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Plant–Animal Interactions in Forest Ecosystems

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Introduction

Flowering plants, being sedentary, have co-opted animal partners for purposes of gene exchange and propagule dispersal, through pollination and seed dispersal. To secure these services plants provide a variety of flower or fruit rewards creating some of the most common and obvious mutualistic interactions in the natural world. However, plants are also eaten by animals which graze on leaves, bore through stems, or predate seeds. Plants have therefore evolved mechanisms to promote the efficiency of mutualistic interactions and protect against herbivores and seed predators. This article describes the range of ecologically significant plant–animal interactions that commonly occur in temperate and tropical forest systems.

Mutualistic Interactions

Pollination

Most flowering plants are animal pollinated, and indeed the function of flowers is to attract animal vectors for pollen dispersal. Most flowers offer a reward to pollinators which is usually nectar or pollen, but can also include resins (e.g. Clusiaceae), waxes, or oils (orchids). Pollinators attracted to flowers collect the resources and in the process pick up pollen through contact with the anthers and deposit pollen they are carrying onto the stigma where pollen germinates and ultimately fertilizes the ovules. Not all flower visitors act as pollinators, however, and there is widespread 'theft' of floral resources where animals benefit from the floral resources but fail to pollinate the plant, either because they are the wrong size or shape to contact the anthers or stigma, or because they obtain nectar by piercing the sides of the corolla thereby bypassing the reproductive tissues.

Pollinators vary in their degree of effectiveness, and the extent to which they are specialized to pollinate one or a few flowering species. Pollination can be passive, where pollen is picked up and deposited inadvertently by the pollinating vector, or it can be active where pollinators seek out pollen. Active pollinators often have specialized morphological traits, such as the pollen combs and baskets on the hind legs of honeybees, used to collect and store pollen.

Some plants have developed alternative and deceptive ways of securing pollination services by temporarily trapping pollinators or by attracting them with floral displays that offer no reward. Other plants, including some large dipterocarp trees in Southeast Asia offer only pollen as a reward which, although consumed by the pollinators, is also carried by them to neighboring plants.

Pollinators range in size and diversity from tiny fig wasps and thrips to large fruit bats and terrestrial mammals, although by far the most important pollinators are bees. Honeybees pollinate many forest trees in tropical regions including many large canopy species, but solitary or semisocial species are also widespread pollinators occurring in forest canopy and understory. Although honeybees are very effective pollinators they are generalist in their foraging behavior and forage preferentially on species occurring at highest frequency or density. Such frequency-dependent foraging behavior does not, therefore, favor rare or highly dispersed plants which become more dependent on pollinators that may be more specialist in their floral resource requirements. Many anthropogenically altered forest habitats have suffered a decline in the richness of pollinator communities and introduced honeybees may to some extent ameliorate these impacts. Plants with generalist pollination systems may be resistant to such changes but plants pollinated by insects and animals other than common bees could potentially suffer a decline in reproductive output through pollination failure.

Other invertebrate pollinators include beetles, flies, butterflies, moths and thrips. Flowers pollinated by each of these groups have, evolved morphological structures and phenological patterns to increase the probability of successful pollination and to limit access to the flowers by other flower visitors that are relatively ineffective as pollinators. Tropical forests contain many invertebrate-pollinated species, while in temperate forests wind pollination is more widespread.

Vertebrate pollinators primarily include birds and bats, but a variety of terrestrial mammals also act as pollinators, including possums and shrews. Even lizards have been noted to pollinate some plant species but such examples are notable by their rarity.

One of the best known highly specific interactions among plants and animals is the fig pollination system. Fig species (*Ficus*) have evolved to be entirely dependent on specialized fig wasps for pollination. The tiny wasps live as adults for only a few days and spend almost their entire life within figs. Figs are actually clusters of flowers enclosed within a spherical or cylindrical structure termed a syconium. Female wasps enter the syconium through a narrow hole to seek out the tiny flowers upon which they lay their eggs. Wasp larvae feed on floral tissue destroying ovules in the process. Larvae develop into adult wasps that emerge into the central chamber of the syconium where they mate, after which the males die. During this time pollen either adheres to female wasps passively or is actively collected by them prior to their emergence from the syconium in search of another fig tree. Pollination occurs when the wasps enter another syconium to lay eggs. Although many flowers are destroyed, sufficient remain to produce pollen and seed. This highly coevolved system is all the more remarkable in that each *Ficus* species is exclusively pollinated by a single, or rarely two, fig wasp species. Despite the potential vulnerability of such highly specialized mutualisms to the loss of one of the partners, the fig–fig wasp mutualism seems very resistant to anthropogenic impacts on forested landscapes.

Seed Dispersal

A second mutualism associated with plant reproductive processes is that of dispersal of seed by animals. In the immediate vicinity of the parent plant competition for resources is intense and the risk of death from pathogens or seed predators is disproportionately high (see below). Thus if seed production is to be translated into seedling recruitment dispersal of seeds away from the parent into uninhabited sites suitable for growth is necessary. Plants achieve this by a variety of biotic and abiotic mechanisms. In tropical moist forests transportation by biotic mechanisms is much more important than it is in temperate or tropical dry forests where wind is an effective dispersal agent.

Plants that use animal agents to disperse seeds may offer inducements in the form of a nutritious reward to attract dispersal agents. Many tropical plants, as well as temperate ones, surround their seeds with fleshy fruit that is sought by animals that consume the fruit and in so doing disperse the seed. The seeds are spat out or may be swallowed along with the fruit, only to be ejected with the feces having passed through the digestive tract unharmed. Indeed, many seeds require exposure to digestive acids in vertebrate guts before they are able to germinate. Dispersal of internally transported seed is a function of animal movement and the duration of passage through the gut. Asian rhinoceroses and elephants both consume and defecate seeds, but while elephants defecate at more or less random locations, rhinoceroses repeatedly visit latrines that can accumulate tens of thousands of seeds.

Animal foraging behavior also dictates the pattern of dispersal. Many forest rodents ‘scatterhoard’ seed, that is they store a little food in each of numerous caches which results in widely dispersed small seedling clumps. Burial of oak seeds by squirrels, for example, results in seedling distribution that is not unlike dispersal by wind, where most of the seeds are within a few meters of the parent tree with a much smaller proportion distributed further away. Such behavior is contrasted with ‘larderhoarding’ in which all food is stored in one or very few locations, resulting in a much higher density of seedlings per clump. Seed hoarding by animals can be a highly effective means of dispersal. Jays that hoard pine nuts in North America can disperse seed 20 km from the trees at which the seed were collected.

Other plants offer a small amount of fleshy tissue that is attached to the end of the seed and serves the same function as fruit. In the case of the cashew nut trees (*Anacardium* spp.), the fleshy aril is consumed by bats usually some distance from where they were collected and the seed is discarded. Thousands of other plants offer a similar reward, termed an elaiosome, that is collected by ants. Elaiosomes contain chemicals that attract ants and stimulate them to carry the seeds back to the nest where the elaiosome is consumed leaving the seed to germinate in the environmentally nutritious and safe surroundings of the ant nest. Ant-dispersed seeds occur in a wide variety of plant families, notably the Fabaceae, Mimosaceae (acacias) and Sterculiaceae, and in several forest habitats including tropical rain, savanna, and sclerophyll forests.

Seed dispersal mutualisms are usually fairly generalist with a wide variety of animal seed dispersal vectors being attracted to the fruit of any particular tree. The fruit of bird dispersed seed tend to be smaller than those of mammal dispersed seed though there are few specialized plant-seed disperser mutualisms. One exception is the Australian mistletoe bird (*Dicaeum livuninaceum*) which specializes on mistletoes.

It is estimated that around 10% of flowering plants have fruits that bear hooks, barbs, claws or a sticky surface by which they become attached to the hair or feathers of passing animals. These seeds are passively carried by the animal until they fall off or are brushed off. Such dispersal does not constitute a mutualistic plant–animal interaction as the seeds or fruit can be an irritation to the animal concerned.

Seeds may be moved to their ultimate location in several stages, with different agents responsible for each stage. Thus a fruit that is initially dropped from a tree into a stream may be later picked up by a rodent that only partially consumes the fleshy tissue before dropping it to be harvested by ants that drag the seed into the nest. Seed dispersal can therefore consist of a complex array of sequential events involving a suite of dispersal agents.

Plant Protection by Ants

Ants are important mutualistic partners to a variety of plant species in tropical forests, protecting plants from herbivores, providing plants with essential nutrients and, as has already been described above, dispersing seeds and fruits. In most ant–plant mutualisms plants provide ants with accommodation, in the form of hollow stems, roots or thorns, or swollen petioles or leaf pouches, and food such as extrafloral nectar or food packages that are rich in protein and lipids. In return ants provide protection from herbivores by attacking any insect or vertebrate that contacts the plants. In the most famous plant–ant mutualism in central America *Pseudomyrmex* ants not only provide protection from herbivores but also clear competing seedlings from around the base of the host *Acacia* trees. Ant protection from herbivory has been observed in a wide variety of plant families common in tropical or subtropical forests. These include bamboos, fast growing pioneer species (*Macaranga* and *Cecropia*), rattan palms, and understory woody plants (*Cordia alliodora*). The mutualism is also geographically widespread and has evolved independently at least twice among *Acacia* trees in Central American dry forests and African savanna forests, and the ferocity of weaver ants (*Oecophylla*) which construct nests from freshly woven leaves of a variety of trees is familiar to forest workers throughout Southeast Asia.

In some cases (as for the plants *Hydnophytum formicarium* and *Myrmecodia tuberosa*) ants provide food for the plants by depositing their refuse in absorptive chambers that house the ants. Such specialized myrmecotrophic plants are in the main tropical epiphytes in open forests and savannas growing on nitrogen-deficient soils, thus acquisition of nitrogen from ant waste is the principle benefit to the plants. A far greater number and diversity of plants that house ants for protective purposes may additionally benefit nutritionally, though to a lesser degree, from ant waste products and discarded prey that accumulate in nesting cavities.

Ants are well known for their habit of maintaining colonies of sap-sucking homopteran insects on plants. Homopterans take sap directly from the plant phloem and excrete unwanted organic acids and sugars in the form of honeydew that is harvested by ants. The ants tend and protect the homopterans from parasites and predators, hence this interaction could be construed as being antagonistic as far as the plant is concerned. However, some evidence suggests that ants regulate homopteran populations and prevent outbreaks that might be highly detrimental to plants, and the presence of ants can also provide protection against herbivory. Currently there is little conclusive information on the balance of costs or benefits to plants of homopteran-tending ants, although in one study the presence of homopteran-tending ants on birch in Finland greatly reduced damage by leaf feeding caterpillars.

Antagonistic Interactions

Animals cause damage to plants by consuming vegetative tissue or propagules, or by mechanical destruction such as trampling. Plants tolerate a certain amount of tissue loss but such damage may make them susceptible to secondary infestation by pests and pathogens or place them at a disadvantage relative to unscathed neighboring competitors. In response to the onslaught of primary consumers plants have evolved a variety of physical, chemical, and biological defenses, albeit at some cost of production.

Herbivory and Plant Defenses

Animals that feed on plant tissue are varied and abundant. Vertebrates graze and browse leaves and gnaw at roots and tubers. Insects chew, mine, or gall leaves, as well as suck sap and bore stems, and even an entire tree may be defoliated by a single caterpillar outbreak (**Figures 1–3**). Plants can usually recover from such damage as only a portion of the plant is consumed and, owing to their repeating modular construction, lost parts can be readily renewed (although continued intensive attack will eventually kill a plant).

Despite the huge abundance of leaves in forests there are few canopy mammals that are able to effectively digest cellulose, the main component of leaves. Those that do, such as sloths and howler monkeys in the Neotropics, and orangutans, proboscis monkeys, and chimpanzees in the Old World tropics, rely on a suite of symbiotic gut microorganisms to digest cellulose in their large stomachs. Among birds, the large stomach required to digest leaf material has limited such a widespread food to only a single species, the hoatzin of South America. Vertebrate grazers and browsers are, however, abundant on the ground and ruminants such as deer, giraffes, and oxen as well as other forest mammals such as elephants, consume large amounts of leaf material. Their impacts on forest composition and succession can be dramatic as they may preferentially feed on seedlings and saplings thereby preventing tree regeneration and succession to mature forest. Overstocking of deer in Scotland, for example, has a severe impact on the regeneration of native pine woods. In African savannas the balance between grazers which feed on grasses and browsers which attack trees can have long-term effects on the extent of trees in the landscape.

Figure 1 *Alcidodes ramezii* (Curculionidae) recently emerged from the fruit of *Dipterocarpus obtusifolius* (Dipterocarpaceae). Weevils are important seed predators of many tropical trees and in some cases can destroy over 90% of the entire seed produced in a particular fruiting event. Photograph courtesy of Richard Davies.

Figure 2 The caterpillar of the emperor moth *Imbrasia belina* (Saturniidae), commonly called the mopane worm, feeding on the leaves of its host plant the mopane tree *Colophospermum mopane* (Colophospermaceae). Mopane woodlands are dominated by this one tree species, and because few other herbivorous species find the leaves of the mopane tree palatable, *I. belina* often achieves very high population densities in sporadic outbreaks. Widespread defoliation of mopane woodlands occur during such outbreaks.

Figure 3 An unpalatable caterpillar on *Shorea leprosula* (Dipterocarpaceae). Many caterpillars sequester the toxic secondary compounds produced by leaves for their own defense against predators.

The most important herbivores in tropical forest habitats in terms of the amount of plant biomass consumed are insects, in both adult and larval forms. Grasshoppers, katydids, some beetles and ants, and the larvae of moths, butterflies, and many flies and sawflies consume vast quantities of leaf material. Many other insect grazers, such as springtails, feed on root tissues. A large number of insects belonging to the orders Coleoptera (beetles), Lepidoptera (moths), Diptera (flies), and Hymenoptera (sawflies) consume tissue between the epidermal layers of leaves creating conspicuous mines or blotches. Leaf-mining insects lay their eggs on the leaf surface or directly into the leaf. Larvae may feed on leaf tissue or just on sap exuded from damaged tissue.

In Neotropical forests leaf-cutting ants (*Atta* spp.) are the dominant herbivores consuming more vegetation than any other group of animals, and it has been estimated that 12–17% of all leaf material produced in Neotropical forests is harvested by *Atta* ants. Species selection appears indiscriminate and leaf-cutting ants will even harvest agricultural crops. Consequently, leaf-cutting ants contribute greatly to nutrient cycling in tropical forests with each colony using about 50–250 kg of dry matter each year. The underground nests of *Atta cephalotes* can cover several tens of square meters and contain up to 5 million workers. In these huge nests leaf material is used to culture specialized fungi on which the ants feed.

Gall-forming invertebrates induce plants to form abnormal growths within which the insect gains both shelter and food. Gall formers include species of mites, gall-wasps, flies, weevils and aphids and are abundant on both temperate and tropical trees, the tree families most heavily galled in Europe being Fagaceae (oaks and beech) and Salicaceae (willows and poplars). All parts of a plant may harbour gall formers, with leaves being most commonly attacked, though nematodes are unusual in attacking roots. Each galling species produces a characteristic gall structure the formation of which is usually induced by egg laying into the plant tissues. The larvae feed inside the gall where they are relatively protected from predators and desiccation. Gall-forming insects appear to increase in relative abundance with increasing aridity, presumably due to the protection a gall affords the developing larvae from desiccation.

Wood-boring beetles can cause extensive damage to trees particularly as they can also be a means of spread of pathogenic fungi. Bark beetles, for example, bore into tree trunks and excavate the wood just beneath the bark causing extensive damage. Trees often respond by flooding bore holes with sap but bark beetles may recruit to injured trees ultimately overcoming the trees' defenses.

Another important mode of consumption is to use strawlike mouthparts to suck fluids from plant vascular tissues, the phloem and xylem, which transport water, nutrients, and photosynthate. The most common sap feeders are aphids and other hemipteran bugs, although spider mites also follow this strategy.

Plants have, in turn, evolved a wide array of defensive compounds or physical structures that impede insect or vertebrate attack. Chemical defenses can reduce the digestibility of leaf tissue, or may have a toxic or repellent function. Tannins are large carbon-rich compounds that bind proteins making them difficult to digest. Toxic compounds include phenolics and alkaloids and these may poison or kill animals that consume them. Some plants have responded to attack by leaf miners by secreting latex which impedes or kills larvae. Mechanical defenses include the obvious spines and thorns to defend plants against vertebrate herbivores, and the less obvious silica structures that render grass and nettle leaves less palatable to vertebrates and invertebrates alike. Leaf hairs, called trichomes, sticky surfaces and often a combination of the two also limit herbivory, while structural tissue such as cellulose and lignin lining leaf veins is not easily digestible constraining herbivores to limited leaf areas. Plant chemical repellents may also deter insects from laying their eggs on plant tissues causing the insects to look elsewhere.

Many animals and insects have evolved mechanisms to overcome or tolerate plant defenses leading to a high degree of specialization on the host plants they infest. Insect larvae may even assimilate poisons rendering themselves unpalatable to predators. Repellents, on the other hand, do not kill herbivores so there is much weaker selection to develop counteractive mechanisms and, consequently, much less herbivore specialization.

Seed Predation

Seeds are highly nutritious packets of carbohydrates, proteins, and lipids that are readily consumed by vertebrates and invertebrates, but are only briefly available and less predictable than other plant tissues. Broadly, two groups of seed predators are recognized, those that consume seeds prior to their dispersal, and those that attack seeds that have already dispersed. Predispersal seed predators are mostly specialist sedentary feeders belonging to the insect orders Diptera, Lepidoptera, Coleoptera, and

Hymenoptera. Postdispersal seed predators are larger, more mobile, and generalist herbivores like ants and vertebrates, particularly rodents and birds. Predation rates are highly variable but can be as high as 100% of seeds produced. Although seed predation is an antagonistic interaction, some seeds that escape predation may be benefited by being dispersed into favorable microhabitats. Squirrels and other rodents cache large numbers of seeds a few of which will escape predation by being forgotten (see above). Nevertheless the vast majority of seeds encountered by seed predators are killed.

High rates of seed predation are thought to have led to the evolution of mast seeding among many tree species. Masting is the periodic synchronous production of seed that leads to such an abundance of seed that seed predators are satiated. As a result there is a greater probability of seedling recruitment following mast years. In nonmast years the dearth of seed resources may limit seed predator populations making them less able to exploit effectively periods of resource abundance. In Europe oak and beech trees produce mast crops once every two to ten years, while dipterocarp trees in Southeast Asia are well known for supra-annual mast fruiting events in which species belonging to several genera participate over areas extending to hundreds of square kilometers.

Mechanical Damage

Physical disturbance by large vertebrates is an important structuring component of forest systems. Large herbivores such as elephants can open up the canopy and disturb the soil by digging and scraping, creating opportunities for seedling recruitment especially for fast growing pioneers. In the tropical dry forest of Mudumalai Wildlife Sanctuary, southern India, very high tree mortality, largely a result of elephant damage, has been documented. Elephants are also known to play an important role in determining the abundance of trees in African savanna forests. In North America dam building by beavers can dramatically alter forest riparian habitats and, because they feed preferentially on deciduous species beavers cause an increase in the relative proportion of conifers. Animals that cause long-term and dramatic physical modification of habitats have been termed ecosystem engineers and may be important for maintaining high species and structural diversity by increasing habitat heterogeneity. At smaller scales and in temperate forests squirrels and deer cause damage to young beech and other trees by stripping bark. Such damage can cause considerable financial loss to plantation owners. Rodents attack tree roots even below ground, though such impacts are most significant in arid rather than forested environments.

Conclusion

There is a multitude of plant–animal interactions ranging from the antagonistic to the mutually beneficial. Both antagonistic and mutualistic interactions have enormous importance for the structure, composition, and functioning of forests as well as all other natural habitats. Often it is not easy to separate apparently antagonist behavior, such as seed predation, from mutualistic behavior such as seed dispersal, as the same animals often perform both functions. Furthermore, while antagonistic interactions such as herbivory, seed predation, or mechanical damage, are certainly detrimental to the individual plants affected, such behaviors may raise habitat diversity and richness by increasing heterogeneity and preventing dominance by fast-growing or competitively superior species. Additionally, many ecosystem functions are dependent on the interactions between plants and animals. Nutrient cycling and decomposition, for example, are functions of herbivory and the breakdown of organic matter by numerous soil-living invertebrates. The reproduction of flowering plants, particularly in the tropics, is dependent on the availability of pollinators. Humans are, of course, dependent on the continued functioning of these plant–animal interactions for crop production and soil fertility and the continued existence of viable diverse forests and their natural renewable resources.

See also: **Biodiversity**: Plant Diversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation; Human Influences on Tropical Forest Wildlife; Natural Disturbance in Forest Environments; Reproductive Ecology of Forest Trees. **Entomology**: Bark Beetles; Foliage Feeders in Temperate and Boreal Forests; Population Dynamics of Forest Insects; Sapsuckers. **Environment**: Impacts of Elevated CO_2 and Climate Change. **Silviculture**: Natural Stand Regeneration.

Further Reading

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