nutrients from prey. Comparisons of greenhouse and field studies suggest that plant growth is generally restricted by the rate of prey capture and that plants could utilize many more prey than they are able to catch. Carnivorous plants also tend to be frugal with their nutrients, practicing particularly efficient internal recycling of nitrogen and phosphorus.

Many elegant methods have been used to examine in more detail nutrient uptake from prey in carnivorous plants (Adamcewicz, 1997). In particular, putatively carnivorous plants can be offered insects reared on media

enriched in the stable nitrogen isotope ^{15}N . If the plant tissues subsequently become ^{15}N enriched, this indicates that their nitrogen supply has been supplemented by insect proteins. Using this method, Hanslin and Karlsson found that *Drosera rotundifolia* and several species of *Pinguicula* in a subarctic environment took up 29–41% of the nitrogen available in insect prey they were offered. Further, root uptake of nitrogen was stimulated by prey capture, an unanticipated additional benefit of carnivory. Experiments performed in glasshouse or laboratory environments generally reveal even greater uptake efficiencies.

Carnivorous plants show interesting developmental changes during maturation of their carnivorous organs. For example, using fluorescent dye tracers, Owen and colleagues found developmentally regulated bidirectional transport by leaf glands in the pitcher vine, *Nepenthes alata*. In mature leaves, the glands transport fluids directly from the pitcher fluid to the plant vasculature (internal plumbing system), apparently functioning in nutrient uptake. However, in immature, closed leaves, the glands secrete fluid from the vascular tissues into the pitcher, building up a supply of fluid in which to eventually trap prey. Gallie and Chang examined developmental regulation of hydrolase expression in *Sarracenia purpurea* pitchers. Hydrolase is an enzyme involved in prey digestion. Hydrolase expression commenced when the pitcher first opened upon maturity, increased for several days, and would largely cease after 2 weeks without prey. However, adding prey-derived resources such as amino acids to the pitcher fluid could induce hydrolase expression in pitchers that had ceased expression due to lack of prey.

4. Nonprey Guests—Iniquiline Communities

Prey-digesting guests (iniquilines) are very common in pitfall traps and provide for some carnivorous plants the sole means of benefiting from prey. In fact, the food webs of iniquilines in pitcher plant (*Sarracenia* spp.) traps have been the subject of numerous highly informative community and population ecology studies.

In one of the most arcane modes of nutrient uptake, *Roridula gorgonias* hosts a bug, *Pameridea roridulae*, that feeds on insects trapped on its sticky leaves. Although the plant has no known method of digesting its prey, stable-isotope studies indicate that it acquires ^{15}N label from prey. It apparently derives nutritional benefit via exudations from the bug guest that has dined on the labeled prey. This example, however, highlights the vulnerability of insectivorous plants to kleptoparasites

(animals that steal prey). Spiders, in particular, frequently compete with carnivorous plants for prey that have been attracted by the plant's attractive structures.

III. MUTUALISTIC INTERACTIONS

In addition to antagonistic interactions in which one party feeds on the other, plants and animals may also interact in ways that can benefit both parties. Far from being pleasant affairs, however, mutualistic associations can be highly vulnerable to cheating, which often makes them evolutionarily uneasy truces between parties. The delicate evolutionary and ecological balances that can be achieved by these organisms are truly fascinating and lead to some common evolutionary issues.

One important question regards the degree of specialization between mutualists. Specialization is useful because it allows the evolutionary development of elaborate lock-and-key mechanisms that exclude cheaters and maintain the mutualism. However, specialization is an evolutionarily vulnerable position because extinction of one partner species can spell doom for the other. Further, in mutualistic interactions that must be reconstituted each generation, which is the case for all animal-plant interactions, specialization may doom individuals that cannot find the correct partner in the environment.

A. Plant-Protecting Ants and Plant-Feeding Ants

As described previously, plants have evolved a variety of mechanisms that defend them against herbivores. One of the strangest defenses, though, is provided when plants are guarded by ants. Once thought to be rare and unusual, myrmecophytes (ant plants) are now recognized as widespread and ecologically important. In many cases, these relationships appear to be quite casual. Visiting ants may rob nectar from flowers, but perform some guarding services in return. However, the term myrmecophyte is generally reserved for the more specialized case in which an ant colony resides in special structures provided by the plant.

1. Benefits to Ants—Costs to Plants

Tropical myrmecophytes display the most sophisticated development of this type of interaction. In the neotropical regions alone, associations between plants and myrmecophytes have been described for about 250 plant species, from 19 families, and up to 180 ant species

from 5 subfamilies. These ant plants may provide ant housing in specially modified stems, hollow thorns, or specialized leaf pouches called leaf domatia. The trees or shrubs often feed ants with amino acid- or sugar-based solutions produced by extrafloral nectaries. The most developed myrmecophytes may also provide food in the form of specialized structures composed of lipids (Beccarian bodies), proteins (Beltian bodies), glycogen (Müllerian bodies), or some combination. In the most elaborate cases, plants may provide everything—room, board, and drink—to their ants.

Food provision for ants may be quite costly to myrmecophytes and studies show that plants regulate production of food structures. For example, in Central American *Cecropia* (Moraceae) trees grown at intermediate nutrient availability, removing Müllerian bodies stimulates their production. In contrast, when Müllerian bodies accumulate, which would happen if ants were not present, plants cease production.

In many ant-plant interactions, however, there is an important third partner through which the ants obtain benefit: sap-sucking homopterans tended by ants. Ants derive benefit from these homopterans in two ways. They may keep “milk herds” of homopterans from which they obtain honeydew, or they may be in the “beef business” and eat the homopterans they tend. Rather than simply supporting ants, the plants in these situations must also support homopteran consumers. Homopterans increase plant risks as well. They are often important vectors of plant diseases. Further, colonization by ant queens is a relatively rare event; presumably colonization by both ant queen and homopterans would be even rarer.

The homopteran mode of ant benefit appears to provide few options for control by the plant. This problem is illustrated with the African myrmecophyte *Leonardoxa africana*, on which the same ant species (*Aphomyrmex afer*) may tend one or both of two different homopteran species. Gaume and colleagues found that homopteran identity influenced the costs and benefits to the plant of ant patrol. One homopteran, the pseudococcid, could support larger colonies of ants, leading to better plant defense. This homopteran was also more efficient at producing ant biomass; ants tending pseudococcids did not use other plant resources. However, when ants tended coccids, the other homopteran, they also used plant resources from the extrafloral nectaries. Thus, when ants tended coccids, the only control that plants had over homopteran feeding was indirectly through nectary production. Plants that produced fewer nectaries supported fewer ants and fewer ants could tend fewer coccids. The plant could control pseudococ-

cid colony size more directly via domatia volume. Plants that provided a smaller total volume of the swollen stems used as domatia supported fewer pseudococcids and therefore fewer ants.

2. Benefits to Plants—What Motivates Ants?

Ants can benefit plants in three ways. First, they may patrol the plant and discourage or repel would-be herbivores. They also prune neighboring plants, thereby reducing plant competition for their host. Finally, some ants feed their host plant (myrmecotrophy).

Ants have frequently been observed killing and removing insect herbivores, and numerous experiments demonstrate the efficacy of this defense. For example, Fonseca observed four times as many herbivores on *Tachigali myrmecophila* plants from which he removed *Pseudomyrmex concolor* ants as on plants with intact ant colonies. Further, the daily rate of herbivory was about 10 times lower when ants were present, resulting in experimental plants without ants exhibiting about twice as much cumulative herbivore damage during the 18-month experiment. Leaf longevity was also substantially higher on plants with ants. It is interesting to note that these ants do not eat the herbivores they kill. Instead, they feed exclusively on catenococcid insects they tend inside the domatium, which is the hollow rachis of the compound leaf.

Ants are also effective deterrents of mammalian herbivory. For example, the African myrmecophyte *Acacia drepanolobium*, possesses two kinds of thorns. The swollen thorns are domatia in which *Crematogaster* ants live and rear their broods. Stapley has shown that the unswollen thorns slow plant damage by browsing mammals, but that browsers may compensate by feeding longer. Ants were far more effective defenses. When a browsing mammal encountered and was stung by ants, it stopped feeding immediately and could not be induced to feed further on that tree.

A second benefit that patrolling ants may provide is in competition with neighboring plants. Ants will prune vines (lianas) and branches of neighboring trees, effectively preventing their host tree from being overgrown. The result of this vigilance is that the host tree occupies a dramatically open cylinder of space amid otherwise densely packed tree canopies. Although such pruning of neighbors clearly benefits the host tree, it also benefits the ant colony by reducing the number of directions from which it may be attacked by competing or predatory ants.

In certain circumstances, ants may harm their own host by pruning it rather than its neighbors. For exam-

ple, Stanton and colleagues discovered a situation in which *Crematogaster nigriceps* so severely prunes its host tree, *Acacia drepanolobium*, that the tree cannot flower and is sterilized. In the habitat studied, four species of ants compete strongly for hosts, and *C. nigriceps* fares poorly in the violent conflicts over nest space. Instead of pruning neighboring trees, *C. nigriceps* prunes its own tree, apparently because it cannot prune neighboring trees occupied by competitively dominant ants. Indeed, careful observation of a large number of trees occupied by *C. nigriceps* revealed that these trees were always pruned in such a way as to avoid canopy contact with adjacent trees occupied by competing ant colonies. Canopy pruning of its own tree appears to be a defensive response by a *C. nigriceps* colony to competition with dominant ants that prevent it from pruning their trees.

3. Feeding Plants—Myrmecotrophy

Finally, a very different group of plants receives nutrients from the ants they house. These plants are also known as ant epiphytes. Epiphytes are plants that live on, but derive no nutritional benefit from, the branches of other plants. Myrmecotrophic epiphytes provide ant domatia in hollow or inflated roots, hollow rhizomes, or folded leaves. Ants then act as “mobile roots,” gathering food items for the nest, processing them, and then depositing the resulting waste and fecal matter within the plant. The best studied of these systems is *Myrmecodia tuberosa* (Rubiaceae), an epiphytic shrub of Southeast Asia and northern Australia. This species also has elaiosome-bearing seeds, a typical feature of ant-dispersed seeds. The ants feed on these food bodies and then “plant” the seeds along the walkways they create in the canopies of the trees their plant “homes” inhabit.

B. Plant Pollinators

An important and obvious characteristic of plants is that, with few exceptions, they are rooted to the ground and cannot move. This poses a crucial problem for sexual reproduction: Immobile mates must exchange gametes, meaning that pollen must be moved to the ovule. Pollen can move passively with fluid flow in the physical environment. Wind pollination has been successful among the gymnosperms and water pollination is found among many aquatic angiosperms. However, as many allergy sufferers know too well, most of the pollen produced by wind-pollinated plants never reaches its intended target. Many land plants avoid this inefficiency by using animals as pollen vectors. Most

temperate angiosperms and almost all tropical angiosperms are animal pollinated.

Of course, animals will not move pollen around as a favor to the plant. An important evolutionary problem for plants, then, has been to attract pollen vectors. It seems quite clear that the need to attract pollinators has been a primary driver in the evolution of flower morphology. Animal-pollinated flowers often have large, brightly colored structures that function as “advertising” for the “goodies” available to the visitor. The rewards may be nectar, other more specialized chemicals, or even the pollen itself. As with any purveyor of delectables, the flower also must contend with thieves. For example, nectar-robbing bees may drill through the flower wall and gain access to the nectar without transporting pollen. Other visitors, such as ants, may be too small to trip the elaborate pollen application mechanisms of some flowers.

The potential for cheating selects for specificity in pollinator attraction. Another advantage of specificity is that it can promote pollinator fidelity. Simply attracting a pollinator once is not sufficient. To ensure fatherhood, the plant must attract an animal that will visit other flowers of the same species. Moreover, to avoid inbreeding, the flowers must be on different individuals.

Thus, the twin needs to avoid exploitation by cheaters and ensure pollinator fidelity create strong evolutionary pressure for plant traits that promote pollinator specificity. As might be expected when sex is involved, response to this selection pressure has led many plants and animal pollinators to exhibit fascinating and baroque relationships (Darwin, [1877] 1984; Grant and Grant, 1965). For example, male euglossine bees depend upon flowers of plants in the euphorb and orchid families for fragrances that they convert to pheromones with which to attract mates. In another instance, male insects are tricked by orchids into thinking they have found a mate, when in fact all they have discovered is a cleverly shaped and scented mimic.

1. Role of Plant Pollinators in Plant Diversification

An important aspect of these highly specialized relationships is that they can prevent mating between individuals of otherwise very closely related populations, a phenomenon known as reproductive isolation. Evolution in a trait that promotes reproductive isolation can quickly lead to speciation. Traits that create the opportunity for rapid speciation by exploiting novel resources such as new pollinators are considered “key innovations.”

Identifying such key innovations is a sticky problem in evolutionary biology. Circularity arises because the

characteristic that best defines a group, and therefore allows it to be identified as speciose (having lots of species), is frequently also the character postulated to be the key innovation responsible for the radiation. One way out of this thicket is to identify a causal link between the putative key innovation and one of the processes that determines diversity.

a. Floral Nectar Spurs as a Key Innovation

One particularly persuasive example of a key innovation is floral nectar spurs. These structures are critically involved in pollinator specialization because they hold nectar deep within the flower and make it available to only a narrow range of floral visitors. Animals must either be small enough to enter the spur or have sufficiently long and narrow mouthparts to sip nectar from the spur. Observing the 11½-in.-long nectaries of a Madagascar orchid prompted Charles Darwin (1877, pp. 162–163) to predict correctly the existence of a moth with a sufficiently long proboscis to pollinate this fantastic flower. Nectar spurs have evolved independently in several distantly related families and genera of flowering plants. They may be constructed from petals, sepals, or both, and genetic studies suggest that simple genetic differences can produce quite different shapes, which might favor different pollinators. Comparative studies suggest that, as would be expected were spurs driving diversification, spurred groups have significantly more species than closely related groups without spurs (Hodges, 1997).

Detailed studies within genera also corroborate the putative link between nectar spur morphology and pollinator fidelity. Within two groups of orchids, experimental manipulation of spur length significantly decreased both pollinia removal by pollinators and fruit set. This observation demonstrates that spur morphology directly influences pollinator-mediated reproductive success. Another study examined the effect of spur morphology on pollinator attraction across a hybrid zone between two species of columbines. Hybrids varied in floral characters, including spur length and orientation, and these morphologies differentially attracted either hummingbirds (primary pollinators of *Aquilegia formosa*) or hawkmoths (primary pollinators of *A. pubescens*), and thereby promoted reproductive isolation. On the other hand, the presence of a hybrid zone indicates that floral morphology has not prevented pollination “mistakes.”

b. Insect Pollination and the Angiosperm Radiation

The role of plant-pollinator interactions in reproductive isolation has also led to the much grander hypothe-

sis that insect pollination was a “key innovation” leading to the co-radiation of flowering plants (angiosperms) and anthophilous insects, which are those groups most involved in pollination, including certain bees and wasps (Hymenoptera), various families of flies (Diptera), and butterflies and moths (Lepidoptera). Fossil evidence suggests that the angiosperms diversified very rapidly, and many hypotheses have been advanced to explain this phenomenon. Like most hypotheses in the historical sciences, however, these have been very difficult to test. One necessary prediction of the insect-pollination angiosperm radiation hypothesis is concurrent diversification of the angiosperms and anthophilous insects.

Considerable controversy surrounds the dates of diversification of angiosperms and anthophilous insects. As early as the Carboniferous, seed ferns had large pollen that was probably too heavy for wind transport and may have been pollinated by paleodictyopteran insects found in the same formations. The first direct evidence associating insects with plant pollen appears in the Lower Permian. However, the radiation of the insect groups that today are most strongly associated with angiosperm pollination probably occurred in the late Middle to early Upper Cretaceous, the period most commonly thought to have witnessed the radiation of the flowering plants. While not proving the codiversification hypothesis, these estimates at least do not rule it out.

2. Pollination Syndromes

Many plant species that share animal pollen vectors also share similar suites of floral traits, such as color, shape, symmetry, and scent, which appear to attract those kinds of animals. For example, hummingbirds fly by day, have excellent color vision, possess long beaks, and visit flowers while in flight. Correspondingly, hummingbird-pollinated flowers are day-blooming and tend to be brightly colored, often red, bilaterally symmetrical and tubular in shape, and frequently pendant. Floral traits also may correspond to the physiological needs of pollinators, as with hummingbird-pollinated flowers, which tend to produce copious sucrose-rich nectar that helps fuel the notoriously high metabolic rates of their pollinators. A number of these trait combinations, which are called pollination syndromes, are summarized in Table III (Howe and Westley, 1988).

Implicit in the concept of pollination syndromes is the assumption that floral evolution has been strongly entrained by interactions with specific classes of pollinators, leading to strong specialization. Specialization, however, may be an evolutionary dead end. A plant

highly specialized and dependent upon one or a few species of pollinator is seriously vulnerable to extinction of its pollinators. Dependence upon specialized pollinators can also lead to Allee effects, which arise when populations become too sparse to persist. For example, individuals in small, isolated populations of the annual plant farewell-to-spring (*Clarkia coccinea*) were visited by so few pollinators that they could not produce enough seeds to replace themselves. If individual reproductive rates dip below replacement levels for very long, a population can dwindle to extinction.

Figs may provide a particularly impressive example of this problem. Fig trees are ecologically important components of tropical forests because the fruits they produce support frugivorous animals that are important seed dispersers for many other forest plants. Figs do not have large showy flowers to attract pollinators. Instead, fig reproduction is exquisitely dependent upon minute wasps that pollinate small flowers held tightly inside the closed fig. The wasp's end of the bargain is met when the eggs it lays inside the fig hatch and its larvae feed on a few of the many developing seeds. Individual fig trees flower synchronously for a relatively short time but fig wasp populations cycle constantly. Maintenance of the wasp population requires that female wasps emerging from a fig find and lay eggs in figs of other trees of the same species that are flowering at times other than their host individual. Genetic evidence shows that, despite their minute size and short life span, these wasps routinely move pollen between trees 5 to 14 km apart. This interdependence argues that viable fig populations may require a higher density of trees than is generally assumed necessary for plants not involved in such a tight mutualism. The only study to test this contention, however, found that despite heavy forest fragmentation by humans, banyan tree (a type of fig) populations on the Cook Islands have not yet suffered from Allee effects.

As demonstrated in a comprehensive study of a group of Hawaiian shrubs by the laboratory of Weller and Sakai, plants can sometimes escape the grips of their pollinator addiction. Here, species derived from insect-pollinated ancestors have evolved wind pollination, apparently by passing through a transitional stage characterized by a relatively generalized pollination system.

Indeed, several researchers have questioned the assumption that most plant-pollinator relationships are highly specific (Jordano, 1987; Waser *et al.*, 1996). First, they argue that even specialization in insect pollinators is usually defined at the level of plant genus or family, not species. Further, insect species confined to

TABLE III
Pollination Syndromes: Putative Characteristics of Flowers Associated with Particular Groups of Pollinators^a

Animal	Flower					
	Opening time	Color	Odor	Shape	Symmetry	Nectar
Entomophilous						
Beetles	Day/night	Dull or white	Fruity or aminoid	Flat or bowl-shaped	Radial	Often absent
Carrion or dung flies	Day/night	Brownish or greenish	Fetid	Flat or deep; often traps	Radial	Rich in amino acids, if present
Bee flies	Day/night	Variable	Variable	Moderately deep	Radial	Hexose-rich
Bees	Day/night	Variable, but not pure red	Sweet	Flat or broad tube	Radial or bilateral	Sucrose-rich for long-tongued bees; hexose-rich for short-tongued bees
Hawkmoths	Night	White or pale green	Sweet	Deep, often with spur	Radial	Ample and sucrose-rich
Butterflies	Day/night	Variable; often pink	Sweet	Deep or with spur	Radial	Often sucrose-rich
Vertebrate pollinated						
Bats	Night	Drab, pale; often green	Musty	Flat "shaving brush" or deep tube; often on branch or trunk; hanging; abundant pollen	Radial	Ample and hexose-rich
Birds	Day	Vivid; often red	None	Tube; often hanging	Radial or bilateral	Ample and sucrose-rich

^a Adapted from Howe and Westley, 1988.

one plant species in one geographical area often visit other plant species in other parts of their range (Thompson, 1994). They also argue that specialization by pollinators may be more a function of which plants are available. Short-lived insects are more likely to visit only one or a few plant species with which they temporally co-occur whereas social insects, which have long-lived colonies and thus the opportunity to overlap with many plant species, often exhibit serial specialization on a large variety of plant species. For example, the only bee species on the Galapagos Islands is colonial and has been recorded visiting flowers of at least 60 plant species in 28 families. Finally, clustering of flowers into certain categories thought to be canalized through selection by pollinators may actually reflect physiological or morphological constraints in plants. For example, Chittka has argued that clustering of flower colors into particular narrow ranges may be a function of the physical and chemical constraints imposed by plant pigments rather than constraints im-

posed by the vision systems of different pollinators. If these arguments are true, the pollinator syndrome concept may be clouding our thinking about and study of plant-pollinator interactions. Researchers may be oblivious to, or fail to record, flower visitation by the "wrong" pollinators (Waser *et al.*, 1996).

3. Competition for Pollinators

Pollinators are an important resource that plants may compete over. Whether plants compete for pollinators is determined by the factors that limit seed production. In many situations, plant reproduction is limited by mineral resources, in which case plants are unable to increase fruit set with increased pollinator availability. However, there are many examples of plants in which reproduction is limited by pollinator availability. Pollinator limitation has important implications for plant conservation. For example, prolific flowering by invading plant species may negatively impact native plant communities by depriving native species of pollination.

C. Fruit and Seed Dispersers

Many plants depend upon animal dispersal of seeds and fruits (diaspores). Unlike pollen dispersal, in which insects are major players, diaspore dispersal is dominated by vertebrates. Seed dispersal is important because plants generally cannot develop successfully in the shade of their mother. Seed dispersal may also be an important mechanism by which seeds escape the predator or pathogen populations that are well adapted to exploit them, having built upon and become adapted to their parents. Finally, seed dispersal is important for plants to colonize newly opened habitat.

1. Types of Dispersers

a. Vertebrates

i. Fish Perhaps the most unexpected and amazing diaspore dispersers are fish. This phenomenon has been most extensively studied along the Amazon River. However, it is likely to be important in many areas with extensive seasonal flooding. In the Amazon basin, where the timing of plant reproduction corresponds with the seasonal flooding, some fruits are adapted to passive dispersal by water (hydrochorous). However, even these fruits can derive facultative benefit from fish dispersal. Plants with heavy fruits or with seeds embedded within hard shells are apparently obligately fish dispersed. Fish differ in their efficiency as dispersers. Catfish are effective dispersers whereas characins are destructive and act largely as predators of all but the smallest seeds.

ii. Mammals Many mammals are important seed dispersal agents. Primates and bats are the most important mammalian dispersers in tropical areas. Both types of animals can move quickly across the landscape, thereby dispersing diaspores long distances. Diaspore dispersal by bats is particularly important for forest regeneration after land abandonment in the neotropics. In temperate regions, diaspores may be dispersed by ungulates (e.g., antelopes, elephants, and zebras) and by many supposed carnivores. For example, black bears consume prodigious quantities of fruit, sometimes competing with humans for delectable berries (McCloskey, 1948).

iii. Birds and Reptiles Birds are arguably the most important class of fruit and seed dispersers. The earliest known examples of animal-dispersed plant propagules include the fleshy seeds of cycad progenitors, which appear to have been consumed by ancient reptiles (Howe and Westley, 1988). Many dinosaurs were cer-

tainly important fruit and seed eaters and may have functioned as dispersal agents. However, except perhaps for birds, modern reptiles are only rarely important diaspore dispersers today.

Birds can be hard on seeds. Beaks may break up the seed coat, rendering the embryo vulnerable to digestive acids and enzymes. Seeds may be ground up in the gizzard. However, the guts of frugivorous birds tend to be short and gentle (not highly muscular). In fact, many seeds require a trip through a bird's digestive tract to germinate successfully.

Although large numbers of a broad range of birds feed on fruits, few depend solely on fruits. Even waxwings, perhaps the most specialized frugivores in the temperate region, also feed on insects when they are available. Nevertheless, fruits are an important resource with which many birds produce body fat prior to migration. Moreover, in the tropics, where seasonal constraints on fruit production may be weaker, several groups of birds depend almost exclusively on fruits (e.g., quetzals, toucans, and barbets).

b. Invertebrates

i. Ants The only major insect seed dispersers are ants. Myrmecorous seeds, those adapted to ant dispersal, often possess a starch- or lipid-rich body called an elaiosome attached to a tough and smooth seed coat that is difficult for ants to crack. Seed size is also constrained by selection by ants—large ants tend to carry larger seeds than small ants.

In comparison with vertebrates, ants do not carry seeds very far. Nevertheless, ants can be important dispersers for many plants. Ants may either store seeds in the nest or remove the elaiosome and then discard seeds at the nest entrance or colony waste pile. Both locations tend to have well-aerated, nutrient-rich soil that can improve plant growth. Seeds collected by ants may also gain some protection from other seed predators through their association with active ant nests, which are generally avoided by most other animals.

An important conservation issue in many areas has been loss of native seed-collecting ants to competition from invading Argentine ants (*Iridomyrmex humilis*), which are not strongly attracted to myrmecorous seeds. Red imported fire ants (*Solenopsis invicta*) do feed on seeds, though, and their arrival in an area may have a negative impact on myrmecorous plant populations by competitively excluding other more effective seed-dispersing ants.

ii. Other Insects Occasionally seeds are dispersed by insects other than ants. For example, scarab beetles

TABLE IV
 Characteristics of Fruits and Seed Dispersed by Different Animals^a

Animal	Fruit			
	Color	Odor	Form	Reward
Vertebrate dispersers				
Hoarding mammals	Brown	Weak or aromatic	Indehiscent thick-walled nuts	Seed itself
Hoarding birds	Green or brown	None	Rounded seeds or nuts	Seed itself
Arboreal mammals	Yellow, white, green, or brown	Aromatic	Arillate seeds or drupes; often compound and dehiscent	Pulp protein, sugar, or starch
Bats	Pale yellow or green	Musky	Various; often hanging	Pulp lipid- or starch-rich
Terrestrial mammals	Often green or brown	None	Indehiscent nuts, pods, or capsules	Pulp lipid- or starch-rich
Highly frugivorous birds	Black, blue, red, green, or purple	None	Large drupes or arillate seeds; often dehiscent; seeds >10 mm long	Pulp lipid- or starch-rich
Partly frugivorous birds	Black, blue, red, orange, or white	None	Small- or medium-sized drupes, arillate seeds, or berries; seeds <10 mm long	Pulp often sugar- or starch-rich
Feathers or fur	Undistinguished	None	Barbs, hooks, or sticky hairs	None
Insect dispersers				
Ants	Undistinguished	None to humans	Elaiosome on seed coat; seed <3 mm long	Oil or starch elaiosome with chemical attractant

^a From Howe and Westley, 1988.

may bury seeds with dung. It is also likely that grassland termites aid in dispersal of grass seeds.

2. Plant Adaptations to Diaspore Dispersers

a. Dispersal Syndromes

Animal dispersers impose selection on fruit and seed characters. As with the suites of floral traits ascribed to selection by particular groups of pollinators, biologists have also described "dispersal syndromes," suites of characters that appear to be shared by propagules sharing certain groups of animal dispersers or particular modes of transportation (Table IV). For example, most dog owners can describe the common characteristics of propagules dispersed on animal fur and feathers, which include barbs, hooks, and barbed hairs that cause these annoying passengers to attach firmly to socks as well as fur. However, as with pollination syndromes, considerable controversy exists over whether these suites of traits are the result of selection by particular groups of animal species or whether they instead reflect the evolutionary constraints imposed by the morphol-

ogy and physiology of plant ancestors (Jordano, 1987).

b. Plant Adaptations to Frugivores

The ripe fruit, of course, functions as the attractant and reward for many seed dispersers. The problem for the plant in this case is to ensure survival of at least some of the seeds. First, the plant must ensure that the fruit remains on the plant long enough for the seed to develop and be provisioned by the mother. Consequently, immature fruits share with other plant organs various mechanisms that deter animal consumption. Unripe fruits often contain toxins and palatability-inhibiting compounds (Stiles, 1989). Perhaps for some readers the most memorable example of this phenomenon will be the inadvertent bite into an unripe persimmon.

A ripe fruit is advertising for dispersal of mature seeds. During ripening, fruits often change color, from an inconspicuous green that is poorly discernable amid the foliage to a contrasting color such as red, blue, yellow, or black, which is conspicuous to visually

searching frugivores. The ripe fruit may contain various nutritious goodies that attract prospective dispersers, including sugars, minerals, water, lipids, and proteins. These resources are costly for plants to provide, and some plants produce fruits or seeds that mimic more nutritious fruits but either lack any nutritional value or are much less nutritious than their model fruits.

Occupying an attractive and nutritious fruit, seeds must possess traits that promote survival of fruit consumption and digestion. Sometimes seeds can be easily separated from the pulp and are discarded by frugivores prior to digestion (remember watermelon seed spitting contests). Other seeds are relatively indigestible, due either to hard seed coats, toxins, or simply the incompetence of the frugivore gut, and pass through unharmed.

Frugivores vary in where and how they deposit seeds. Those that discard seeds as they are eating often deposit seeds individually, but may also fail to move seeds any distance from the parent. Dispersers that regurgitate seeds may move them further and often deposit seeds individually. When seeds are defecated, however, they may be concentrated at high densities. If no secondary dispersal process spreads these seeds, they may experience extremely competitive growing conditions upon germination. Such dense concentrations of seeds may also attract seed predators or secondary seed dispersers. Ants, for example, often remove seeds from dung piles. Nevertheless, some seeds require passage through a vertebrate gut before they will germinate (Traveset, 1998).

Frugivores function as seed dispersers only if they move away from the parent plant before defecating, regurgitating, or otherwise discarding the seed. Fruits often contain mild toxins, which are thought to improve dispersal by deterring foraging frugivores from finishing all the fruits at a bonanza tree. Specialization on particular fruits is rare among frugivores, perhaps because no one species of fruit provides a complete diet. This, too, may be a mechanism that benefits plants because it encourages frugivores to move about to achieve a complete diet.

c. Seed Predators as Dispersers

Many diaspores lack a fleshy fruit or other enticement with which to attract frugivores. These seeds may benefit from dispersal by their predators. Many rodent and bird seed predators hoard seeds for future use. To the extent that they forget or lose buried seeds, they may be extraordinarily effective dispersal agents. Many members of the crow and jay family are important seed hoarders and dispersers. For example, Clark's nutcrack-

ers carry pinyon pine seeds up to 22 km and bury seeds in small clumps (scatter-hoards). Behavioral studies indicate that these birds are highly effective at finding hoarded seeds and will even dig into a meter of snow to find known hoards. However, individual birds will commonly store more than twice as many seeds as needed, perhaps to protect themselves against theft. Theft may be common, especially among social seed predators, such as pinyon jays. Pinyon jays that observe other individuals burying seeds can also find and exploit those hoards.

Caching may have significant effects on the local ecosystem. For example, Clark's nutcracker initiates forest succession after large fires by moving in limber pine seeds from long distances. Genetic structure of tree populations may also be influenced by the seed-caching behavior of Clark's nutcracker.

Seeds dispersed by predators have interesting adaptations that promote offspring survival. Oaks, for example, are dispersed by their seed predators, which include birds and rodents. Both types of animals crack open acorns and feed on the cotyledons of the embryo. During germination, the embryo root (radical) emerges from the apical (pointy) end of the acorn. Several studies by Steele and colleagues have discovered that digestibility-reducing astringent tannins are concentrated at the apical end of the acorn. Further, all acorn consumers studied, including insects, birds, and rodents, preferentially consume the basal (cap) end of the acorn, which leaves the embryo intact and viable. Partially eaten acorns can germinate, sometimes at higher rates than found for intact acorns. Finally, Frost and colleagues have found that in the European oak *Quercus robur*, experimentally removing cotyledons from seedlings does not reduce their germination success when compared with seedlings with intact cotyledons. These authors suggest that the primary function of the cotyledons is to attract seed dispersers.

d. Evolutionary Dead Ends?

As with other forms of specialized dependence, specialization to a particular dispersal agent can be an evolutionary dead end. Perhaps the most famous example involves the fruits of the *Calvaria major* tree on the island of Mauritius in the Indian Ocean. This tree had not been observed to recruit young seedlings for over 300 years when Temple surmised that it was lacking its essential fruit disperser, which was the dodo, a large flightless pigeon that had gone extinct in the late 1600s. Temple was able to mimic dodo digestion by feeding the *Calvaria* seeds to turkeys.

Turkeys were not available to rescue *Calvaria* on Mauritius, but Janzen has argued that another tree has survived the loss of its dispersal agent in Central America through such a substitution. Huge, rare guanacaste (*Enterolobium cyclocarpum*) trees in Costa Rica produce fruits that are readily eaten by domesticated horses and cattle. Janzen speculated that these fruits were once dispersed by the native Pleistocene horse (*Equus fraternus*), which went extinct some 10,000 years ago. He demonstrated that most seeds pass unharmed through the guts of domesticated horses and went on to argue that these animals, which were introduced by Spanish conquistadors 500 years ago, have replaced the lost dispersal agent. Thus, adaptation to one seed dispersal agent preadapted the fruit to other similar agents.

IV. SUMMARY

Plant-animal interactions are ubiquitous and important. A common theme throughout the study of plant-animal interactions is the enormous effects that these interactions have on plant and animal evolution. There is strong evidence that the interaction between plants and insect pollinators is the primary driver of diversity in flowering plants and the groups of insects most involved in pollination. Selection by animal consumers has driven the evolution of numerous plant defense traits. These traits form the basis of many of the uses that we make of plants today. Plant-based fibers, pharmaceuticals, and flavorings all derive from plant evolutionary responses to consumers. The plant fitness trade-offs between these defensive traits and competitive ability also play an important role in determining the composition of biotic communities.

The primary benefit that plants obtain from animals is mobility. Many, perhaps most, plants depend upon animals to transport pollen and propagules. In many cases, the interactions between plants and their animal transportation providers are highly specialized and mutually beneficial. These specialized mutualisms can be quite vulnerable to extinction of either party, which is an important issue in both plant and animal conservation.

Finally, plant photosynthesis converts solar energy into chemical energy and thereby provides the energetic basis for most of the world's life. Plants are therefore the foundation of the global ecosystem. Aside from the decomposition of plant litter through the microbial food chain, this energy flows into the global ecosystem via

animal consumers of plants. Understanding how plant-animal interactions influence this process is crucial to understanding how intact ecosystems provide the goods and services upon which human endeavor, and indeed all life, depends.

See Also the Following Articles

ADAPTIVE RADIATION • COEVOLUTION • DEFENSES, ECOLOGY OF • FOOD WEBS • GRAZING, EFFECTS OF • PLANT-SOIL INTERACTIONS

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