Coevolution and species interactions

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Ecosystems are characterized by a network of interrelationships among species and species groups which leads
to community homeostasis. Occasional mutations or recombination in one component of the coevolving species
pair may lead to a new set of defense characteristics making it possible for that component to enter a new
adaptation zone from which evolutionary radiation might follow. The other component of the pair through genetic
feedback might evolve to develop morphological, behavioural or biochemical features to overcome the new
characteristics of the other component. Selection would carry this population to new adaptive zone allowing it to
diversify further. Coevolution thus is a manifestation of selective evolutionary interactions between species or
species groups with a close ecological relationship. Coevolutionary instances are illustrated in plant-herbivore,
host-parasite, plant-pollinator and several similar relationship. In coevolution, the biotic environment plays an
active role within a relatively passive physical environment. However, change in the physical environment might
favour or disfavour one component of the coevolved pair more than the other component. This differential
response might lead to disruption of the relationship and may even result in loss of species.

Key-words—Coevolution, Plant-animal interaction, Herbivores, Pollinators, Parasites, Predators.

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सारांश

सहविकास एवं जातियों की पारस्परिक क्रिया

एम० अग्रवाल, ए० एस० रघुबंशी, जे० एस० सिंह एवं बी० के० रॉय

पारिस्थितिक-तंत्र जातियों की अन्तरबन्धुता एवं जाति समूह, जिनसे समुदाय समस्थापन होता है, के परिपथ-जाल से अभिलक्षणित हैं। सहविकासीय
जाति युग्म के एक अवयव में प्रायः उत्परिवर्तन अथवा पुनः संयोजन से एक नया लाक्षणिक समुच्चय बन सकता है तथा इसी से ही बाद में विकास सम्भव हो
सकता है। इसी युग्म का अन्य अवयव आनुवंशिक पूर्वजता के फलस्वरूप दूसरे अवयव के लक्षणों पर प्रभुता स्थापित करने हेतु आकारिकीय, व्यवहारिक
अथवा जैवरासायनिक लक्षण उत्पन्न कर सकता है। वरण-प्रक्रिया इस नव-समुदाय को नये अनुकूल मंडल में स्थापित कर सकती है जहाँ पर इसका और
विकास हो सकता है। अतः सहविकास घनिष्ठ पारिस्थितिक सम्बन्ध के साथ-साथ जातियों अथवा जाति समूहों के मध्य वरण विकासीय अन्तरक्रियाओं की
अभिव्यक्ति है। पादप-शाकभक्षियों, पोषी-परपोषी, पादप-परागणक एवं अन्य सदृश बन्धुताओं के माध्यम से सहविकास के उदाहरण प्रस्तुत किये गये हैं।
सहविकास में जैव-वातावरण की महत्वपूर्ण भूमिका है। हालाँकि भौतिक वातावरण में हुआ परिवर्तन सहविकसित युग्म के एक अवयव हेतु अनुकूल अथवा
प्रतिकूल भी हो सकता है। इस विभेदी प्रक्रिया के फलस्वरूप इनकी बन्धुता भी समाप्त हो सकती है अथवा जाति का अस्तित्व भी समाप्त हो सकता है।

COEVOLUTION, with all of its ecological ramifications, has attracted increasing attention during the past three decades or so. It is fairly well established that the evolutionary competence differs among organisms. Evolution consists not of one or two important processes but often of a consortia of processes of various sorts affecting different taxa differently (Endler & McLellan, 1988). While the community is itself a major determinant of the selective milieu of its component populations, its characteristics change frequently due to evolution of and coevolution among the species' populations.

Communities often change by the immigration and/or local extinctions of species.

The term coevolution was popularized by Ehrlich and Raven (1964) in their classic paper describing the interactions of butterflies and plants. These authors considered coevolution as the joint evolution of two (or more) taxa that have close ecological relationships but do not exchange genes. Ricklefs and Cox (1972) have suggested that biotic

responses to competition and predation determine the counteradaptation of the species in a community. The evolving interactions among species due to adaptations and counteradaptations against constraints lead to coevolutionary instances. Reciprocal relationships among the taxa work as selective pressures resulting in one species evolving in response to another species. According to Lindroth (1989), coevolution refers to closely integrated, reciprocal evolutionary adjustments between two interacting populations. Coevolution can thus be considered to result from population interactions such as competition, predation, parasitism and mutualism. Gilbert and Raven (1975) have edited the first book on coevolution.

Janzen (1980) defined coevolution as "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change of the first". This definition overemphasizes the specificity and reciprocity since the traits of each population are due to the traits of the other population and both sets of traits must coevolve (Futuyma & Slatkin, 1983). Schemske (1983) defined coevolution as the joint selective effects on characters of interacting taxa and argued that coevolution could occur either simultaneously or sequentially among interacting taxa. Coevolution requires genetic variations in the characters relevant to the interactions as well as in those characters that are genetically correlated with selected characters (Schemske, 1983).

Coevolution may result both from macroevolutionary as well as microevolutionary processes (Brooks, 1988). Microevolutionary processes refer to short term interactions between individual ecological associates, and denote the mutual modifications among them. Macroevolution is a long term phenomenon of associations between evolving linkages of ecological associates and denotes the degree of cospeciation or mutual associations. Coevolution may be strict where pairwise evolution of reciprocal nature occurs, or it may be diffused when species interact with many other species, and when all may affect each others' evolution (Rothstein, 1990). Although reciprocal coevolution may be rare, diffuse coevolution is relatively common (Janzen, 1980; Futuyma & Slatkin, 1983). Diffuse coevolution, such as broad spectrum plant chemical defenses, may consist of events widely separated in evolutionary time or involve selection pressures created by a guild of species (Abrahamson, 1989). Diffuse coevolution may however, be hard to identify because coevolutionary traits are weakly expressed.

In this article we view coevolution as representing a range of situations from specific, reciprocal and sequential flux of genetic changes to simultaneous events or to those separated widely in evolutionary time, but all leading to heritable ecological adaptations among interacting populations. We review a variety of coevolutionary patterns in ecological systems with illustrative examples. We suggest that most coevolutionary processes are based on interactions involving availability and patterns of resource utilization.

PLANT HERBIVORE INTERACTIONS

Plant-insect interactions

The plant and insect association has its root back to the time of their origins. Insects started colonizing terrestrial environments approximately 320 to 280 million years BP during the Carboniferous Period when the early plants had already encroached upon the terrestrial system. Primitive plants are still used by many insect groups that arose during the Permian. Smith (1979) has reported that many sawflies, members of the primitive suborder Symphyta of the Hymenoptera still feed on ferns and gymnosperms.

Biochemical or behavioural specificity in overcoming chemical defences may be an important force in the evolution of feeding specificity in plant-insect interactions. At the same time, selection pressures exerted by herbivores may be an important force in directing the evolution of plant secondary chemicals (Weis & Berenbaum, 1989). Ehrlich and Raven (1964) examined the phylogenetic relationship among butterflies, a group that contains many specialist herbivores, and their host plants. For example, the Danaidae feed on the Asclepiadaceae, and the members of subfamily Pierinae feed on the Capparidaceae in the tropics and the closely related Brassicaceae in the temperate zones. Ehrlich and Raven (1964) proposed a five-step process for the evolution of butterfly feeding habits and brought the term coevolution into general usage to describe this scenario. The five steps are:

(i) An angiosperm produces a novel secondary compound or class of compounds due to a random genetic event,

(ii) By chance, these compounds render the plant less suitable as food for insects,

(iii) These plants undergo evolutionary radiation in a new adaptive zone because they are now free from herbivore pressure.

(iv) By a random genetic event an insect evolves

resistance to the secondary compound.

(v) The adapted insect enters a new adaptive zone and undergoes its own evolutionary radiation because it is now able to exploit a plant resource previously unavailable to herbivores.

Many plants produce and store secondary products such as alkaloids, terpenes, phenolics, and steroidal, cyanogenic and oil glycosides, which when released function as a contact poison or a volatile inhibitor. However, such chemical defences are overcome by specialist herbivores which have developed the capability to absorb or metabolically detoxify these substances. When the feeding environment offers few or no choices for herbivore, selection favours feeding specialisation and forces the herbivore to develop physiological adaptations against chemical defences of available food plants. For example, the monarch butterfly feeds on cardic glycoside-containing milkweeds and incorporates the toxin in its tissues. If in turn the butterfly is eaten by birds, the stored toxin causes illness in the latter (Sondheimer & Simeone, 1970). Weis and Berenbaum (1989) described the interaction between plants of the family Umbelliferae and swallotail butterflies and oecophorid moths. In Umbelliferae three biochemicals, hydroxycoumarins, linear furanocoumarines and angular furanocoumarins, have arisen in sequence and are sequentially less suitable to polyphagous insects. However, some oligophagous species have counteradapted to furanocoumarins through behavioural and biochemical means. Genera within the Umbelliferae containing these chemicals have more species than those lacking coumarins, and the insect taxonomic groups that can handle these chemicals are more diverse than related groups that cannot (Berenbaum, 1983).

The genetics of furanocoumarin production in the wild parsnip with respect to its major herbivore, parsnip webworm, was examined by Berenbaum et al. (1986). When the plant genotypes that produce high levels of two different furanocoumarins are grown in insect free environment, they exhibit lower fitness compared to the situation when they are grown in presence of insects. These plant genotypes evidently are protected from herbivory and therefore show high fitness in the presence of insects. Within the plant populations, the levels of secondary compounds may change as herbivore populations fluctuate and different plant genotypes are favoured (Weis & Berenbaum, 1989).

Small invertebrates do not feed upon cyanogenic plants of Lotus curniculatus, whereas many acyanogenic plants are heavily grazed by slugs and snails (Jones, 1966). This chemical polymorphism in L. corniculatus is controlled by pairs of alleles at separate loci which are not linked. In this species glucoside presence is a dominant character compared to glycoside absence. The species is also polymorphic for the enzyme which hydrolyses glucoside to produce cyanide. The combination of glucoside and enzyme loci on the one hand and their joint absence on the other, resulted into differentiation of cyanogenic and acyanogenic plants (Atwood & Sullivan, 1943). Larvae of the butterfly Polyommatus icarus show no preference for acyanogenic plants over cyanogenic plants. These insects have developed the capability of rendering the cyanide harmless by converting it enzymatically into thiocyanate.

In oak leaves, tannin (deposited in vacuoles) combines with leaf proteins rendering the proteins undigestable to caterpillars that eat the leaves. Growth of the caterpillars is checked. Larvae of certain leaf mining beetles, however, have evolved in such a way that they can burrow through and selectively consume the inner leaf tissues while completely avoiding the tannin-filled vacuoles. There are some examples where mutual relationship of plants with animals protect plants from certain herbivore species. Janzen (1966) showed that some species of Acacia which are deprived of their normal epiphytic fauna are more palatable to herbivore insects as compared to those which do not have such an association.

Thus, in the course of evolution, plants may develop chemical substances that are toxic to most herbivores. If during this process one herbivore develops a strategy to cope with this offensive chemical, that herbivore will be assured of a continuous food supply. This kind of coevolution is highly specific involving a single herbivore and plant species. Drosophila pachea is the best example of this type of coevolution. This species of fruit fly can only exploit the senita group of cacti because the alkaloid produced by plants is fatal to the larvae of all other fruitfly species. D. pachea has, however, evolved a means of detoxifying this chemical (Kircher et al., 1967). Such antiherbivore chemistries force reciprocal evolution of herbivore specialists by reducing the efficiency of generalized herbivores. Phylogenies of certain herbivorous insect (particularly butterflies) closely parallel the phyletic relationships of their host plants (Ehrlich & Raven, 1964).

The degree of herbivory and the effectiveness of defenses vary widely among plant species. Many investigators have recognised the importance of resource availability in directing the evolution of plant antiherbivore defence mechanisms. Janzen

(1974) suggested that plants in nutrient-poor soils can less afford to lose biomass to herbivores. He reasoned that the cost of replacing materials eaten by herbivores would be greater in areas of nutrient-poor soils than on sites richer in nutrients. He predicted that vegetation growing on impoverished soils would be found to contain greater concentrations of anti-herbivore compounds. Mckey *et al.* (1978) measured herbivore deterrent phenolic compounds in two African rain forests and concluded that vegetation of low nutrient soils contains higher concentrations of secondary compounds. They hypothesized that the level of defence investment increases as the plant's potential growth rate decreases. Coley *et al.* (1985) proposed that resource availability in the environment is a major determinant of both the amount and type of plant defence. Fast-growing plants adapted to resource-rich habitats suffers higher rates of damage from herbivores and have both lower amounts and different types of defensive chemicals than slow-growing species. Secondary chemicals of slow-growing plants from resource limited sites have low turnover and the absolute concentrations of defensive compounds in leaves tend to be at least twice as high as those in leaves of fast growers from resource rich sites (Coley *et al.*, 1985; Mckey *et al.*, 1978). Thus conservation of resources is the factor dictating patterns of secondary chemical production; moreover, it dictates the impact of resource removal by herbivores (Weis & Berenbaum, 1987).

Plant-insect interaction can also take the form of a host-parasite relationship. A close genetic inter-relationship has been observed in Hessian fly (*Mayetiola destructor*) and wheat (Gallun & Hatchett, 1968). Planting of resistant wheat varieties in the United States has placed heavy selection pressure on Hessian fly populations, leading to development of Hessian fly biotypes that can overcome the resistance of wheats governed by specific genes. During genetic analysis, H_1H_2, H_3, H_5H_6 and H_7 H_8 genes for resistance to Hessian fly were identified in wheat (Gallun, 1984). Laboratory populations of Hessian fly were subjected to selection pressure from wheats having H_3 genes for resistance. Within the population some variants occurred, that survived on the resistant wheat variety and stunted them. Following the gene-for-gene concept (see later), it was suggested that for each gene conferring resistance in wheat plant against Hessian fly, there is a comparable gene for virulence in the insect. Studies have shown that for every new gene placed in the wheat plant for conferring resistance, the gene base for virulence of Hessian fly has increased. Since Hessian fly has existed for centuries, many genes for virulence against wheat resistance may have accumulated (Gallun, 1984).

Southwood (1961) has studied the association between insect species and tree species in England and found that the more abundant the occurrence of a tree species, measured by the number of records in fossil pollen samples, the greater the number of species of insects that can be collected from living trees of that species. Few insects have evolved to exploit the relatively less abundant mountain-ash, hornbeam and maple compared to the number of insects feeding on more abundant willow, oak and birch. Evidently the intensity of interactions is influenced by the opportunity each species had to evolve with respect to others.

Plant-mammal interactions

Coevolution calls for reciprocal evolutionary responses in plant-herbivore systems, and the degree of reciprocity varies among populations in different communities (Lindroth, 1989). Diffusive coevolution between plants and mammals is best documented with respect to grasslands and large grazing mammals (Mack & Thompson, 1982; McNaughton, 1985). The two groups have closely associated evolutionary histories, exert strong selection pressures on one another, and have developed a variety of adaptations for avoiding, tolerating, or abetting herbivory (Lindroth, 1989).

Evidence regarding the coevolution of grass flora and herbivores in North and South America has been presented by Stebbins (1981). Detailed analyses of landborne sediments of Middle Eocene (45 million years ago) shows the existence in South America of semiarid conditions associated with open savannas similar to the pampas of present day temperate South America (Spaletti & Mazzoni, 1978). Most dominant forms of grasses (monocotyledons) originated in West Gondwana (Africa and South America before their separation) in vast arid and semiarid tracts of tropical latitudes. Stebbins (1981) suggested that Poaceae entered South America from the old world most probably during the Palaeocene or the uppermost Cretaceous. Presence of opaline siliceous bodies in sediments indirectly suggests that the coevolution of grasses and herbivores continued in Oligocene. Janis (1976) has reported that coevolution of floral components of grasslands and large ungulates began during the Early Tertiary, when large ungulates became capable of digesting the structural parts of plants, although direct evidence is scarce. A symbiotic association developed between cellulolytic micro-organisms and ruminal and cecal digestive systems of animals for efficient exploitation of grasslands by large

herbivores.

Some scientists consider plant-mammal interaction as mutualistic because herbivory is shown to benefit some plants. These workers suggest that the responses of grasses to grazing (e.g., delayed senescence, compensatory growth, increased vegetative propagation) increase their genetic fitness. Owen and Wiegert (1981) and Owen (1980) assert "grasses do not defend themselves from grazers, rather they encourage them". They have hypothesized that grasses and their grazers are co-evolved groups to the extent that one would not occur without the other. Herbivores can increase the relative fitness of the plants they eat in a variety of ways. The selection pressures operate in both grazer-plant and plant-grazer directions leading to the evolution of specific mutualistic characters. In his controversial paper Dyer (1980) proposed that saliva produced by grazers stimulates grass growth. In this relationship, increased grass productivity resulted in increased grass biomass and increased life span of individual plants. It was suggested that certain characteristics of the saliva and grasses have co-evolved. Frequent grazing, however, reduces the seed production, but the life span of individual clones increases which otherwise would have senesced earlier due to earlier seed production.

Herrera (1981) argued against the possibility that plants benefit from grazing, and cited McNaughton (1976), who in a study of the effects of grazing showed that increased grass production resulting from wildebeest grazing in the Serengeti Plains of East Africa does not benefit these ungulates but it rather benefits Thomson's gazelles who approach the area after the wildebeest herds depart. In this area large herds of mammalian herbivores migrate in temporal succession (Bell, 1971). Zebra, which feed on tall, protein-poor stems and grass sheaths, migrate first and are followed by wildebeest, which consume grass sheaths and the more nutritious grass leaves. Thompson's gazelles follow the wildebeest and feed on the nutritious regrowth of grasses and the protein-rich herbaceous vegetation. Here, the wildebeest is the commensal of the zebra and the Thompson's gazelle is the commensal of the wildebeest. While the relationships among these animals are commensalistic, the relationship between each of these herbivores and the plant communities on which they feed is predominantly antagonistic (Abrahamson, 1989).

Other opponents of the view of Owen and Wiegert (Silvertown, 1982; Crawley, 1983; Belsky, 1986) argue that herbivory is most unlikely to increase fitness because it causes an appreciable nutrient and energy drain. Increased reproduction induced by grazing does not mean that fitness is enhanced, because fitness is a compilation of many factors in addition to reproduction. Moreover, the presence of physical defences by grasses (e.g., high and inducible concentrations of silica, sharp awns) and counteradaptations by mammals (e.g., high crowned teeth) would suggest that grazing is an antagonistic, not mutualistic interaction. However, Owen and Wiegert (1981) emphasized the fitness related to differential mortality rates rather than that related to differential reproductive success. Further, as we argued earlier, adaptations and counteradaptations lead to coevolution. Therefore, grasses and grazers represent a highly co-evolved system which has developed as a result of mutualistic adaptations for the benefit of both the counterparts.

According to Orians (1974), the abundant plant species evolve quantitative defences, such as, tough leaves with low water and nutrient content and large amounts of relatively nonspecific chemicals. These defences may be overcome over the evolutionary time by coevolution of detoxification mechanisms in herbivores. This leads to host plant specific herbivore species. According to Cates and Orians (1975), late successional plants are fed upon by more host-specific herbivores than early successional plants, allocate fewer resources to chemical antiherbivore defences, and are fed upon by more generalized herbivores. This suggests that plant defence systems are more generalized in early successional species than in the late successional species which have coevolved with herbivore specific demand.

Caughley and Lawlor (1981) described grass and grazer relationships as coevolved predator-prey like systems. Grasses defend themselves against grazers by accumulating silica particles (phytoliths) in the leaf blades and stems. Perhaps phytoliths were intended to make the grass less palatable but this led to an added benefit of wearing down herbivores teeth. This mechanical defence was overcome by more recent grazers by evolution of teeth with very hard slicing surfaces and very complex enamel patterns and continuous tooth growth. Guthrie (1971) thus suggested that abrasive diets have played a most important selective pressure in the evolution of grazers dental pattern.

Plants protect their seeds from predators in a variety of ways. Some plants enclose their seeds in a toxic matrix or in a hard covering. Janzen (1971) has reported that predation on the seeds is higher where predators occur in highest concentrations. Smith (1970) described coevolutionary relationships

between pine squirrels and their coniferous food trees in the pacific northwest of North America. The relationships between red squirrel (*Tamiasciurus hudsonicus*) and lodgepole pine and between Douglas squirrel (*T. douglassii*) and Douglas-fir are interesting examples of coevolution (Smith, 1970). Trees defend squirrel predation in different ways, including producing cones that are difficult to reach or carry; investing seeds with a thick coat which is difficult to open; maturing fewer seeds in each cone; reducing the energy content of seed; periodic cone failure; and by early shedding of seeds from cones. Due to selection pressure from red squirrel populations the lodgepole pine developed a harder texture, thicker cone scales, and only one per cent of the weight of the cone in seeds. In response the red squirrel has developed stronger jaw musculature. Douglas-fir produces fewer seeds per cone and the Douglas squirrel has developed strong jaws but with a different skull configuration than red squirrel. The hard cones of lodgepole pine and fewer seeds in Douglas-fir cones increase the amount of work required to extract each seed. These adaptations have selected for squirrels with stronger jaws. Therefore, there is a marked coevolutionary influence of squirrel predation on reproductive characteristics of conifers. These defence systems in conifers have forced squirrels to coevolve the various ways to effectively get their food.

It is argued that the adaptations of mammalian herbivores evolved in response to plant adaptations that themselves evolved in response to insect herbivores. However, at the other extreme, in some communities the evolution of plants and mammals is more tightly coupled, and insects play a less significant role.

The coevolution of some plants and several species of herbivorous marsupials in Australia may have been chemically mediated (Mead *et al.*, 1985). Numerous species in the Fabaceae evolved fluoroacetate in response to herbivory by mammals. But the mammals counter adapted by evolving resistance to fluoroacetate. Presently, populations of kangaroos and bush rats, whose ranges include the fluoroacetate producing plants, are highly resistant to the compound. But the same species of bush rat and related species of kangaroos whose ranges do not encompass the plants are susceptible.

Changes in genotypic structure in rye grass (*Lolium perenne*) populations induced by grazing have been studied by Brougham and Harris (1967). They found major changes in population composition within 4 months of the application of differnetial grazing pressure. This situation has been suggested to arise automatically by the dominance

modification as a result of heterozygosity due to chromosomal translocation. The frequent spatial temporal heterogeneity in grass populations has been suggested to result from direct consequences of foraging and disturbance by animals (Pickett & White, 1985).

Plant-bird interactions

Competition for dispersal agents is another selective pressure. Plant species have evolved fruits that attract specialist frugivores. This requires production of nutritionally-rich fruits so that the frugivore may not have to turn to alternate food sources. Fruit ripening occurs at a time when only few other plants using the same frugivores as dispersal agents are producing fruits. Such plants produce large soft-coated seeds in nutritionally-rich fruits. Bird frugivores develop thin-walled, little-muscularized stomachs and an efficient means for regurgitation of seeds before they reach the intestine. The plant becomes an important part in the diet of the bird and the latter repeatedly visits the plant so that seeds are removed quickly after maturation and are not left to rot on the plant.

Marine plant-herbivore interactions

Herbivores have profound effect on seaweed communities of temperate and tropical marine systems. Hay and Fenical (1988) have discussed the potential of coevolutionary relationships in marine and terrestrial communities. In coastal communities, fishes and sea urchins are the primary herbivores and their life cycle patterns track those of the many seaweeds. This circumstance may promote greater coevolutionary instances in marine system as compared to the terrestrial communities where herbivores have shorter life histories than many of their food plants. However, due to differences in dispersal modes of common herbivores, chances of true coevolution between seaweeds and marine herbivores is unlikely (Lewis, 1986).

PLANTS AND POLLINATORS

It has been proposed that plants and nectarivorous animals have coevolved simultaneously due to adaptations in flowers that either attract specific pollinators or exclude other potential nectar thieves (Raven, 1972; Baker & Baker, 1975; Faegri & van der Pijl, 1979). Structural organization of flowers, the colour or aroma of flowers, the time of nectar production and quality and quantity of nectar produced determine the choice of a particular pollinator to harvest the nectar (Hainsworth & Wolf, 1979). This highly specialized

requirement leads to coevolution of flowers and pollinators. For example, hummingbirds visit plants with flowers that have bright colour, tubular corolla, little aroma, and that can be readily seen from above, all of which are visual clues (Raven, 1972; Faegri & van der Pijl, 1979). Interaction between plants and their pollinators is suggested to be a driving force in the evolution of angiospermic flowers (Bierzychudek, 1981).

Beetles and flies were first of the modern group of pollinators. However, the first pollinators were probably mandibulate insects that visited flowers to consume pollen, ovules, and other floral parts (Crepet, 1979). If some pollen transfer was accomplished incidentally during such activities, selection pressure would have favoured floral traits that enhanced pollen transfer and minimized damage to critical flower parts (Bertin, 1989). Selection would also have acted on plants visited by a variety of insects to favour traits encouraging visits by those taxa most effective in pollination and to discourage visits by the poorer pollinators.

Hymenoptera, the most important modern order of insect pollinators and Diptera appear in the fossil record in the Triassic. These orders as well as the beetles (Coleoptera) underwent major radiations during the Jurassic. The remaining important order of insect pollinators, the Lepidoptera, appeared and underwent a major radiation during the Cretaceous. Other pollinators, such as bats and birds were probably not important until much more recently. Crowding of cones to decrease access to herbivorous insects and fossilized plant parts showing insect damage suggest increasing insect visits to cycad cones in the Jurassic and Cretaceous. By the Cretaceous there existed bonafide angiosperms and their four major orders of insect pollinators (Bertin, 1989).

Angiosperms are much more successful than the gymnosperms because the closed carpel of angiosperms promote self-incompatibility, and pollen tube competition, both of which enhance offspring quality (Bertin, 1989). Regal (1976) suggested that animal pollination allows angiosperms to achieve a higher rate of outcrossing among widely dispersed individuals than does wind pollination found in gymnosperms. This permits angiosperms to be successful when growing at low densities. Animal pollination is more efficient because ,it also increases the likelihood of a pollen grain reaching a conspecific stigma, and is more likely to result in outcrossing.

Bertin (1989) and Grant and Grant (1965) give examples of the phlox family (Polemoniaceae) to illustrate the potential importance of pollination in the radiation of a particular angiosperm group. Here, bee-pollinated ancestors have given rise to species pollinated by beetles, hummingbirds, and several kinds of Lepidoptera and Diptera, as well as to autogamous species. Such evolutionary shifts have apparently taken place many times during the evolution of the family. Several species currently possess two or more races visited predominantly by different types of pollinators. This situation could be an early stage in the speciation process. Given adequate time and genetic isolation, complete reproductive isolation is produced by plants by making modifications which could accumulate in each race resulting in the flowers more suited to the local pollinators, and less likely to be visited by members of other pollinator groups (Bertin, 1989).

Orchids present cases of well developed plant-pollinator relationships. The relationship between the euglossine bee *Eulaema* and the orchid *Stanhopea* is noteworthy. Various species of orchids produce different fragrances which attract different species of euglossine bees. The differential placement of pollinaria on bees by the orchids and specific differences in fragrance precludes accidental interspecific pollination (Dressler, 1968).

Stiles (1975) has reported that 9 species of *Heliconia* in a Costa Rican area are visited by 9 species of hummingbirds which serve as pollinators in return for nectar. Five of the *Heliconia* species have long, curved corollas and are visited by hermit hummingbirds with long, curved bills. Species with short, straight corollas are visited by non-hermit hummingbirds having shorter, straight bills. The non-hermits hold territories about clumps of short-corolla *Heliconia* species which are able to supply birds their total energy requirement at the time of peak flowering. Hermits, which feed on long corolla-species with low rates of flowering and nectar production, on the other hand, seldom hold flowering-centered territories; their feeding strategy involves traplining (travelling different clumps of flowers along a definite route).

Figs and fig-wasps constitute an extremely interesting example of plant-pollinator coevolution. Fig-wasps are species specific. Many of the 800 fig species require specific pollinators. Within an individual fig plant the female phase may be separated from the male phase by more than four weeks. The pollinating wasps enter the syconium when it is in the female phase, deposit pollen, oviposit, and die. A new generation of wasps, which matures inside the syconium, collects pollen when exiting from the syconium which is now in the male phase, fly to another tree which is in the female phase, enter the syconium, deposit pollen and

oviposit (Wiebes, 1979). Figs thus have developed a high level of asynchronous blooming to which the life cycle of fig-wasps has adapted.

Pollinator-induced reproductive isolation has played a substantial role in generating the present diversity of angiosperms. In two interfertile species of *Ceracidium* (Fabaceae) hybrids are uncommon in nature, despite the physical proximity and flowering synchrony of individuals of the two species. Jones (1978) showed that bee pollinators rarely moved from one species to the other. This pollinator specificity seemed to result specially from the different ultraviolet floral patterns of the two species.

PLANT-ANT INTERACTIONS

Direct plant-ant interactions are probably mutualistic because of the dissimilarity of the two organisms. Since ants cannot digest cellulose, only very specialized ants (harvesters and leaf-cutters) can feed on plants. The mutualism must increase fitness, but many, such as extra-floral nectary-ant mutualisms, are not critical for plant or ant survival, nor do they seem likely to determine the distribution of pairs of species. Plants have evolved more than ants in response to ant-plant mutualism. In defence nectaries, myrmecochory, and any pollination, no change in any structure or behaviour has been demonstrated, while the nectary, elaiosome, perhaps floral structure, and numerous associated traits have evolved to fit the plant to interact with ants (Keeler, 1989).

However, ant-*Acacia* associations in Central America range from total independence to facultative dependence to total interdependence showing probably the stages in coevolution. Complete mutual interdependence is exhibited by *Acacia cornigera* and *Pseudomyrmex ferruginea*. These ants form the colony by boring a hole at the base of enlarged thorns and defend the plant against herbivorous insects. In turn, plant houses the ants and provides them food from nectaries at the base of leaves and beltian bodies at the tips of some leaves (Janzen, 1966). Coevolution has occurred such that *P. ferruginea* is active 24 hours a day, rather unusual among ants, providing round the clock protection to the plant, and *Acacia cornigera* has leaves throughout the year and provides continuous source of food for the ants. The other examples are *Barleria fistulosa* (plant) and *Tetraponera aethiops* (ant), *Leonardoxa africana* (plant) and *Detalomysmex phylax* (ant) interactions. Schemske (1983) demonstrated that multispecies (interspecific competition of ants) interactions have played major

role in the evolution of pairwise associations in ant-plant symbioses. Behavioral adaptations of ants and morphological preadaptation of plants were the selective traits for such coevolution.

HOST AND PARASITES

Host-parasite relationships have often been described as coevolved systems (Brooks, 1988). Host specificity and defense mechanism are the two determinants of this coevolved system. There are two theories to explain this relationship.

1. The parasite is associated with the host because its ancestors were also associated. This is termed association by descent.
2. The parasite evolves in association with one host species and later transfers to an another species. This is association by colonization.

It has been suggested that possibilities for associations by colonization, or departures from association by descent increase in direct proportion to the number of species that can serve as suitable hosts. A good example of coevolution between the nematode genus *Enterobius* and its primate hosts has been documented by Mitter and Brooks (1983) and Brooks and Glen (1982). Brooks (1988) has suggested that such coevolution must be based upon strong directional selection leading to speciation, otherwise a reversible process may occur. However, certain studies have reported very little or no congruence between host and parasite phylogenies for tapeworms occurring in seabirds and in carnivorous mammals.

Coevolution is a result of mutual adaptive responses of host and parasite leading to predictable coadapted trait complexes. Host defences and reciprocal adaptations in parasites result in fully congruent coevolved phylogenies of host and parasite. Brooks (1988) has described various methods for comparing host and parasite phylogenies. Consensus tree analysis and parsimony techniques have been suggested for identifying the linkages during coevolutionary processes.

The coevolution of suitable traits in hosts and parasites may sometimes occur quickly. European rabbit (*Oryctolagus cuniculus*) was introduced in Australia in 1859. By 1900, the rabbit population became a critical problem. A myxoma virus was introduced in 1950. The first epidemic of myxomatosis killed 99 per cent of the local rabbit population. During the second and third myxomatosis seasons (corresponding with the disease vector mosquitoes) only 90 per cent and 40-60 per cent of infected rabbits were killed (Fenner 1971). Presently myxoma virus has little effect on

rabbits. In the coevolutionary adjustment the rabbit population besides passive immunity to myxomatosis passed on to the offsprings by the immune females, developed a genetic strain which provided an intrinsic resistance to the disease. The virus in its turn evolved by mutation attenuated genetic strains replacing more virulent strains (Thompson, 1954). Thus the coevolution permits the rabbits infected by non-virulent strains to live longer and the virus to increase its total population in the ecosystem.

The exploitation of unmanageable food resource can also be achieved by the host with the aid of its parasites. Siricid woodwasps and their obligate fungal associates combine to kill or debilitate their common host trees. The larvae of these woodwasps obtain cellulases and xylanases by ingesting the host-cultured fungi, which the female woodwasp inoculates into the tree during oviposition (Madden & Coutts, 1979; Kukor & Martin, 1983). *Dacus oleae* has evolved to feed on olive fruit by acquiring a preadapted bacterial pathogen of olive trees. This inherited symbiont is established in the larval cecum, where it hydrolyses protein and synthesizes required amino acids (Hagen, 1966).

More than 400 totally achlorophyllous species of angiosperms are epiparasites through their mycorrhizal fungi. The fungal partners of such epiparasites accelerate the death of otherwise resistant trees and increase the nutrient gathering efficiency of plant-fungus association (Price *et al.*, 1986).

The genetic basis of coevolution in host-pathogen systems, has been discussed and summarized by Allard (1991). A gene-for-gene hypothesis was proposed for the close genetic interrelationship between hosts and parasites (Flor, 1956). This hypothesis states that for every gene controlling resistance in the host, there is a corresponding gene in parasite controlling pathogenicity. Thus coevolution of hosts and their pathogens can be understood in the context of integrated gene-for-gene host resistance-pathogen virulence systems (Allard, 1991).

The results of long term studies of coevolution in Barley (host) and *Rhynchosporium secalis* (pathogen) showed complementary genetic systems. There exists a gene-for-gene interaction among loci which affects many traits, leading to self-regulating adjustments over generations between host-pathogen populations. Different pathotypes differ widely in their ability to damage the host and different host resistance alleles differ widely in their ability to protect the host from the pathogen. In the

specific host population of barley, 29 resistance loci were identified. Among resistance loci, several played major roles in providing stable resistance, but many had detrimental effects on yield and reproductive ability of the host. The proportion of resistant alleles that protect against the most damaging pathotypes increased sharply in the host population. The host population adjusted genetically to pathogen in ways that minimised losses in reproductive capacity and yield, whereas the pathogen adjusted genetically to the host in ways that allowed it to survive on each host population.

AVIAN BROOD PARASITISM

This relationship represents an excellent example of coevolution. This is a social parasitism in which individuals of the parasite receive parental care from unrelated individuals of the host. The most prevalent examples are in birds and hymenopterans (Davies *et al*, 1989a, b; Rothstein, 1990). This parasitism reduces host reproductive output and results in selection of host defenses. The reciprocal relationships coevolved simultaneously in an arms race (Dawkins & Krebs, 1979). Intraspecific as well as interspecific parasitism occurs in birds. Intraspecific parasitism shows less prominent host defenses because the host and parasite are usually identical in appearance and behaviour. Examples of interspecific parasitism are more numerous (Lack, 1968; Rothstein, 1990). Eighty bird species, including two subfamilies of cuckoos (Cuculinae and Neomorphinae), two types of finches (*Anomalospiza imberbis*, the cuckoo-finch and whydans in the Viduinae), the honey guides (Indicatoridae), the cowbirds (Icterinae) and the black headed duck (*Heteronetta atricapilla*) are classic examples of interspecific parasitism. Brood parasitism occurs in 1 per cent of total bird species especially among passerines. Over 200 cuckoo species lay their eggs in the nests of birds belonging to different families. Their eggs are incubated and nestlings fed by the foster parents. Some species are strictly adapted to one type of host. Some of them are polymorphic in respect to their parasitism (Southern, 1954). In early times, development of parasitism was perhaps a common phenomenon in many birds, but in cuckoos, the transitional stages between parasite behaviour changed into complete dependence upon foster parents (Rothschild, 1965).

Social brood parasitism can be of mutual benefit to both the host and parasite. The giant cowbird (*Scaphidura oryzivora*) lays eggs in the nests of host oropendolas (*Zyrhynchus* sp.) and cacique (*Cacicus* sp.). A botfly that feeds by burrowing into the chick's

body causes substantial mortality to the host chicks. However, when nestlings of cowbird are present in the nest, they remove bots and eggs from nest mates and protect themselves by snapping at adult botflies. As a result a greater number of host offspring survives in cowbird parasitized nests compared to nonparasitized nests (Smith 1968).

Brown headed cowbirds (*Molothrus ater*) parasitize about 220 species, of which most are passerines. Fleischer (1985) has shown that female brown headed cowbirds parasitize more than one host species within few days. *Malothrus rufoaxillaris* (screaming cowbird) and all Viduinae species are highly specialized as they parasitize only one host species. Host defences include avoiding parasitism, foreign ' egg rejection, adaptations during the nestling stage, etc. Parasite counter defences include egg and nestling mimicry. Host and parasite incubation periods may become shorter in response to one another. It has been suggested that parasite host coevolution will become more refined as the parasite becomes more specialized on one to a few hosts as a result of different counter-defences needed for different hosts (Hamilton & Orians, 1965). Davies and Brooke (1989a, b) have indicated the likely sequence of events in coevolution of parasite—host relations: (a) The host has no egg rejection tactics before being parasitized, (b) With the start of parasitism, egg rejection starts as adaptive process, (c) When hosts start rejecting eggs, mimetic parasite eggs start evolving, (d) The host learns egg discrimination, (e) Heightened egg mimicry by the parasite results, and (f) Recognition errors may occur. The host, thus, undergoes directional selection with the parasite lagging just behind leading to a never ending race for stabilizing parallel egg polymorphism in parasites and hosts. Davies and Brooke (1989a, b) have suggested that parasitic egg mimicry spreads faster than host egg rejection. The adaptive significance of host rejection depends on the frequency of parasitism and parasite egg mimicry depends on the frequency of host rejection.

It has been suggested that mimicry of the cuckoo depends upon a genetic mechanism combined with an appropriate behaviour learnt in the nestling stage (Ford, 1971). Female European cuckoos have been subdivided into groups called 'genetes' (Newton, 1893), each laying a certain type of egg and parasitizing the host suited to it. The inheritance of egg colour is not maternal because necessary genes for egg colour are carried in the Y chromosome (Punnett, 1933). Birds are heterogametic in the female sex and therefore selection favours translocations of the requisite autosomal genes in the nonpairing region of Y. The general similarity between the colour pattern of cuckoo's eggs and those of its host is due to selection operating on the gene complex to adjust the effect of the controlling gene in Y (Ford, 1971). This selection pressure is powerful because the host species frequently destroy the parasitizing eggs and there is a need for accurate similarity between the two. For example, the Indian Koel, *Eudynamis scolopaceus* correctly mimics the eggs of crows (*Corvus splendens*) both in size and colour. The black headed offsprings are also similar to crow. But as the nestling stage is completed, the cuckoo moults and the head becomes brown.

PREY AND PREDATORS

Prey-predator systems are suggested to be coevolved systems (Dawkins & Krebs 1979; Schaffer & Rosenzweig, 1978). In predator-prey relationships the predator exerts selective pressure on prey which in turn develop more efficient defence mechanisms. Genetic changes in the prey feed back as a selection pressure on the predator for developing more effective mechanisms of prey exploitation until the demand is balanced against the supply. Some predators are highly specialized on fewer types of prey. By diversifying their strategies of predator avoidance over evolutionary time, prey species may reduce predation. The predator in response counteracts by various mechanisms in morphology, anatomy or behaviour to make best use of the prey. These adaptations may be sound, smell, colour, pattern, form, pasture, and/or movement.

An example of counter adaptation of prey to predators leading to a coevolutionary race was given by Dawkins and Krebs (1979) for foxes and rabbits. They have suggested that over the evolutionary time scale the fox evolved improved adaptations for catching rabbits, whereas rabbits improved adaptations for escaping foxes. Coevolution of predator and prey has been suggested as an example of an evolutionary arms-race. This arms-race has been described as a evolutionary escalation of ever more refined mutual counteradaptations. Co-evolution of prey and predators affects the population dynamics of the two species (Schaffer & Rosenzweig, 1978). According to Schaffer and Rosenzweig (1978), the two species evolve at the same rate which can be judged by their number; if one will become abundant, that will suffer from resource depletion. They concluded that predation results in the evolution by prey of features that reduces the absolute success of predators, and vice versa.

CONCLUSIONS

Ecosystems are characterised by a myriad of interdependent interactions among species and consortia of species, such as plant-herbivore, prey-predator, host-parasite, plant-pollinator, etc. These interactions have been established through, often long, coevolutionary processes.

Coevolution represents a range of situations from specific, reciprocal and sequential flux of genetic changes to simultaneous or to those separated widely in evolutionary time, but all leading to hereditable ecological adaptations among interacting populations. The coevolution of organisms and its process lead to well organised, functionally operating ecosystems. In coevolution, while the physical environment remains rather passive, the biotic environment plays an active role. Most of the coevolutionary relationships are based on interactions involving utilization of resources. Nevertheless, the influence of the physical environment cannot be ignored in maintaining the coevolved patterns. Profound changes in global climate have been predicted in view of the increasing atmospheric loading of greenhouse gases and ozone depletion. In such situations, if the responses of coevolving species are not similar then considerable disruption in ecological relationships will occur. Interactions may break and an entirely different gamut of interrelationships may result.

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