Plant-Animal Interactions

Broadly defined, any relationship occurring between organisms in the kingdoms Animalia and Plantae is classified as a plant-animal interaction. Plant-animal interactions are common features of virtually every environment, including all marine, freshwater, and terrestrial biomes. Many such interactions demonstrate evolutionary principles and the myriad ways that species interactions influence the functioning of the biosphere.

Biologists and naturalists have long been fascinated with plant-animal interactions (PAI), the relationships between organisms in the kingdoms Animalia and Plantae. The seeming simplicity of the formulation conceals an enormous number and diversity of ecological relationships and fundamental processes, ranging from the obscure to the ubiquitous. As a result, there is an extensive history of investigation into these often fascinating relationships. The preeminent biologist Charles Darwin wrote extensively about PAI in *On the Origin of Species by Natural Selection*, although many PAI were the focus of a considerable amount of descriptive ecology prior to Darwin's text. Today, PAI remain a centerpiece within many of ecology's central theories, including, among others, coevolution and consumer-resource theory.

General Categories of PAI

Plant-animal interactions range from the general to those that are highly specific and involve elaborate evolutionary adaptations. An example of a general PAI is a plant that provides shelter for an animal, such as a tree that provides critical habitat for a nesting bird. Some animals are flexible in their choice of plants; in contrast, some insects are highly specialized, living and laying eggs on only one plant species. In an attempt to categorize and describe the plethora of PAI , biologists further categorize PAI as being commensal, in which one partner benefits while the other is unaffected; antagonistic, in which the interaction is detrimental to at least one partner; or mutualistic, in which both the plant and animal partners both benefit. Interactions are classified by whether an individual partner has more, less, or the same number of offspring as a result of the relationship, in terms of higher or lower fitness. Although the ultimate value is the reproductive success (fitness) of the interacting plants and animals, this can be quite difficult to measure. Thus other metrics such as photosynthetic carbon gain, growth rate, longevity, and survival are often used as surrogate estimates of fitness.

Commensal Interactions

Commensal plant-animal interactions, while straightforward in theory, are somewhat difficult to demonstrate. This is because there is always some question whether an interaction has a completely neutral effect on one of the species involved. Take the previous example of a bird nesting in a tree, which clearly benefits the bird but may or may not influence the tree. If the presence of the nest has no effect on the tree's growth and reproduction, then the relationship is truly commensal. The bird may eat herbivorous insects that feed on the tree, thus having a positive effect. Alternatively, the nest may block sunlight or weigh down branches away from sunlight exposure, thus having a negative effect. The task of conclusively demonstrating commensalisms in this type of interaction involves experimentally removing nesting birds from some trees and leaving others unchanged and comparing the fitness of the two groups.

Antagonistic Interactions

The most common plant-animal interactions are antagonistic and involve the direct consumption of plants by animals (called herbivores) for food. This general PAI serves as the fundamental process for transferring the energy of sunlight to the animal biomass in all ecosystems. Herbivores can be highly specialized or unselective generalists and span a huge range of body sizes, from tiny leaf-eating and sap-sucking insects to large herbivores such as elephants, or the selective Chinese giant panda whose diet consists almost entirely of bamboo. Herbivores have evolved a variety of feeding styles to consume plants. For example, insects in the order Hemiptera, such as aphids, leafhoppers, and scale insects, have piercing and sucking mouth parts specialized to suck fluids directly from the vascular system (xylem water and phloem sugars) of the plant. Other insects, such as those belonging to the orders Orthoptera (grasshoppers and crickets) and the larvae of Lepidoptera (moths and butterflies), have chewing mouthparts that allow them to bite and tear leaf material. Vertebrate herbivores also come in a variety of types and sizes, including fresh- and saltwater fish that feed on algae, small rodents that eat parts of leaves, and large-bodied mammalian herbivores that forage on woody plant species (called browsers) or that eat more ground-dwelling herbaceous plants (grazers). Large-bodied mammal herbivores have high-crowned teeth and specialized digestion to facilitate the internal decomposition of plant material. Some ecosystems throughout the world, such as Serengeti National Park in Tanzania, Africa, and Yellowstone National Park in Wyoming, are famous for the abundance and diversity of these large mammal herbivores (also termed megaherbivores). These ecosystems have been labeled grazing ecosystems or browsing ecosystems because of the large proportion of energy transferred from primary producers to the primary consumers, grazers, and browsers.

Plants have evolved a broad spectrum of defenses against herbivory, ranging from tolerance to resistance of defoliation. Herbivory-tolerant plants have high growth rates and are able to reallocate stored carbohydrates to defoliated stems rapidly. Additionally, plants tolerant of herbivory often have architectures that protect carbohydrate-rich storage organs, found below ground or out of the bite range of herbivores. Plants that are resistant to herbivory employ either structural or chemical defenses that deter or even harm herbivores. The most basic structural defense of plants is the production of cell walls and fibrous tissues composed of cellulose and lignin, a main component of wood, which are difficult for herbivores to chew and digest. More specialized structures include thorns, barbed spines, hooks, and hairs that protect especially the photosynthetic tissue of plants. Plant chemical defenses, also known as secondary compounds (or metabolites), are metabolic products not necessary for primary growth and reproduction. The chemistry of plant secondary compounds is complex but well studied because of the deep historical connection with humans. For example, plant secondary compounds are responsible for a rich array of chemicals used by humans, including herbal stimulants (coffee, nicotine), narcotics (cocaine), spices (nutmeg, mint), and a vast array of medicines that treat everything from headaches (aspirin from willow bark) to cancer (taxol from the Pacific yew tree).

Many small rodents and birds, known as granivores, consume seeds rather than plant tissues. Another group of specialized herbivores called frugivores feed specifically on plant fruit; this is a diverse group including a wide variety of insects, birds, and mammals. Although less well studied than their above-ground counterparts, there is also a diverse community of below-ground herbivores, composed of nematodes, insects, and rodents, that forage on plant roots.

Not all antagonistic relationships involve animals eating plants. One of the more interesting deviations from the typical pattern is that of the carnivorous plants. Currently there are more than six hundred species of carnivorous plants described, including the well-known Venus fly trap and pitcher plant, which trap and slowly extract nutrients from decomposing arthropods. The first popular scholarly text on carnivorous plants was written by none other than Charles Darwin in 1875.

Mutualisms

Plants and animals also engage in a wide diversity of interactions that benefit both partners. One ubiquitous example is pollination, in which animals feed on nectar and pollen from flowers, transferring pollen to other plants, the foundation of the highly successful sexual reproduction of flowering plants. The vast majority of pollinators are insects, but the group also includes birds, bats, rodents, monkeys, and even lizards.

A second type of common mutualism between plants and animals is seed dispersal. Animals benefit by consuming fruits that house the seeds, while plants benefit by having their seeds dispersed long distances by animals, thus increasing their offspring survival probability. Especially for large-seeded plants, long-distance dispersal of seeds would be physically impossible without animal vectors. In this regard, the human domestication of fruits and vegetables may represent one of the most extensive plant-animal mutualisms on Earth. Another type of mutualism involves animals that protect plants from other animal herbivores.

Ants and Acacias The PAI involving ants and acacias is one of the best-known examples of mutualism. In tropical woodlands and savannas throughout the world, trees belonging to the genus *Acacia* produce hollow, swollen structures on their twigs that provide shelter for stinging ants. Moreover, these trees also have glands at the base of their leaves that secrete carbohydrate-rich nectar on which the ants feed. Thus, the ants benefit by receiving both a place to live and a source of energy-rich food. This relationship is mutualistic because the trees benefit in return: the ants swarm to attack leaf-eating mammal and insect herbivores. This relationship is very effective and even protects acacias from African elephants, the largest terrestrial herbivore on Earth. Interestingly, the ants do not attack bees that pollinate the acacia flowers because of a chemical released by the plant that somehow prevents ants from approaching during pollination.

Yucca and Yucca Moths Another classic example of mutualism is the close association between yucca plants and yucca moths. This interaction is a highly specialized relationship in that each species of yucca has only a few, and sometimes just one, species of moth with which it interacts. Also, the yucca moths are entirely dependent on the yucca plants for their own reproduction, while yucca plants require cross pollination between different individuals and rely completely on the yucca moths for pollen transfer. The moths pack the pollen into the stigma of the yucca plant, ensuring fertilization. While adult moths do not feed, female yucca moths lay eggs in the flowers, and the emerging larvae then feed on the developing seeds. This relationship is classic in that it provides an example of extreme specificity between partners and a relationship in which mutualism and antagonism are balanced in a strong coevolutionary relationship.

Bees and Bee Orchids A final example of PAI mutualism is the "deceptive" plant pollination that occurs between bees and bee orchids. Bee orchids have evolved a mechanism to deceive bees into pollinating their flowers through both visual and chemical mimicry of the female bee. The bee orchid produces floral structures that look like a female bee and emits volatile chemical compounds that mimic female reproductive pheromones. Bees are attracted to the plant and are deceived into "mating" with the flowers. In reality, the male bees distribute pollen between individual plants but receive nothing in return.

Coevolution and the Antiquity of PAI

The two most species-rich groups of macroscopic terrestrial organisms are plants and insects. One body of theory suggests that the global diversity of these groups is a consequence of their long coevolutionary history, which has persisted since the first invasion on land over 450 millions years ago. Evidence of ancient herbivory, in the form of fossilized insect dung containing plant pollen, begins to show up regularly at the transition between the Silurian and Devonian periods around 420 million years ago. The radiation of the modern angiosperms (the very plant group that is dominant on Earth today) and the modern insect fauna that prey upon them extends from the

Cretaceous period, around 115 million years ago. Although fossil evidence of herbivory is more abundant than evidence for pollination or seed dispersal is, the great species diversity among plants and insects is believed to have been enhanced by both antagonistic and mutualistic coevolution. Indeed, the morphological diversity of flowers, fruits, seeds, and animal pollinators and dispersers observed today provides compelling evidence of a rich and lengthy coevolutionary history.

Sustainability and Ecosystem Management

The sustainability of ecosystems throughout the world depends on an elaborate network of plant-animal interactions that facilitate ecosystem function (energy flow and nutrient cycling). Habitat destruction and the loss of biodiversity, brought about by rapidly expanding human populations and increased resource consumption, is threatening to unravel these core plant-animal interactions to the detriment of natural ecosystems and at great cost to human societies. The remarkable agricultural prosperity of the human race relies profoundly on the persistence of functioning plant-animal interactions. Chief among them is our dependence on insect-pollinated crops and food production for domestic livestock, such as cows, sheep, donkeys, and goats, which provide meat, natural fibers, and labor. Plant-animal interactions are also at the heart of natural processes that threaten human well-being and economic stability, such as the long history of cataclysmic crop damage by insect pests. Consequently, understanding and preserving the coevolutionary relationships between plants and animals is a critical component for a responsible stewardship of natural and agricultural ecosystems on which humans depend.

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See also Agricultural Intensification; Agroecology; Biodiversity; Boundary Ecotones; Community Ecology, Complexity Theory; Food Webs; Global Climate Change; Human Ecology; Microbial Ecosystem Processes; Mutualism; Population Dynamics; Refugia

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