Plant-animal interactions: an overview

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Plant–Animal Interactions: An Overview

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Introduction

Interactions among organisms can strongly influence the morphology, behavior, and ecology of those organisms. Why else, for instance, would many angiosperms produce elaborate and brightly colored petals, copious amounts of nectar and extralfloral nectar, or diverse types of compounds toxic to herbivores? Natural history has recorded countless examples of adaptations that are clearly the result of past selective episodes created by species interactions. Although these interactions are more ephemeral and less tangible than a species’ morphological traits, interactions are just as fundamental in a species’ evolution. Not only can interactions produce the selective forces necessary to cause evolutionary changes within organisms, but these interactions linking the life histories

of the Earth’s inhabitants are themselves the products of evolution. As is argued later in this chapter, interactions can create new resources (e.g., nectar) that in turn allow the development of additional interactions. Species interactions contribute to the complex networks that link species into communities and ecosystems. Interactions should be viewed as one of the major organizers of community and ecosystem functions.

Until the 20th century the interactions of species, particularly those among plants and animals, received limited investigation. Ecologists now realize, for instance, that the bizarre synchronous fruiting of many bamboo species is related to seed predation and that the extinction of the common dodo more than 300 years ago may be responsible for the loss of Calacatia forests on the Indian Ocean island of Mauritius. In order to understand the evolutionary basis of the ecology of various species, it is necessary to critically evaluate the ways in which they interact with other species. Studying organisms without considering their interactions is akin to thinking that species exist only as collections in geological parks or botanical gardens rather than in natural communities. Interactions are fundamental to all living organisms.

This book is about plant–animal interactions and how they have evolved. By surveying a variety of interactions and the natural history of the species involved, some general patterns will become obvious; the patterns for other, more subtle interactions have yet to clearly emerge.

The following chapters focus on specific examples of interactions that represent a wide range of species relationships. These chapters do more than merely describe; they also provide a conceptual framework for understanding the evolution of interactions. Continued research and reflection on organismal interactions will allow advances in our understanding of the ecology and evolution of the biosphere.

Types of Plant–Animal Interactions

Plants and animals evolve in response to a background of selective pressures created by their physical environment and the other organisms with which they interact. This setting provides for numerous kinds of interactions, some of which are mutualistic, while others are antagonistic (e.g., parasitism, predation) or commensalistic. These types are defined on the basis of whether the effects of the interaction are beneficial, harmful, or neutral for each interacting species (Table 1–1). It is important to realize, however, that sharp boundaries often do not occur among these types of interactions and that interactions, whether beneficial, harmful, or neutral, can change in time and space. Thus, these distinctions are unclear in many cases.
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*Interaction 1-10 (shown in parentheses are beyond the scope of this text.*

Mutualism

The mention of plant–animal interactions commonly invokes thoughts of mutualism, a relationship beneficial to both participating species. There are numerous examples of mutualism involving both plants and animals. The usual relationship between a pollinator and a flower for instance includes a plant-produced reward (e.g., nectar, brood-place) that benefits the pollinator and an animal activity (e.g., carrying pollen to another blossom) that benefits the plant. As described in the next chapter, however, not all pollinator–plant interactions are mutually beneficial. In some cases (e.g., carrion flowers, Stapelia), plants deceive floral visitors and gain pollen transfer but without providing any benefit to the pollinator.

Mutualism is very common, and Thompson (1982) has argued that the high frequency of mutualism in communities depends evolutionarily on the richness of antagonistic interactions. There is good evidence, for example, that the majority of the early insect interactions with plant reproductive structures were detrimental to the plants (Crepet, 1979; Mulcahy, 1979) has argued that the highly successful closed carpels of angiosperms were likely to have evolved as a defense against antagonistic floral visitors. Whatever the precise evolutionary pathway might have been, the point remains that the interaction itself can evolve from an antagonistic to mutualistic relationship. Antagonistic interactions are usually less specialized than mutualistic ones, creating the opportunity for selection to produce mutual benefits. In addition, Thompson (1982) theorized that because mutualisms often create new resources (e.g., fruits, nectar), they can become foci for the development of new interactions. Thus, mutualisms contribute to the complex network of interactions and the organization of communities.
Antagonism

Antagonistic interactions occur between populations because organisms are concentrated parcels of limited resources such as energy and nutrients (Thompson, 1982). Plants, for example, fix carbon dioxide, producing carbohydrates and other energy-rich products. These plant products are essential to the survival of almost all animals, many of whom feed directly on plants, stealing materials crucial to the plant's survival. Over evolutionary time, this process results in selection pressure favoring plant genotypes with adaptations that reduce the loss to herbivores. Simultaneously, these processes will favor herbivores that can counter plant modifications with their own set of adaptations enabling them to detoxify plant toxins, digest plant parts that are high in fiber, or circumvent a plant's physical barriers such as spines or thorns.

One form of antagonism is parasitism, an interaction in which an organism (parasite) spends much of its life either attached to or within a single host organism taking nourishment from the host. This relationship typically results in reduced reproduction and/or survival of the host. Traditionally, the term parasite is used in reference to microorganisms or small animals that attack larger animals. But many other organisms, including invertebrate herbivores such as gall-makers or aphids that spend the immature portion of their life on a single host, are clearly parasitic.

Another form of antagonism is predation, an interaction in which one organism, the predator, obtains energy or nutrients by consuming, usually killing, another organism, the prey. Typically, a predator is thought of as an animal that catches, kills, and consumes its prey. However, predation can also include the capture and digestion of insect prey by carnivorous plants or the consumption of seeds by insects.

Predation is similar to parasitism in that it is a means of feeding that brings harm to the consumed organism. The distinction between predation and parasitism is often not clear cut, especially for insect populations. There is actually a continuous gradation of interactions from predation to parasitism. Just as not all pollinator–plant interactions are mutually beneficial, not all predator–prey relationships are entirely antagonistic. For example, Givnish (Chap. 7) suggests that certain pitcher plants may actually be involved in a mutualism with their social insect prey.

Commensalism

Commensalisms include those interactions in which one species, the commensal, benefits from another unaffected species. There are numer-
Competition

In simple terms, competition is an interaction in which one organism consumes a resource that would have been available to, and might have been consumed by, another (Begon et al., 1986). Although competition is not often directly considered within the context of plant-animal interactions, it virtually always affects these interactions in many indirect ways. Rubenold and Bromer (Chap. 8) show the important role competition plays in determining animal distribution. For example, slight variations in adaptations to feeding in a particular plant community inevitably lead to differences in efficiency. These differences result in either a segregation of similar species to different resource bases within a habitat or extirpation of one of a pair of very similar species from a habitat. Thus, the variety of resources provided by plants and their attendant fauna determines the likelihood of coexistence of similar species by controlling the degree to which niche separation is possible.

It should be apparent from the foregoing discussion of mutualism, antagonism, commensalism, and competition that the division of species interactions into such categories is somewhat arbitrary, but nonetheless useful. The fundamental issue is not which category is to be applied to a given example; rather, it is the recognition that there is a continuum of interactions ranging from antagonistic to mutualistic. This recognition is crucial to our understanding of how and why such interactions exist at all.
Multitrophic-Level Interactions

Much of the ecological theory of plant-animal interactions addresses only two trophic-level systems. For instance, most discussions of herbivore–plant interactions exclude the effects of the herbivore’s natural enemies (Abramsson et al., 1983; Weiss et al., 1985). Studies have shown that parasitoids (parasites that kill their hosts as a consequence of their own development) that could potentially control herbivore populations can be adversely affected by the host plant’s defenses against its herbivores (van de Merendonk and van Lenteren, 1975). This suggests the necessity of evaluating not just the plant-herbivore interaction but also the plant-herbivore-natural enemies interactions if the evolution of a plant and its herbivores is to be understood.

Price et al. (1980) pointed out that all terrestrial communities based on living plants are composed of at least three interacting trophic levels, not merely two (Fig. 1–1). Some communities may have four or more interacting trophic levels. A further complication is that each trophic level typically consists of a number of species that not only interact with other trophic levels but also interact with the species within the same trophic level. These guilds of species generate selective pressures as a

![Diagram of multitrophic interactions](image-url)

**Figure 1–1.** Many ecological studies isolate trophic-level interactions, as shown in the upper portion of the figure, by considering only the reciprocal effects of a plant population and its herbivores or the reciprocal effects of a herbivore and its enemies. When all three trophic levels are considered simultaneously, as illustrated in the lower portion of the figure, the additional effects of interactions involving the first with the third trophic levels become apparent. Modified from A. E. Weiss (unpublished).
group (e.g., insect herbivores attacking a host plant population) that can provide opportunity for the evolution of interactions. Thus, theory on plant–animal interactions will not progress realistically without consideration of all trophic levels that can influence a given system of interactions. Many studies have begun this holistic approach to plant–animal interactions, but as the succeeding chapters show, much more needs to be learned about multitrophic-level interactions. Studies of this type have become an exciting bridge between the traditionally separate fields of population and community ecology.

Evolution of Interactions

Interactions can occur as a result of a number of different ecological or evolutionary processes. These processes include reciprocal coevolution, diffuse coevolution, mutual congruence, and evolutionary tracking. Although plant–animal interactions can be studied without reference to the particular process that created the interaction, investigation of the evolution of interactions is currently an active field within biology.

Reciprocal Coevolution

Various definitions for coevolution have been proposed including Janzen's (1980a) restrictive definition that defines coevolution as

\[
\text{an evolutionary change in a trait of the individual in one population in response to a trait of the individual of a second population, followed by an evolutionary response by the second population to the change in the first.}
\]

Although this is one of the better working definitions for coevolution and one adopted by many, it does have a drawback: its overemphasis of specificity and reciprocity between the interacting populations. The definition requires specificity and reciprocity since the traits of each population are due to the traits of the other population and both sets of traits must evolve (Futuyma and Slatkin, 1983). Coevolution could, for example, occur either simultaneously or sequentially among interacting taxa (Schenske, 1983).

Some ecologists have approached the problem of creating an adequate definition for coevolution by relaxing restrictions. Roughgarden's (1979) definition, for instance, simply states that coevolution is "the simultaneous evolution of interacting populations." However, Schenske (1983) points out that this definition is inadequate because it does not sufficiently emphasize that coevolution results from selective pressures
on heritable traits that are created by the interactions between taxa. He further argues that the definition should emphasize that coevolution requires genetic variation in the characters relevant to the interaction as well as in those characters that are genetically correlated, with selected characters. Schemske (1983) has defined coevolution as the joint selective effects on characters of interacting taxa, based on heritable variation in these characters.

The term coevolution was popularized by Ehrlich and Raven (1964) in their classic paper describing the interactions of butterflies and plants. Unfortunately, Ehrlich and Raven’s paper did not define coevolution, and the example they chose to illustrate it was inappropriate. In their example, the butterflies were neither stated nor implied to have been the single populations or array of herbivores that generated the selective pressures on plant traits that produced the observed butterfly distributions on host plants (Janzen, 1950a).

The following hypothetical example illustrates the concept of reciprocal coevolution. Since all organisms are potentially food resources for other organisms, it is expected that individuals should have adaptations (e.g., chemical, physical, behavioral, morphological) to defend themselves. Evison, for example, a plant population that varies in its chemical defense against an herbivore population that in turn varies in its ability to deal with the plants’ defenses. Those herbivores that are best able to circumvent the plants’ defenses are likely to leave the most descendants; and through many generations their traits are likely to spread among the herbivore population. But the interaction should not stop there. Because of its variable resistance, the plant population should also change evolutionarily by acquiring either greater quantities of the defensive chemical or a novel chemical. A dynamic evolutionary interaction should develop that would continue as long as there is close interaction of the plant and herbivore populations. In this coevolutionary situation, the evolution of each interacting taxon is partially dependent on the evolution of the other. This concept is logical, unifying, and aesthetically pleasing; however, the role of reciprocal coevolution as a widespread and important evolutionary force, at least in Janzen’s restrictive sense, is not yet established (Begon et al., 1986). Futuyma (1983) has suggested that in most cases it may be difficult to show that reciprocal coevolution has ever occurred since the reasons for the evolution of a plant’s chemical defense or an herbivore’s detoxification adaptations are lost in unobservable past evolutionary events.

But, reciprocal coevolution is still a tenable concept. Ecology does offer a number of examples that are likely the result of coevolutionary events. For example, many ant–plant interactions (e.g., bullhorn acacia–ant relations, see Chap. 6) appear to be the result of reciprocal
coevolutionary interactions as do the impet–corallite alga association (Steneck, 1982) and some pollinator–plant associations (e.g., promiscuous moth–Yucca, see Chap. 2).

The term coevolution has often been misused, probably because of the lack of a rigorous working definition for the concept (Janzen, 1980a; Schemske, 1983). In some literature, coevolution has been incorrectly used synonymously with interaction, symbiosis, mutualism, or even animal–plant interactions, processes that do not necessarily involve coevolved traits (Janzen, 1980a).

The following examples from Janzen (1980a) illustrate the interpretative dangers inherent in the misuse of the term coevolution:

1. It is commonly assumed that a pair of species whose traits are mutually congruent (i.e., coinciding traits, such as long floral tube and long pollinator mouthparts) have coevolved. Janzen (1980a) offers the example that fruit traits of a mammal-dispersed seed could have coevolved with the mammal’s dietary needs. However, it is also possible that the mammal entered the plant’s habitat with its dietary preferences well established and subsequently began feeding on the fruits of those species that fulfilled them. The mammal whose dietary requirements are most congruent with the plant’s fruit characteristics may appear the most coevolved, yet as Janzen points out, is likely to be the least coevolved.

2. Invertebrate herbivores attacking a plant are typically assumed to be coevolved with the plant’s chemistry or morphology. In many situations, however, the herbivore may arrive in a new habitat and simply begin feeding on those plant species whose defensive traits it can circumvent. Unfortunately, such cases cannot be distinguished from ones in which, during the course of feeding on the plant, the herbivore evolved the ability to circumvent the defenses.

3. Janzen provides an additional example in which coevolution is assumed because a parasite has traits that circumvent the defenses of its host. However, there is no reason to conclude that the defense overcome was the result of selective pressures created by that parasite. The plant’s defense could be the product of its earlier coevolution with a parasite no longer present in its habitat or no longer parasitizing that particular plant species.

These examples should make it clear that biologists must be careful when invoking coevolution. Further, the point remains that the study of plant–animal interactions will yield important results regardless of
whether reciprocal coevolution is or is not involved in the development of a particular interaction.

**Diffuse Coevolution**

Some authors (Janzen, 1960b; Fox, 1981; Feeny, 1983; Putnam, 1983) have suggested that although reciprocal coevolution may be rare, diffuse coevolution may be relatively common. Diffuse coevolution occurs when either or both interacting populations are represented in an array of species that generates selective pressures as a group. Diffuse coevolution, in contrast to reciprocal or pairwise coevolution, may consist of events widely separated in evolutionary time or involve selection pressures created by a guild of species. For instance, most plants are simultaneously attacked by a wide variety of insect herbivores. Selection should therefore be most effective for plant traits that provide a broad-spectrum defense. Indeed, most plant chemical defenses are active against a wide variety of insects, vertebrates, and pathogenic microorganisms (Putnam, 1983). Such broad-spectrum defenses are most likely the result of diffuse coevolution, not reciprocal coevolution.

**Mutual Congruence and Tracking**

It should now be clear that interactions can evolve through a number of different evolutionary processes. Some interactions, for instance, are simply the result of the mutual congruence (i.e., coincidental co-occurrence) of traits possessed by the interacting organisms (e.g., an introduced pollinator able to forage on the flowers of native plant species). Others may occur because one of the interacting species responds to (tracks) the evolutionary changes of another population, while still others, as just seen, may be due to reciprocal or diffuse coevolution.

Figure 1-2 illustrates the difference between an animal that simply tracks the evolutionary modifications of the plant with which it interacts and reciprocal coevolution. The traits of the plant population are shown as notches, while the traits of the animal population are indicated as eggs. Also illustrated are the selection intensities created by pressures on the plant population by the animal population, $s_a$, and those selection effects produced by the plant population on the animal population, $s_p$. In the example labeled "tracking," the plant population is unaffected by the animal population. This is indicated by the unchanging zero value for the selection intensity $s_a$. However, as the plant population's traits
evolve through time in response to other selective pressures in the environment, the animal population responds to these plant modifications with changes of its own and thus improves the congruence of characters important to the interaction. During the times of nonconformance of traits, the selection intensity created by the plant population on the animal population is greater than zero. This process favors those animal genotypes with traits more congruent to those of the plants.

In the case of reciprocal adaptation or coevolution (Fig. 1-2) both the plant and the animal population create selective pressure on each other. An alteration of animal traits, for example, produces selection, \( s_A \), on the plant population. Those plant genotypes most congruent with the modified animal traits should, on average, leave more offspring and eventually restore a degree of congruence in the interaction. Later, a change in plant traits is countered by modification in animal traits.

It should now be evident that the term interaction is not synony-

![Diagram](image)

**Figure 1-2.** Differences between (a) evolutionary “tracking” and (b) reciprocal adaptation or coevolution. Plant traits are shown as notches, while animal traits are indicated as coogs. Selection intensities created by pressures on the plant population from the animal population are indicated as \( s_A \), while the selection effects produced by the plant population on the animal population are indicated as \( s_p \). From A. E. Wed (unpublished).
notion with coevolution, and that it is a fallacy that interactions are necessarily coevolved. Schemke (1983) in discussing flower specialization in North American bees suggests that there is virtually no evidence that the tremendous diversification and specialization of these bees is related to coevolution between plants and bees. One must proceed with caution in studies of plant-animal interaction. Without a quantitative assessment of selection intensities on the characters involved in an interaction between taxa, coevolution cannot be assumed. Further, plant-animal interactions can be highly asymmetrical, both in the selective pressures that the interactions create and in the evolutionary responses to those pressures. Thus, in many cases there is no reason to expect coevolution at all.

Certainly, coevolution is a process that could potentially influence the patterns of variation and adaptation in plants and animals. But progress toward understanding coevolution will be markedly slowed if the concept is misapplied.

Fitness

Every organism possesses an immense number of adaptations as a result of natural selection acting on an organism’s traits. Many of these adaptations are concerned with gas exchange, internal transport, regulation of fluids, and other processes not necessarily influenced by any plant-animal interaction. But others, such as the leaf morphologies of carnivorous plants or the extraloral nectaries of an ant-tended plant, are at least partially the product of selective pressures influenced by plant-animal interactions. These adaptations are genetically controlled traits that increase an organism’s fitness. In evolutionary biology, fitness refers to an individual’s (or gene’s or allele’s) genetic contribution to future generations relative to the contribution by other individuals (or genes or alleles). Thus, an adaptation is a trait that increases the probability of genetic representation in succeeding generations. It is important to recognize that adaptations do not necessarily enhance the individual’s survival probability at all stages of life. Since an adaptation must improve the chance of leaving descendants to future generations, it would be expected to increase prereproductive survival, but not necessarily postreproductive survival. Indeed, in some species (e.g., century plant, Agave), evolution has resulted in monocary (i.e., the “big bang,” reproductive pattern of reproducing only once and dying in the process).

Fitness is generally based on the reproductive performance of genotypes (or alleles) relative to one another and in a particular habitat. Genotypes, for example, vary in their reproductive success (relative fitness) in a given environment and the relative fitness of a given
Figure 1-3. The ability of the offspring of 12 goldenrod ball gallmakers, *Eurosta solidaginis*, to stimulate gall growth vary on one genotype of tall goldenrod (*Solidago altissima*). Offspring of fly 16, for instance, were less successful in stimulating gall growth on this plant genotype than offspring of fly 9. If tested on another plant genotype, the relative abilities of these flies to stimulate gall growth would likely change. From A. L. Weis and W. C. Abrahamson (unpublished data).

individual can change according to the environment in which fitness is measured. Although the offspring of certain gall-maker genotypes perform poorly on one host plant genotype (Fig. 1-3), those offspring might perform well on other host plant genotypes (Weis and Abrahamson, 1986). As a result, the alleles responsible for the gall-maker’s ability to manipulate its hosts should change over evolutionary time in response to alterations of the host plant. A given allele or set of alleles may increase in frequency in some localities while declining in others. Recognition of the genetic basis of plant-animal interactions is critical to the development of theory within the field.

Principle of Allocation

Each individual organism has a limited amount of resources available to devote to such primary activities as growth, maintenance, and reproduction. Because of this limit, the resources spent on one activity are unavailable for allocation to other activities. For example, increased reproduction during one growing season will reduce current growth. A large commitment to reproduction in the early years of a long-lived organism’s life will decrease fecundity (an organism’s reproductive capacity) in future years. In long-lived perennial plants (e.g., aspens, goldenrods, mayapples), for example, clonal growth should be favored.
over fecundity, especially when space for clonal expansion is available. This strategy increases lifetime reproductive output (Altmannson, 1980; McCrea and Altmannson, in preparation). Alternatively, in species with short life-spans the strategy of allocating more resources to reproduction rather than growth is expected.

This principle of allocation is applicable to many evolutionary alternatives faced by organisms. There are trade-offs between seed size (i.e., provisioned of the embryo) and seed number, between fruit size and number, and between floral secondary attractants (e.g., petals or colorful stipples) and primary attractants (e.g., sector, pollen). In discussions of plant-animal interactions, it is useful to keep this principle in mind when considering the evolutionary alternatives implemented by a given species in a particular situation.

It must also be emphasized that organisms are not perfect in their design, even though there is close correspondence between an organism’s morphology, physiology, and behavior, and its environment. As Gould (1980) has argued, design is not inherent to the process of natural selection. The environment itself is the template for the pattern seen in organisms. Selection merely acts as the process that creates the pattern. Gould (1980) has illustrated this point with the imperfection of the panda’s thumb. The panda’s thumb is functionally a sixth “digit” that is derived from a wrist bone. This unusual development converts what would otherwise be a paw into a manipulative hand able to grasp stems of bamboo, the panda’s primary food. The panda’s thumb is not an ideal design in the sense of engineering perfection, but it works. Natural selection can only act on the heritable variation available to bring about evolutionary change. Organisms are constrained by their evolutionary past.

In discussing the evolution of plant and animal traits important to an interaction, it is tempting to perceive organisms as completely malleable by selection pressures. However, the form that an adaptation may take is strongly limited by the species’ prior evolution (Gould, 1980). Natural selection can only work with existing genetic variability. This evolutionary history along with the randomness of mutation and recombination constrain the possibilities and directions of new evolutionary modifications. As a consequence, perfect correlations between theory, or what a designer would produce, and what nature (or human selection of domesticated plants and animals) creates are not realized.

Ecological vs Evolutionary Time

A considerable amount of ecological theory deals with competition among species. Virtually every student taking an introductory course in
ecology is introduced to the competitive exclusion principle (the hypothesis that two or more species cannot coexist on a single resource that is limited relative to the demand for it). This principle provides various theoretical outcomes of interspecific competition depending on numbers of individuals initially present and the competitive ability of the interacting populations. But these outcomes consider only the immediate, or ecological, time frame. More important to the discussions of the subsequent chapters are the implications of competition (see especially Chap. 8) and other types of interactions in an evolutionary time frame. Thus, one can view competition for floral visitors among flowering plants as a selective force that can alter the representation of plant genotypes in future generations. The nectar rewards or floral morphology of some genotypes may be such that these genotypes set more seeds than other genotypes resulting in higher fitness. The study of plant–animal interactions has an evolutionary time perspective. Although interactions may be ephemeral in a palentological sense, they are the evolutionary outcome of ecological processes.

Plant–Animal Interactions as a Subject of Study

The study of plant–animal interactions encompasses much of the disciplines of evolution and ecology and therefore cannot claim any distinction as a separate field of study. However, as Futuyma and Slatkin (1983) suggest, progress is frequently made by drawing attention to particular definable subjects within a field. Focus on plant–animal interactions facilitates an evolutionary approach to classical ecological studies. Studies addressing various plant–animal interactions have initiated a highly analytical view of ecology. The theories are based on the fact that genetic shifts can occur in the populations of interacting species as a result of selective pressures. These pressures are created by the interactions themselves and act on the heritable variation in the organism's traits. These genetic shifts can be driven both by the immediate interactions and by feedback through the rest of the community as a result of diffuse coevolution (Roughgarden, 1983).

An important attribute of many studies on plant–animal interactions is their perspective of evolutionary time. These interactions are dynamic and change as selective pressures are altered. While discussing coevolution, Futuyma and Slatkin (1983) note that if one species is considered alone, it might be expected to evolve until it has resolved whatever challenges it has met and then stop. But if two or more species respond evoluntarily to one another, then continued evolutionary change should be expected. A plant species could continually elaborate new chemical defenses while its herbivores evolve adaptations to over-
come those compounds. Recent studies of plant-animal interactions, regardless of whether they involve coevolution, have utilized this dynamic, evolutionary time perspective. It is now clear that this approach is fruitful and should provide important insights into the evolutionary history of many groups of organisms.

There are practical spin-offs to these studies in fields such as medicine and agriculture. For example, a number of plant chemicals, presumably evolved in response to herbivores, have useful therapeutic effects on humans. Cardiac glycosides, defensive chemicals common in foxglove (Digitalis), possess cardiotoxic (having a tonic effect on the heart) activity which is of value in the treatment of congestive heart failure. Digitalin increases the force of heart muscle contraction without a concomitant increase in oxygen consumption, making the heart a more efficient pump (Lewis and Elvin-Lewis, 1977). Indeed, most useful drugs originated as plant products that serve ecological functions in nature. There is an abundance of species yet to be discovered and screened for possible human uses.

Other applications of studies of plant-animal interactions will be particularly obvious in this book’s final chapter on plant-animal interactions in agricultural systems. The fundamental processes of ecology and evolution operating in natural ecosystems also operate in managed ecosystems. Understanding the biology of plant-herbivore-natural enemy interactions in natural ecosystems, for example, can provide

Figure 1-4. Calathea ovandensis (Marantaceae) hosts a variety of mutualistic and antagonistic plant-animal interactions. These interactions include relationships with pollinators, seed dispersers, ant guards, and herbivores. A = Eugenia heterogyna (Hymenoptera: a common pollinator), B = Drosophila sp. (Diptera: adults oviposit in older Calathea inflorescences and the resulting larval seed on reproductive tissue), C = Solenopsis geminata (Hymenoptera: ant tending the specialist herbivore larva, Euryzota elvana, see also L. Solenopsis geminata also serves as a Calathea seed disperser), D = Crematogaster sumichrasti (Hymenoptera: feeds on extrafloral nectaries while serving as an ant guard against generalist herbivores; this ant, like other ants visiting Calathea, feeds on the nectarlike secretions on Euryzota elvana), E = Aculea sp. (Hymenoptera: leaf-cutting ant and its damage), F = Pachycnema lurida (Hymenoptera: seed disperser), G = Calathea ovandensis seed with its lipid-rich elaiosome, H = Calathea ovandensis (Marantaceae), I = Hesperia heelei (Coleoptera) damage to Calateza leaf, J = Heliconius erato (Lepidoptera: an occasional pollinator), K = Euryzota elvana (Lepidoptera: specialist herbivore as a larva but the adult visits Calateza flowers), L = Euryzota elvana larva. Lepidoptera: specialist herbivore that secretes a nectarlike fluid harvested by ants such as Solenopsis geminata, while feeding on flowers and developing frass. M = various members of the Hesperiidae (Lepidoptera: common flower visitors but poor pollinators), N = Saliara sp. (Lepidoptera: herbivorous larva and its leaf damage), O = Podalia sp. (Lepidoptera: herbivorous larva), P = Orthopteran leaf damage (herbivores). Illuminations created from materials provided by C. C. Horvitz and D. W. Schenske.
crucial understanding of such interactions in systems based on crop plants.

Progress made in the field of molecular genetics involving the direct transfer of genes from one organism to another raises expectations for the improvement of modern crops using these techniques. Host resistance could be obtained through the transfer of genes responsible for resistance to a particular set of herbivores from a wild plant species to a domesticated crop species. Knowledge of natural plant defenses against herbivores will be important to these attempts.

Breadth of Plant-Animal Survey

A comprehensive survey of plant–animal interactions is beyond the scope of this textbook or any single volume. The approach taken here is one of providing description and theory for a set of important, representative types of plant–animal interactions. There are obvious omissions (e.g., marine plant–animal interactions), but this approach does provide a theoretical framework useful in considering virtually any interaction. This textbook offers a way of thinking about organisms rather than detailing as many types of interactions as could possibly be described.

There are many well-studied plant-animal interactions including the New and Old World Acacia tree systems, goldenrod-herbivore interactions, and many pollinator-plant systems. A series of studies by Carol Horvitz and Douglas Schemske and their coworkers nicely illustrates the complexity of such interactions within one plant species. *Calathea ovandensis* (Marantaceae, arrowroot family). This neotropical herb hosts a variety of mutualistic and antagonistic plant–animal interactions, each of which affects several stages of the plant's life history (Fig. 1–4, Table 1–3). These interactions include pollinators, seed dispersers, ant guards, and herbivores of both reproductive organs and leaves (Horvitz and Beattie, 1980; Horvitz and Schemske, 1984, 1986; Schemske and Horvitz, 1984).

In *Calathea* there are at least three mutualistic interactions. There is a pollination system with bees as primary pollinators, but also other *Hymenoptera* (bees and wasps) and *Lepidoptera* (butterflies and moths), each of which vary in pollination efficiency (Schemske and Horvitz, 1984). It has a seed dispersal system with ants that are attracted by the *Calathea* seed's lipoid-rich elaiosome (edible oil body; attached to the outside of some plant species' seeds). Mature fruits deliver (split open) so that seeds are scattered onto the forest floor near the plant. Here they attract several ant species that vary in their ability to disperse seeds (Horvitz and Beattie, 1980; Horvitz, 1980, 1981). These ant dispersal
<table>
<thead>
<tr>
<th>Stage</th>
<th>Pollinators</th>
<th>Ants at Ectocarpal Membranes</th>
<th>Herbivores of Repro. Tissues</th>
<th>Post-dispersal Seed Predators</th>
<th>Dispersal Agents</th>
<th>Total Herbivores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovules</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Seeds (on plant)</td>
<td>0</td>
<td>+</td>
<td>-</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Seeds (in soil)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Seedlings</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Larger Plants</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>+ (Survival)</td>
<td>(Growth)</td>
</tr>
</tbody>
</table>

*Effects are indicated as beneficial (+), harmful (-), or of no appreciable benefit or harm (0) by each guild of animals that interact with Calathea.*

From: D. W. Schremke and C. C. Vanatta, personal communication.
agents probably have important effects on seedling establishment and long-term effects on seedling success because the ant determine where seedlings will grow (Horvitz and Schemske, 1984). Finally, there is an ant guard defense system based on the plants extrudal nectaries (Horvitz and Schemske, 1984). Variation in the magnitude of beneficial effects by ant mutualists is likely. Factors such as the distance of plants from ant nests as well as the spatial and temporal variation in the particular ant species involved can markedly influence the ant’s benefit to the plant (Keeble, 1977; Schemske, 1989b).

Calathula has antagonistic interactions with (1) an herbivorous butterfly larvae, Eurybia erina (family: Biodaidae) which, while feeding on the flower and developing fruits, secrete a nectar-like fluid harvested by ants (Horvitz and Schemske, 1984), and with (2) herbivores feeding on vegetative tissues, particularly leaves. The numbers of interactions involving this one plant species themselves create complexity. Moreover, the relationships are far more complicated because some of these interactions are isolated from one another. For example, the inflorescences of Calathula possess extrudal nectaries that provide sugar-rich food to several ant species. But, in addition to feeding on nectar, these ants prey on most but not all herbivorous herbivores encountered while patrolling Calathula. These same ants that offer Calathula defense against generalist herbivores also tend the larvae of the specialized herbivore E. erina, which in turn produces a nectar-like fluid used as food by the ants (Schemske, personal communication).

The Calathula system demonstrates the complexity of interactions among species on several trophic levels. But this example is not unique. Most systems are equally complex. In the clusters that follow, these types of interactions and many others will be explored. The examples will be drawn from a diverse selection of plant and animal taxa. The organization of chapters moves from population-level to community-level interactions and from interactions involving plant reproductive organs to vegetative organs.

Chapter Topics

The second chapter, written by Robert Bertin, discusses the interactions between flowers and their pollinators. Many of these interactions are mutualistic. The chapter examines plant fitness, floral mechanisms for pollinator attraction, plant breeding systems, pollinator sensory abilities, and pollinator behavior and energetics. A discussion of fruits, seeds, and dispersal agents follows the pollination chapter. Here Edmund Stiles explores fruit and seed characteristics (e.g., structure, chemistry, phenology, allocation) in relation to
the characteristics of frugivores (fruit-eating animals) and seed predators. Throughout, there is an emphasis on the evolutionary responses to the potential selective pressures resulting from the interaction.

Next, Arthur Weis and May Berenbaum shift attention to antagonistic interactions involving insect herbivores with plants. These authors consider the ecological impacts of insect herbivores on plants and the resultant evolutionary responses. Also outlined are the evolutionary responses of insects to plants. Weis and Berenbaum deal with natural enemies of herbivores providing a holistic look at multitrophic-level interactions.

Insects are not the only herbivores of plants. Richard Lindroth guides an examination of herbivorous mammals and their relationships to plants. This chapter describes these interactions from both the plant’s perspective (e.g., plant adaptations, impacts of mammalian herbivores on plant populations and communities) and the mammal’s perspective (e.g., mammalian adaptations to herbivory, effects of plants on herbivore population dynamics and community organization).

Kathleen Keeler’s chapter on ant–plant interactions describes the many relationships that ants and plants have evolved. Ants are seen as fungus gardeners, seed harvesters, plant defenders, and herders. These interactions, illustrating both mutualistic and antagonistic interactions, provide some of the best examples of coevolution.

Some plants, the carnivorous ones, seem to have turned the tables on insects. Thomas Givnish details much of what is known about the ecology and evolution of carnivorous plant species. This chapter explores predaceous plants includes, among other topics, the mechanisms of prey attraction, capture, and digestion as well as the nutritional benefits, possible mutualism with social insects, and a cost–benefit analysis of plant carnivory. The chapter concludes with a discussion of the evolutionary pathway to carnivory.

The remaining two chapters emphasize community and ecosystem patterns. Kerry Blackwell and William Broner look at plant communities as animal habitats. The theme running throughout their chapter is that plants form much of the physical and biological environment for animals and thereby greatly affect animal population dynamics (e.g., competitive interactions) as well as the patterns of animal distribution and abundance. The approach of this chapter is, of necessity, more one-sided that that of all but the preceding chapter, but in this case considers primarily animals rather than plants.

In the final chapter, Benjamin Stinner and Deborah Stinner examine plant–animal interactions in human-created agricultural ecosystems. They draw heavily from the theories developed for natural ecosystems and the theories discussed in the earlier chapters to provide an understanding of current problems in agriculture. The problem of limited
Genetic variation in crop species, for instance, is outlined relative to attempts to enhance a crop’s genetically based resistance to pests. This chapter offers an opportunity to consider the application of basic ecological and evolutionary theory to an economically relevant situation.

These topics provide a wide variety of natural history descriptions of interactions but also offer a solid theoretical framework in which to consider the evolution of these interactions. The topics included represent the broadest of the editor rather than an attempt to comprehensively examine all possible types of plant-animal interactions. The goal was to initiate a reader’s discovery of the complexity and wonder of ecological interactions.

Selected References