

Interspecific Interaction

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Organisms are not isolated, and to survive and reproduce most have evolved in ways that require them to use a combination of their own genetic information and that of other species. Hence, interspecific interactions, or interactions between individuals of different species, are one of the most important processes influencing the patterns of adaptation and variation of species.

Interspecific Interactions

Interspecific interactions, or interactions between individuals of different species, are one of the most important processes influencing the patterns of adaptation and variation of species. The history of evolution and biodiversity is basically a history of the evolution of interspecific interactions. Similarly to species, interactions also evolve and multiply; they are links between the histories of species, and mould their future evolution. Organisms are not isolated, and to survive and reproduce most have evolved in ways that require them to use a combination of their own genetic information and that of other species. However, not much is known about how genomes of separate species become intermeshed in the process of coevolution, or reciprocal evolutionary change through natural selection. The types of interaction are defined on the basis of whether the net effect or outcome of the interaction is an increase or decrease in fitness, or no effect (neutral) for each interacting species. Basically, two types of interactions can be considered: antagonistic and mutualistic. Other terms such as commensalism, neutralism and amensalism are common in the literature, but are beyond the scope of this article (Table 1).

Interspecific interactions are based on an entirely selfish cost–benefit system, which depends on the relative gain to loss in fitness produced by the interaction, so we should

Table 1 Differences among several types of interactions based on whether the outcome is an increase in fitness or beneficial (+), a decrease in fitness or harmful (–) or neutral (0) for each interacting species

Type of interaction	Effect on species 1	Effect on species 2
Antagonism	+	–
Competition	–	–
Mutualism	+	+
Commensalism ^a	+	0
Neutralism ^a	0	0
Amensalism ^a	0	–

^aNot within the scope of this text.

Introductory article

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expect a continuum from antagonism to mutualism. Also, interspecific interactions change in space and time. A species may be antagonistic in one stage of its life cycle, for example a caterpillar which is a herbivore, while the adult, a butterfly, is a potential mutualist when acting as pollinator. A population or species may be antagonistic in one portion of its distribution or habitat while another population of the same species may be mutualistic in another portion of its distribution. For example, the ant *Formica neorufibarbis gelida* (Wheeler) visits the flowers of three plant species, creating a very interesting system of mutualistic and antagonistic interactions: they pollinate the gynodioecious *Paronychia pulvinata* Gray (Caryophyllaceae), are herbivores of the gynodioecious *Eritrichum arentioides* (Chamisso) de Candolle (Boraginaceae) and appear to have little effect on the hermaphroditic *Oreoxis alpina* (Gray) C. & R. (Apiaceae).

Finally, a species does not interact solely with only one other species; thus interactions between species must be studied in this context. A species is immersed in an evolutionary unit of interaction, which is the group of species within which selection acting on one of the pairs of species significantly affects selection on the other species. The system between leaf-cutter ants, the plants they forage and the fungus they grow is a good example of a unit of interactions encompassing several species with interactions producing different outcomes. For example: (1) the ants and their basidiomycetes fungus form a mutualistic pair of species; (2) the ants and the plants are an antagonistic pair of species; (3) a microfungus (*Escovopsis* sp.) and the ants form an antagonistic interaction; and (4) a bacterium (*Streptomyces* sp.) that inhibits growth of the microfungus and increases basidiomycetes biomass mutualistic with the ants.

Antagonistic Interactions

In antagonistic interactions, the fitness of individuals of one of the interacting species increases whereas the fitness of individuals of other interacting species decreases as a result of the interaction. Antagonistic interactions occur

between species because living organisms are concentrated packages of energy and nutrients (i.e. trophic interactions) and because resources are limited (i.e. there is competition). Antagonistic interactions are usually defined as discrete categories: parasitism, herbivory, predation, competition, etc. Also, some of these categories have been used with different meanings, for example predation for grazing or herbivory. Even though these categories are no more discrete than other concepts, such as population or community, they provide a useful tool for comparative studies. However, certain evolutionary patterns may result from the ways organisms feed on other species, differing greatly in how they attack their victims, including whether they kill them, how long they remain to feed on a single victim before killing it or leaving it, and how many victims they feed upon during their lifetimes.

Three basic categories of antagonistic interactions can be considered: parasitism, grazing and predation. Parasites are organisms that live throughout a major period of their lives in or on a single host individual, deriving their food from the host and causing lowered survival or reproduction to the host. Grazers are organisms that feed on parts of several to many victims during their lifetime and cause some detrimental effects on fitness of their victims, excluding immediate death. Predators are organisms that feed on several to many individuals during their lifetime, quickly killing each individual on which they feed. The categories of parasitism, grazing and predation represent pure forms of the antagonistic interactions that occur between species at different trophic levels. An individual species may share characteristics of two or even all three of these categories, but developing concepts of the ideal forms of the categories of interaction can make clearer the evolutionary transitions among feeding modes. The lack of an absolute discrete boundary between parasitism and other kinds of interactions between victims and their enemies is a reminder that we should consider an evolutionary continuum between parasitism and predation.

The other antagonistic interaction, with totally different selection pressures, is competition. Competition can be defined as the use of one resource by an organism that thereby reduces the availability of the resource to others. Competition is considered to act in two ways: exploitation and interference. In exploitation competition, the individuals of one species consume a resource and make it unavailable to the poorer competitor; the competing individuals may never actually meet. In interference competition, the better competitor directly excludes the poorer competitor from access to the resource. Competition differs fundamentally in one critical aspect from the other kinds of interspecific interactions that can lead to coevolution: selection does not act on any competing species specifically to increase the likelihood that an individual will encounter a competitor. Selection acts on parasites, grazers and predators to increase their ability to

find suitable hosts, victims or prey; selection acts on mutualists to increase their probability of interaction. No comparable selection pressure generally holds competitors together. Once one of the species diverges from a competitor in its use of resources, the interaction ceases (or at least decreases) as a selection pressure on the species and there is probably little selection on the other species to diverge also. Therefore, coevolutionary divergence of competitors is probably much less common than divergence of only one of the competitors.

The differences in modes of feeding influence how organisms specialize on their victims, how victims defend themselves against enemies, and how coevolution proceeds between enemies and their victims. Basically, all organisms specialize; thus, parasites, grazers and predators specialize on their hosts, victims and prey. Specialization can be defined as a limitation in the number of other species with which a particular species interacts. An extreme specialist would be a species that relied upon only one species or a few closely related other species for survival or reproduction during a major part of its life cycle. Because the relationship between parasites and hosts is so intimate, the most common specialization of many taxa of parasites is on a single host species or on a few closely related host species. On the other hand, grazers and predators share two potential traits that separate them from parasites in the evolution of patterns of specialization: the potential to become channelled genetically over evolutionary time into requiring a mixed diet, and the potential for individuals to learn which hosts or prey to eat and which to avoid. By definition, neither of these traits influences the patterns of specialization in parasites.

Hosts, victims and prey defend themselves from parasites, grazers and predators. The evolution of defence will depend upon whether the enemy is a parasite, a grazer or a predator, and hosts, victims and prey should differ in their evolutionary responses to inevitable or unavoidable interactions with them. An inevitable interaction is one in which avoidance defences (e.g. camouflage) are ineffective at preventing attack by an enemy. Selection will continually act on parasites, grazers and predators to overcome avoidance defences and increase the probability of successful encounters with hosts, victims or prey. If the probability is high that a host, victim or prey individual will interact with an enemy during its life despite its avoidance mechanisms, then selection may act to favour other lines of defence specifically against inevitable interactions. In these situations selection can act in two ways: either by changing the outcome of the interaction or by decreasing the enemy's efficiency (e.g., physical and chemical defences). Selection to decrease the enemy's efficiency are considered primary evolutionary responses to parasites and secondarily to grazers with limited home ranges. In the case of predators and grazers with large home ranges, the adaptations in victims and prey are based on changing the mode of interaction. If the interaction has a high probability of

occurring during the lifetime of a victim or prey individuals, selection may act to transform a predatory interaction into essentially a grazing interaction. Interactions based on parasitism, grazing or predation may evolve through a change in outcome to interactions that are either commensalistic or even mutualistic. Many mutualisms have evolved in this manner.

Examples of Defence: Insects and Plants

Plants are the most obvious and readily available source of food in terrestrial communities; however, only a fraction of insect orders have adapted to feed on tissues of green plants. Phytophagous insects exploit plants in different ways: some feed externally by biting and chewing, or by sucking from individual cells or from the plant's vascular system; some species mine into their host; a few form galls; and yet others bore into seeds or exploit shed seeds. Phytophagous insects have to overcome the basic problems of desiccation and attachment, but they also have to confront the problems posed by food quality and the defences of plants.

The loss of tissue to consumers is a physiological cost to a plant. Plants are rooted and cannot move, so their defences have to operate at the site of attack. A variety of plant defences have evolved that enable plants to avoid or reduce herbivory and increase their fitness: (1) morphological structures, also known as physical defences (e.g. thick cuticle, trichomes, thorns and spines); (2) 'qualitative' (toxins, effective against specialists) and 'quantitative' (digestibility-reducing compounds, effective against generalists) chemical defences; and (3) the less well studied biotic defences.

Depending on the attacker, most plants use a variety of defences, which can vary in intensity and effectiveness, and can operate over different temporal and spatial scales. Many studies have proposed trade-offs between plant defences, that is a lack of redundancy of defences that act over the same temporal, spatial and/or herbivore scales. However, an absolute trade-off between defence systems is not always found.

The production and maintenance of defences when plants have limited amounts of resources is associated with a cost, which apart from being a function of the concentration of defence substances in leaf tissues will also depend on the turnover rate of these substances and on the relative overlap between resources used for production of defences and resources used for growth.

For example, a general model for allocation to different defences in interactions between ants and plants should take into account the relative effectiveness of each defence, since no single defence is likely to eliminate damage by all herbivores. In the association between the plant *Cecropia* spp. (Cecropiaceae) and its ant inhabitants (*Azteca* spp.),

the plant may use a variety of defensive strategies and adjust them as needed to the environmental conditions. Induced responses to herbivory (i.e. modifications to defensive strategies of plants triggered by changes in environmental cues) have been characterized extensively, and demonstrate that plant defences are very dynamic and create an unpredictable environment for herbivores, complicating their strategies. Most studies have not focused on the dynamic nature of defence in plants that harbour ants, in which many cues and signals controlled by the plant and the environment can enhance defence by influencing recruitment, patrolling, and persistence of ants. It has been shown that ants can select and prefer sugar solutions containing a complex mixture of amino acids over solutions only containing sugars. Moreover, in damaged plants, an increase in the amount and quality (sugar and amino acid concentration) of extrafloral nectar is induced by the damage, which in turn increases patrolling by defending ants (Figure 1). Also, ants prefer homopteran honeydew (Figure 2) rich in trisaccharides and with higher total sugar concentration, over disaccharides, monosaccharides or low total sugar concentration. Finally, the ants' dynamic responses to damage should be controlled by the plant in facultative interactions (mediated by extrafloral nectar) but be predominantly controlled by the ants in obligate interactions (mediated by food bodies and domatia), and, overall, they suggest that induced responses to herbivory are common in plants associated with ants (i.e. ant-plants).

Mutualistic Interactions

In mutualistic interactions, the Darwinian fitness of both (or all) interacting species is increased. However, benefits could be asymmetric, as one species may receive more benefits than the others. Although the participants in mutualisms vary greatly in the services or resources exchanged, or in specificity and degree of dependence, most can be categorized as hosts or visitors. In general, the majority of studies that have addressed mutualistic interactions prove benefits only for the best understood and/or easier to study partner: the host (e.g. plants), and tend to assume that a mutualistic interaction takes place. Mutualistic interactions are very common in nature and many have been described. However, the selective pressures, life-history traits and characteristics of communities that favour and maintain mutualistic interactions are not completely understood. Nevertheless, certain patterns and hypotheses suggest how different kinds of mutualism contribute to the interactive structure of communities and how these interactions are maintained over evolutionary time. There is a strong association between antagonistic and mutualistic interactions; thus, the richness of mutualisms in communities depends upon the

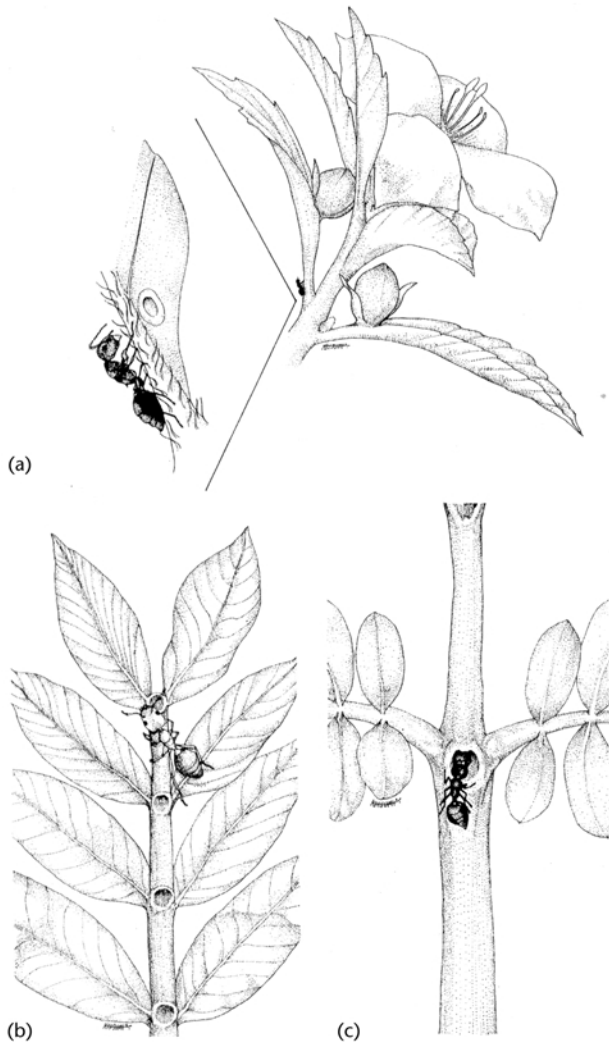


Figure 1 Ants foraging for nectar from extrafloral nectaries. (a) *Crematogaster brevispinosa* on *Turnera ulmifolia* (Turneraceae). (b) *Camponotus abdominalis* on *Inga vera* (Leguminosae). (c) *C. brevispinosa* on the leaf of a shrubby legume.

richness of antagonistic interactions. Some mutualisms evolved from an initial antagonistic interaction; or in many mutualistic interactions the basic unit of interaction are three species or groups of species, encompassing an antagonistic pair and a mutualistic pair of species. Other mutualistic interactions may have evolved because certain life-history traits and habitats may favour mutualistic interactions among potential mutualistic organisms.

The change in outcome from antagonism to mutualism is most likely in interactions that are inevitable within the lifetimes of individuals and may have their evolutionary origin in the defence reactions of species. If it is unlikely that individuals can avoid a specific antagonistic interaction, then selection will favour individuals that have traits



Figure 2 The ant *Camponotus sereceiventris* foraging for honeydew from a honeydew-producing membracid (Homoptera).

causing the interaction to have at less negative effect on them. An example is found in seed dispersal (**Figure 3**) and pollination.

Although some mutualisms involve mostly a change in an interaction between two species from antagonism to mutualism; other mutualisms are built on interactions involving at least an antagonistic pair of species and a

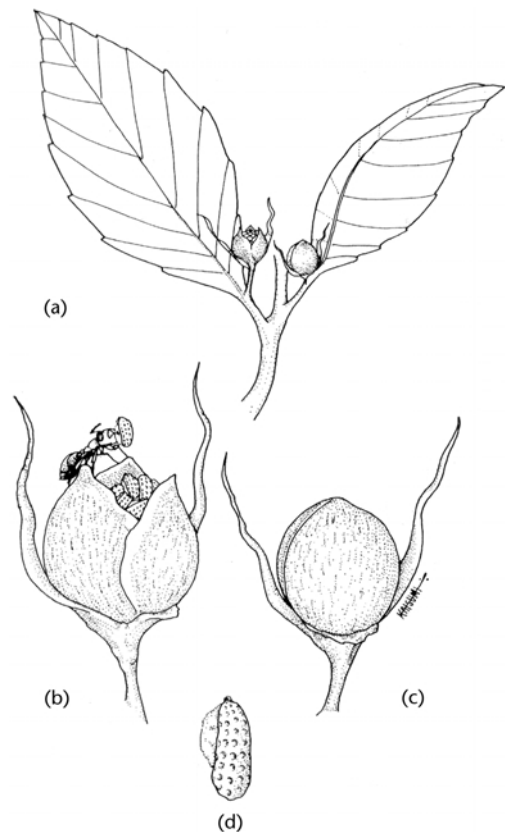


Figure 3 The ant *Crematogaster brevispinosa* removing seeds (b) from the fruits of *Turnera ulmifolia* (a, c). Note the fleshy aril on the seed (d), which acts as reward for the ant.

mutualistic pair of species. Most studies of mutualism consider directly the interaction between two species, yet the evolutionary unit of many mutualisms involves at least three species in a way that emphasizes the evolutionary relationships between antagonism and mutualism. This is the case for two broad classes of interactions between ants and plants: (1) direct interactions, where the plants provide an array of resources (e.g. food, domatia), and (2) indirect interactions, which are mediated by homopterans (sometimes lepidopteran caterpillars) that produce honeydew. In both types the ants, through their foraging and territorial defence, provide defence against herbivores or competitors (such as encroaching vines). The association between the ant and the plant is the mutualistic pair of species, and the association between the plant and the herbivore is the antagonistic pair of species.

Not all mutualisms have evolved from, or are related to, an antagonistic interaction. Some components of life histories predispose organisms to mutualistic interactions. In particular, organisms living in environments characterized by intermediate levels of disturbance and faced with intermediate survival abilities have a higher probability of evolving mutualisms with other organisms than organisms with very high or very low survival abilities in similar environments rich in biotic interactions. Under such conditions, small positive effects of a mutualist can increase survival or growth rates significantly. On a broad scale, some of the most obvious mutualisms in communities, including mutualisms between ants and plants, are associated with intermediate levels of disturbance. Light gaps in forests induce a high richness of biotic interactions through intense competition among plants and interactions between animals and plants. For example, in Costa Rica extrafloral nectaries, and hence associations between ants and plants, are more common along forest edges and in light gaps than in other forest sites. In Mexico there are more interactions between ants and plants in dry, open regions than in more enclosed, humid environments. Organisms living in environments characterized by low richness of antagonistic interactions but high levels of physical stress (e.g. habitats poor in nutrients) have a high probability of mutualistic encounters with other species because a small input by a potential mutualist can affect growth rates significantly.

Mutualism is also favoured by another group of conditions, which includes organisms with a high probability of encounter and very low pre-mutualism growth rates in environments that impose a high level of physical stress but lack the richness of antagonistic interactions that is the basis for selection in many other mutualisms. The mutualisms associated with this set of ecological conditions often involve nutrition of a host by a symbiont in environments poor in nutrients. In these environments, as in those characterized by intermediate disturbance regimes and species with intermediate survival ability, the small

inputs by a mutualist can potentially have major effects on fitness.

Probably the clearest examples of how environments that impose unusual physical stresses on organisms have favoured novel forms of interaction, including mutualism, involve the reversal of the usual trophic order of life. Insectivorous plants and plants fed by ants are the two major ways in which plants have evolved to gain nutrients directly and actively from animals, one in an antagonistic and the other in a mutualistic manner. The mutualistic subset of these reversed trophic interactions involves ants that live within or under a part of the plant that appears specialized for harbouring ants and absorbing nutrients from the ants' debris piles.

Ants are involved in many mutualistic interactions with plants. Studies of mutualism between ants and plants has played a major role in shaping our broad understanding of mutualism, by developing approaches to measure benefits, costs and net outcomes, and by explicit consideration of variability, and also afford an excellent opportunity for analysing the effects of both historical and ecological factors on the evolution of mutualisms. Moreover, the evolution of mutualisms is positively associated with the richness of social behaviour in species such as ants, so that mutualisms should be more common among the more social species within a taxon and the richness of social behaviours within a species may be partly an evolutionary result of mutualisms that allow species to spend less time foraging for food.

Seasonal and Geographic Variation in Interspecific Interactions

The distribution of species is far from even, creating a spatial mosaic of species richness. In general, the tropics contain more species than an equivalent area at higher latitudes, although exceptions are numerous when specific taxa are reviewed. Moreover, the study of the distribution of species, which has long been a central focus of ecology and biogeography, is taking on new urgency as evidence increases of the global crisis of biological diversity. The question of which geographic regions to protect in order to maintain the most biological diversity is central to the design of effective conservation programmes. Thus, areas particularly rich in species, rare species, threatened species, or species with some combination of these attributes (i.e. 'hot spots') are increasingly being delineated to set help priorities for conservation. However, the focus should not only be on the conservation of species but also on the conservation of their interactions, because the diversity of life has resulted from the diversification of both species and the interactions among them.

For example, the structure of ant communities and of interactions between ants and plants has been studied in a

variety of habitats, and it is clear that neither the spatial nor the temporal dimension can be ignored, because variation characterizes ant communities. Ant assemblages are very dynamic and extrapolating from one ant community to another of superficially similar characteristics can lead to erroneous inferences; thus, the spatial and temporal dimensions of community structure in ant communities and their interactions with plants preclude broad generalizations.

Not only are species unevenly distributed, but their interactions also vary spatially and seasonally; consequently, the use of a landscape approach to the study of interspecific interactions should increase considerably. Interactions vary in their probability of occurrence along environmental gradients (e.g. latitudinal or altitudinal) and under different disturbance regimes, they vary in their outcome under different ecological conditions or between habitats; and they vary between seasons. This spatial heterogeneity in interactions may be a major factor maintaining the diversity of species and their interactions over both small and large geographic regions, by reducing the chance that one species can push another to extinction. Moreover, this geographic mosaic of interactions between species may often influence the nature of the coevolutionary process and the evolution of interactions in general, as natural selection integrates geographic differ-

ences both in the species involved in an interaction and in the outcomes of an interaction.

Further Reading

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