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PARASITE MEDIATION IN ECOLOGICAL INTERACTIONS

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INTRODUCTION

The interaction between two populations, whether of the same or different species, can often be influenced by a third population of a separate species. For example, the outcome of competition between two species can be modified by a predator, parasite, or pathogen (57, 88, 105). Consider Figure 1. Competitor *A* affects competitor *B* via three routes. The direct effect ($-a$) is called *interference competition*, and the effect via impact on a common resource ($-g \times +j$) is called *resource competition*. The effect via a common

parasite or pathogen ($+c \times -f$) has no traditional name. Such indirect effects are always present in principle in multispecies systems (70), but we will speak of parasite mediation any time the influence via the third party is important relative to the direct effect or to the effect via a common resource.

By *parasites* we mean here species that draw their food resources from the live bodies of another species; in addition, we mean that much or all of the life of an individual parasite is spent in association with an individual host and that some damage is done to the host (94, 95). Under this definition, parasites include most insect herbivores and microbial pathogens, as well as ecto- and endo-parasites, as they are traditionally defined. Plainly, parasites involved in three-cornered interactions may have some net beneficial effects on one participant or the other. Traditional classifications of between-species interactions focus on the question of whether the net effects are deleterious or beneficial for the participants. When indirect effects are included, it is often unclear whether the net effect of an interaction is positive or negative. Thus, direct parasitic impact may actually result in a net commensal or even mutualistic relationship as a symbiosis evolves or as indirect effects develop. We enter into a cloudy zone of shifting signs of positive, negative, and zero net effects in interactions, but as far as possible we retain the standard names of interactions as they apply to the direct symbiont-host interaction.

Mediation via parasites has characteristics quite different from direct interaction, because the mediating agent is biological and literally has a life of its own. For example, shore birds that were hosts to bird malaria influenced

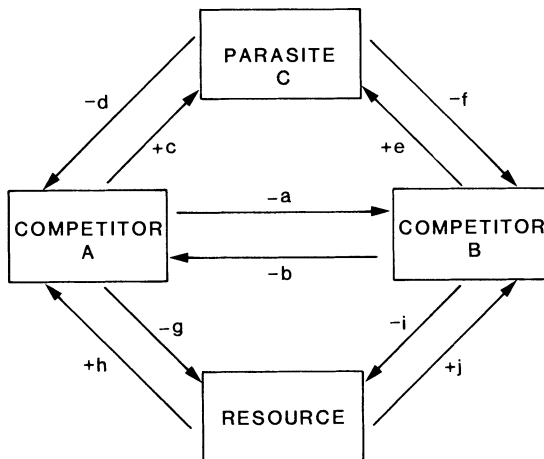


Figure 1 A three trophic level system showing interactions between elements. The effect of each interaction is indicated by + and - signs indicating positive or negative impact of one element on the other. Each interaction is lettered for easy reference from the text.

the survival and distribution of native birds in Hawaii well into the hinterland, when malaria was carried by a mosquito (116). The shore birds did not consume resources needed by the natives, nor did they overlap in distribution with the natives. The malaria had an effect at a distance from the shore birds, and the effect was amplified. The damage to the natives was far greater than the cost to the shore birds. Amplification and remote action can be far stronger through biological agents than through chemical interference or through resource consumption (see also 59).

It might be argued that such examples involving human intervention do not tell us anything about the importance of mediation by parasites in natural assemblages. We would not agree. We think the processes revealed by such examples are general but often are to be seen most clearly when human intervention has provided a natural experiment (see also 10). Besides, ecologists need to understand the dynamics of the new assemblages humans have created, not only of those assemblages that developed over evolutionary time before human influence on the natural world became ubiquitous.

Mediation by parasites is very common in nature and must be regarded as one of the major types of interaction in ecological systems, comparable in importance to direct competition, predation, parasitism, or mutualism. The bulk of this review seeks to convince the reader of its ubiquity by providing examples under various groupings. Mediation by parasites includes: (a) parasites as agents of interference when one species competes with another; (b) parasites as instruments of defense for a species against its enemies; (c) parasites assisting consumers in exploiting the species they eat.

Mediation of competition by parasites has been discussed in the literature using several different terms. Barbehenn (10) used the concepts of "germ warfare" and of parasites as potent weapons of defense in nature. Crosby (27 p. 52) spoke of the "biological allies" of Europeans in their invasion of the New World. Cornell (26, p. 881) mentioned "the host-parasite complex as a competitively superior unit," and Dixon (31) regarded parasites as the "invisible allies" of humans. "Biological warfare" (95, p. 172) "weapons of competition" (56, p. 45), "apparent competition" (57), and "agents of interference competition" (101, p. 43) are all terms associated with the same concept.

Authors who have emphasized that parasites can benefit a host also often suggest that such hosts are under natural selection to make use of the parasite. For example, in Figure 1, competitor *A* could be selected to actively encourage, culture, or accommodate its parasite *C*, provided the effect in reducing the competition *A* suffers from *B* is greater than the increase in direct impact of *C* on *A*; that is, provided the change in $\{+c \times -f \times [-b + (-i \times +h)]\}$ is greater than the change in $(+c \times -d)$. Some of the cases we discuss probably have been selected for in this sense, although there is little direct evidence on the selection pressures (but see 112). Other cases are clearly not at any sort of

evolutionary equilibrium and are fortuitous in nature. Near the end of this review we consider evolutionary aspects of mediation by parasites, but we do not attempt to assess the adaptiveness or otherwise for each example, partly because of the shortage of genetic evidence and partly because the effects are ecologically important whether or not they have equilibrated in an evolutionary sense.

PARASITE MEDIATION IN INTERACTIONS ON ONE TROPHIC LEVEL

At least three different effects of parasites can be distinguished. First, there are cases in which the parasites are endosymbionts of one of the species. In these instances it may be unclear whether it is even worthwhile to consider the parasite as a separate species in the interaction-web. Second, there are cases in which the parasites have been introduced recently to a part of the world beyond their previous distribution and have had marked effects on hosts that had not previously experienced them. They are evolutionary novelties. Sometimes the parasite has been accompanied to its new habitat by a host and/or a vector from its previous distribution. Third, there are the many cases in which two species have a parasite in common, but the parasite's impact on one of the species is much greater than on the other, so that the abundance or distribution of the two species relative to each other is critically affected by the presence of the parasite. In some of these cases the less-affected species may actually have been selected to accommodate the parasite, as a biological interference agent (10, 56, 95, 101). In others it seems fairly clear that both species have been selected to resist the parasite as much as has been possible for them, given the limitations of the biological machinery of resistance; but again resistance probably will not be equally developed.

Endosymbionts mediate many interactions in nature, and knowledge of their action should alter perspectives in ecological studies. *Paramecium* of the *P. aurelia* complex house *Caedobacter taeniospiralis* bacterial symbionts, some strains of which produce toxins (37). *Paramecium* housing such strains are known as "killers." The killer trait behaves as if it were a cytoplasmically inherited character. Killer strains of *Paramecium* can tolerate the toxins produced by their own *Caedobacter* but are killed by others. Nonkiller *Paramecium* are sensitive to any killer. In most cases the impact only comes about when the *Caedobacter* are transmitted by conjugation, so killer *Paramecium* can only kill others of a compatible mating strain. Of 14 species of the *P. aurelia* complex, however, 3 excrete a poison into the culture media. Several strains of the marine protozoan *Paraureonema acutum* also contain intracellular bacteria-like particles that are capable of killing or inhibiting the growth of other marine strains, particularly those of the related genus

Uronema (109). Killer phenotypes are known in other protozoa (54, 109) and fungi (20, 29), and strains of *Escherichia coli* producing bacteriocins have an equivalent ecological role (69).

Evolutionary novelties include the introduction of malaria to native birds of Hawaii already discussed. Another example concerns rinderpest in Africa, introduced in the late nineteenth century. The disease drastically affected African savannas, for almost all artiodactyls were susceptible to the disease, although differentially so. Buffalo, wildebeest, and cattle were most affected at first while zebra were always immune. Less virulent strains began to appear by 1925. Yearlings became the major susceptible class, and smaller ruminants with faster population turnover were thus impacted more severely. The last epidemic was in 1962–1963, but still the relative abundances of species are changing (43, 107, 108). In a similar vein, the soil-borne root pathogen *Phytophthora cinnamomi* has impacted *Eucalyptus* species extensively in Australia, and associated species have also changed in abundance and composition (42, 85, 130).

Introduced hosts have also carried parasites devastating to resident and novel hosts, for example, sturgeon, and brown and rainbow trout introductions (13, 55, 56). Conversely, introductions of potential hosts have been limited by diseases endemic in resident hosts. Examples of such interactions include cattle in Africa and the trypanosome-*Glossina* vector relationship (30, 43, 56), and domestic ducks in parts of North America affected by native waterfowl-protozoan-blackfly vector systems (22). Where landmasses converged through plate tectonics, patterns of extinction frequently are explained more parsimoniously by pathogen action in novel biotas than by competition or predation (9).

The outcome of competition is commonly affected by parasites in between-species interactions. Any time a parasite (or a predator) has a differential impact on two competitors, their relative competitive abilities logically may be affected (57–59, 88). European hares are excluded from some wooded areas occupied by rabbits because they are more susceptible to a stomach worm transmitted from the rabbits, the free-living larvae of which are restricted to woodlands (15). The rhesus monkey is not resistant to malaria and is restricted to regions where malaria is less abundant or to uplands within malaria-infested regions, while the crab-eating macaque, which is closely related but malaria-resistant, is found where the rhesus monkey is not (121). Cornell (26) proposed that gaps in the distribution of bird species may often be caused by the capacity of vectors to carry a parasite from a tolerant population to another population in which the parasite is pathogenic. The woodrat, *Neotoma cinerea*, is very susceptible to sylvatic plague *Yersinia pestis*. When a cave is cleared of *Neotoma* by a *Yersinia* outbreak, the less susceptible *Peromyscus maniculatus* often takes over the cave (83). Other

examples include the well-known cases of the meningeal worm (carried by white-tailed deer *Odocoileus virginiana*) which is highly pathogenic to other cervids (2, 56, 95), and the role of the sporozoan parasite *Adelina tribolii* in competition between *Tribolium castaneum* and *T. confusum* (89). While competition between *Tribolium* species is widely cited in the ecological literature, the role of *Adelina* has been commonly ignored; this is symptomatic of the general attitude towards parasite-mediated interaction.

Rice & Westoby (101) argued that the evolution of heteroecious rust fungi was bound up with competition between their two hosts. The smaller host species loses in competition with the larger host but is less impacted by the rust. The smaller host species also supports stages of the rust with short-range spores, so the competitively dominant species is most impacted close to the smaller host. Other fungi commonly influence competitive interactions between plants (16, 18), while viruses mediate the coexistence of bacteria such as *Escherichia coli* (68).

Local effects on plant distribution may be mediated by soil-dwelling organisms. Allelopathic effects of *Adenostoma fasciculatum* are most likely due to toxins produced by soil microbes that inhibit germination and the growth of herbaceous plants that are potential competitors (64; see also 62). An antibiotic factor produced by *Calluna vulgaris* roots may prevent colonization by birch through inhibition of its mycorrhizal fungi. The potential for complex interaction between plants is illustrated by Chiariello et al (23) who found an extensive but unpredictable transfer of phosphorus-32 between unrelated plants from a single plant source. Such transfer was probably mediated by vesicular-arbuscular mycorrhizae, and this suggests that a given fungus may act as a parasite on some plants and as a host for others.

When one population harbors a parasite, other populations of the same species are even more likely to be affected by it than are populations of other species. The effect is only worth considering as a three-party interaction when the two populations are differentially susceptible to the parasite. Given structured demes (126), differential susceptibility could well evolve and could be an important factor in selection between demes (41, 127, 128). Such interactions have been little studied in nature, but their far-reaching influences on human population interactions are compelling indicators of equivalent forces in nature. McNeill (79, 80) emphasized both the impact of "disease-experienced populations in densely inhabited civilized centers" on "disease-inexperienced peoples" in isolated communities and the devastating impact of epidemic diseases on naive populations when civilization expanded. This "epidemiological-sociological process" may well account for the small number of major civilizations developed in human history. Crosby (27) discussed many aspects of disease-mediated conquests of the New World by Old World populations. Such impact involves transport of diseases that were evolution-

ary novelties to the receiving populations and therefore devastating. The results of interdemetic competition would not have been so clear in the absence of disease.

PROTECTION BY PARASITES AGAINST ENEMIES

Protection against pathogenic parasites may be achieved primarily by preemption of resources by more benign species (3, 31, 75, 76). A fetus is largely uncolonized in the uterus, but colonization by cutaneous microbes is rapid in the birth canal and during contact with the mother. The process is complete in terms of species and population sizes by the ninth day after birth (3). Preemption of resources is so complete that even alternative strains of the same *Staphylococcus* species are usually not found in the nose of a neonate. Such preemption is widespread in human populations and in nature. Benign strains and species prevent infection by pathogenic organisms. If a benign strain of *Staphylococcus aureus* does not colonize a baby, then a virulent strain may well cause serious pathology. The normal microbial flora of the gastrointestinal tract of many vertebrates (ruminants are an obvious exception) are of little nutritional significance (72). Nonetheless, the normal flora can play a critical role in the protection of the host from more invasive microorganisms such as *Shigella*, by making it difficult for these pathogens to make attachment and acquire resources. The indiscriminate use of antibiotics for prophylactic purposes, far from protecting against infection by pathogens, suppresses the normal flora, thereby permitting the invasion of enteric pathogens, many of which have been previously selected for resistance to antibiotics.

The preceding examples illustrate direct, physical preemption of resources by benign parasites, which may protect a host against more pathogenic forms. In contrast to this "spatial" preemption, host immune responses provide a mechanism for "temporal" preemption. That is, the immune response triggered against a benign parasite may confer subsequent immunity to a related, more pathogenic parasite. For example, the very closely related spirochetes *Treponema pertenuis* and *T. pallidum* interact. *T. pertenuis* causes yaws, principally in children. It induces production of antibodies protective against other *T. pertenuis* strains and against *T. pallidum*, the etiological agent of syphilis (124). While yaws is an unpleasant disease, syphilis is probably worse because of its impact on the nervous system (82). As yaws is eradicated, the danger from syphilis increases (75). In a similar fashion, *T. pallidum* causes nonvenereal syphilis in children and so provides a degree of immunity to venereal syphilis when they become adults. When the childhood disease is common in primitive communities, venereal disease is rare; this suggests that human hygiene has actually created the epidemic disease of

venereal syphilis (125). Perhaps the most celebrated example of cross-immunity as a source of protection against more virulent pathogens is the use of the cowpox virus to provoke immunity to the smallpox virus, a process discovered in the late 1700s by Edward Jenner (99).

Other forms of protection are physical barriers or antibiotics generated by symbionts. Fungi associated with herbivorous larvae may produce a sheath that protects the larvae against parasitoids (12, 117). Bioluminescent bacteria housed in fish species such as the pony fish produce a visual barrier to predation by obscuring the animal's silhouette (53, 77). Some mycorrhizal fungi produce antibiotics (51). Bacteria carried by parasitic nematodes may mediate competition through production of antibiotics (90). Chestnut trees have virus-containing strains of the chestnut blight, *Endothia parasitica*, that are less virulent and can arrest the expansion of cankers caused by formerly prevalent, highly virulent strains. In Italy, *E. parasitica* has become noticeably less virulent over much of its range, without any genetic change in the host population. This loss of fungal virulence apparently results from viral transfer (and transformation) following anastomosis with hypovirulent strains (29). Antibiotics secreted from human sebaceous glands, active against some bacteria and fungi, are actually the product of gram-positive bacteria that live on the skin and use sebum as a substrate. Such antibiotics are important in preventing colonization by potentially pathogenic skin and respiratory tract microbes (72, 76).

PARASITES MEDIATING EXPLOITATION OF RESOURCES

Many plant parts, ingested by animals as dietary supplements, act as prophylactics or remedials for parasite infection (33). Wild chimpanzees pick and swallow, without chewing, the leaves of *Aspilia* spp. This unusual feeding behavior is probably associated with the potent antibiotic Thiarubrine A, contained in the leaves (102). "Worm seed," obtained from several *Chenopodium* species, has long been used by humans as an anthelmintic (e.g. 81), with a variety of *C. ambrosioides* sometimes designated as *anthelminticum*. The amount of *Chenopodium* in the diet was negatively related to pinworm infection of humans on the Colorado Plateau around 5,000 BC and it accounted for 72% of the variance (100).

A fascinating case of cultural evolution is the taboo against eating yams in West Africa (34, 35). The taboo lasts for several months, causing people with sickle-cell trait to express their innate resistance to infection by malaria during the infectious period. Subsequently, consumption of yams introduces thiocyanate into the blood which reduces sickling of erythrocytes. With such cultural regulation of a remedial, the impact of both sickle cell anemia and

malaria are reduced. Many other plants may play similar roles, for example, the fava bean (30).

Diet selection can be influenced strongly by parasites. Many insects have speciated onto new toxic plants that confer protection against enemies (14, 97). For example, parasitic nematodes may have selected for amanitin tolerance in mycetophagous *Drosophila* species because it confers resistance to nematode parasitism (61). Diet may often be restricted when such protective mechanisms are linked to particular plant species. In contrast, where ants form the protection against parasitic wasps, as with lycaenid butterflies (91), food plant use becomes idiosyncratic and opportunistic, and ants become essential cues in oviposition (5, 6).

Food is also made available to hosts by mutualists that are parasitic on the host's living resources. The exploitation of previously unmanageable resources is commonly achieved with the aid of parasites carried in specialized chambers such as the mycangium. Parasites make novel foods available to their host partners by: (a) enzymatic conversion of refractile compounds; (b) synthesis of absent or deficient compounds; (c) detoxification of interfering compounds; or (d) otherwise altering the phenotype of their host or their host's food so as to benefit the combined associates. Whether such symbionts occur as single species or in communities, they often provide their associate with more than one type of benefit.

Beetles and woodwasps carry fungi, parasitic on trees, that aid the insects in subduing their hosts and also provide nutritional benefits. The fungal associates of tree-killing bark beetles overcome localized host defenses and generally weaken a tree, predisposing it to subsequent attacks (123). Siricid woodwasps and their obligate fungal associates similarly combine to kill or debilitate their common soft and hardwood host trees (73). 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 (66). Homopterous insects such as leafhoppers and aphids commonly vector plant viruses and nematodes, and infected plant tissues benefit the herbivore (21, 74). Parasitic wasps also carry viruses important in suppressing the cellular encapsulation response of the insect host (36, 111). The olive fly, *Dacus oleae*, has evolved to feed on olive fruit by acquiring a preadapted bacterial pathogen of olive trees. This inherited symbiont becomes established in the larval caecum, where it hydrolyzes protein and synthesizes required amino acids (49). In addition to caecal digestion of seeds in heteromyid rodents, seed management in caches before ingestion maximizes the benefits of fungal growth on seeds (98).

Vascular plants parasitize other plants directly, by the formation of haustoria, or indirectly via mycorrhizal fungi. These haustoria are specialized plant structures that attach to and penetrate foreign plant tissues, forming a direct

vascular connection between host and parasite (65). Considerable circumstantial evidence suggests that these tumor-like structures may be caused by inherited endosymbionts (4, 7), quite possibly a bacterium carried by a fungus (P. R. Atsatt, unpublished data). In addition to these 3000-plus species of haustoria-forming parasites, more than 400 totally achlorophyllous species of angiosperms are epiparasites via their mycorrhizal fungi. Among angiosperms, epiparasites occur in the Burmaniaceae, Gentianaceae, Liliaceae, Orchidaceae, Polygalaceae, Pyrolaceae, and Triuridaceae (48), as well as in the pteridophyta (*Lycopodium*, *Ophioglossum*) and the liverwort *Cryptothalpus miraliths* (52). Like fungus-carrying bark beetles and siricid woodwasps, the fungal partners of such nonphotosynthetic epiparasites probably hasten the death of otherwise resistant trees, thereby increasing the nutrient-gathering efficiency of the plant-fungus association.

Extrachromosomal elements, including plasmids and certain viruses, are nearly ubiquitous in those bacterial species that have been carefully examined (25). While not necessarily of "foreign" origin, these elements appear to be genetic nomads, capable of being transmitted between individuals and species, often even between widely divergent species. Such elements are considered parasitic not only because of this transmissibility but also because they are often assumed (and occasionally demonstrated) to impose some "cost" on their host. Nonetheless, these elements may encode a variety of traits that benefit their bacterial host, at least under certain conditions, and which may permit bacteria to exploit resources they might otherwise be unable to use. For example, extrachromosomal elements are typically responsible for mechanisms of resistance to heavy metals and antibiotics. Such mechanisms enable bacteria to acquire resources in environments otherwise uninhabitable. In some cases, resistance encoded by an extrachromosomal element in one bacterial population can facilitate the coexistence of another bacterial population, which does not carry the extrachromosomal element, as an indirect consequence of the toxin's removal from the environment (S. Hattingh, R. Lenski, unpublished).

Extrachromosomal elements are also sometimes responsible for the pathogenicity of certain bacteria to their animal or plant hosts. For example, the diphtheria toxin is encoded by a virus integrated into the *Corynebacterium diphtheriae* genome, without which the bacterium is nonpathogenic (47). Similarly, in crown gall, the tumorigenic properties of *Agrobacterium tumefaciens* are dependent on the Ti plasmids. These plasmids force dicotyledonous plants to synthesize particular catabolites (the "opines") which the bacteria are able to degrade and use as their sole carbon, nitrogen, and energy source. This mechanism of "genetic colonization" (106) stably alters the host cells to provide a phenotype of selective advantage to the parasite (84). By complete analogy with crown gall tumorigenesis, Truchet et al (114) hypothesize that

nodule development in *Medicago sativa* is initiated by a segment of DNA from the *Rhizobium meliloti* plasmid. Indeed, *Rhizobium* plasmids can be transferred to *Agrobacterium*, enabling the recipients to nodulate clover plants; and reciprocally, transfer of the *Agrobacterium* Ti plasmid to *Rhizobium* produces tumorigenic rhizobia (86). It is now commonly held that *Agrobacterium* and *Rhizobium* are closely related and probably are congeneric (38). As in previous examples, the evolutionary outcome of these bacteria-host plant interactions depends upon the combined characteristics of three interacting genomes; i.e. crown gall is a debilitating disease of many dicotyledonous plants, while leguminous dicotyledons benefit measurably from interaction with closely related *Rhizobium* bacteria and their plasmids.

EVOLUTIONARY ASPECTS

Selection To Use a Parasite

It is a commonplace that strong selective pressures act on host-parasite interactions. Basically, hosts are selected to resist or tolerate the parasite, and parasites may be selected for reduced virulence if the benefits of lower virulence accrue to their offspring, which often is the case (78). Very substantial changes can come about quickly (40, 129). A pathogenic bacterium in *Amoeba proteus* evolved into a commensal and then a mutualist within five years (71). On the other hand populations that have not previously been exposed to a pathogen often are devastated, and this testifies to the strength of the evolutionary effects in populations that have been exposed. Major epidemics caused by human transport of pathogens novel to populations include bubonic plague, smallpox, syphilis, rinderpest, myxomatosis, dutch elm disease, and chestnut blight.

Only under special circumstances can a parasite persist over evolutionary time while remaining highly lethal to a host, and this too testifies to the strength of the selective pressures generated. Such a parasite must be very effectively transmitted so that its lineage persists even though the host dies quickly; most lethal diseases are vector-borne (39). Lethal parasites also usually have an alternate host in which they are not so lethal, with persistence more probable in the less susceptible host. Both these principles can be seen in the events that followed the introduction of myxoma virus to Australia. The virus quickly became less lethal, and the rabbits (*Oryctolagus cuniculus*) acquired some resistance. The pattern of interaction has not changed significantly in recent years, and the effectiveness of the virus is limited by the vectors (24, 40). Barbehenn (10) argued that had the original host (*Sylvilagus spp.*) been introduced with the virus, the evolutionary responses of virus and Australian rabbits would have been much slower and the longer term impact more severe.

Under certain circumstances it should therefore be possible for a host to be selected to "use" a parasite as an agent of interference against another host. The circumstances when this would be expected are specified in the introduction in relation to Figure 1, and the possibility is discussed in relation to certain examples in the body of this review (see also 112). Only for the endosymbiont systems described do we have both experimental evidence that the parasite is a net benefit to one of its hosts because of the impact on other hosts and genetic evidence about the natural selection involved. In the context of this possibility, it is important to distinguish between resistance, which acts by excluding the parasite, and tolerance, whereby the parasite does little damage to the host but survives and perhaps multiplies at the host's expense. Hosts that "use" a parasite must be selected to tolerate it rather than to exclude it.

Diversification and Speciation Mediated by Parasites

The possibility has already been mentioned that allopatric geographical distribution of closely related species may well result from the action of shared parasites rather than from resource or interference competition. Coexisting species would be selected to tolerate each other's parasites or to avoid them by using different microhabitats (95). Studies on the determinants of species diversity have found relatively little evidence for the importance of resource or interference competition, but a strong correlation with physical structuring of the habitat (119, 120). This suggests perhaps that much niche diversification occurs in relation to enemy-free space (63).

By closely associating with a parasite, many species have been able to acquire new biochemical capabilities. The result is an ability to exploit a new kind of resource (49, 103, 104), with the subsequent potential for adaptive radiation of that lineage (95). Many such radiations have involved acquisition of species that become mutualists: wood wasps, ambrosia and bark beetles, cecidomyiid flies, tephritid flies, blood and keratin feeding parasites, termites, parasitoids, attine ants, figs and fig wasps, and many others (96). It is clear that in many herbivore species, their mutualists do differ and were probably very important in speciation and radiation (11).

Reproductive isolation between host populations has resulted from incompatibility between symbionts (32) and may be common in nature (19). Reproductive isolation may also result from pathogens so debilitating to males that parthenogenetic sibling species evolve, as in the web spinner, *Haploembia solieri* (122). Steiner (110) has suggested that sympatric speciation can occur in vectors of pathogens through the action of the pathogen. Disruptive selection may result in vector species that are parasite compatible, parasite sensitive, or parasite resistant. Malaria may be implicated in a similar way in the speciation and allopatric distribution of macaque monkeys (121), just as

pathogens select for divergence of phenology or geographic separation among plants (16). The process of parasite-mediated reproductive isolation between host populations involves both coevolution and cospeciation (113).

Parallel evolution of related hosts, or coevolution through exchanges of resistance genes, may be forced by common parasites in such a way that patterns of resistance and susceptibility correspond on geographical gradients in some relationships (17, 87). For example, the wild oat species *Avena barbata*, *A. fatua*, and *A. ludoviciana* vary together in reactions to the parasite *Puccinia coronata*. In New South Wales, Australia, northern populations are more resistant to the disease, and more variation in disease resistance exists than in southern populations (17).

Many aspects of social organization within populations may also be affected by differential impact of parasites. It has been argued that pair bonding and mate selection (44, 50), choice and tenure of new sites, stability and size of social groups, and acceptance of new group members (44–46) have all been under natural selection principally to minimize parasite impact.

Metabolic and Genetic Integration with Parasites

Ecology has had a research program which we call the “interaction web” program. Communities are conceived as assemblages of species populations, many of which interact with each other. If we could achieve a sufficient understanding of the dynamics of each species population, each pairwise interaction, and the more extensive relationships as they are influenced by the complete web of interactions, we would have understood the ecosystem.

One of the points we emphasize here is that many interactions that appear to be between two species actually involve a third. Unless this is recognized, models will either fail to match field reality or will match it spuriously. It is important to consider the web within which any particular pairwise interaction is embedded and shaped by evolution. Thompson (112) referred to these species complexes as “the evolutionary unit of interaction.” The metabolic and genetic intimacy of hosts and parasites raises problems with which the interaction-web program has yet to deal. When we come to species that are obligate associates of other species, or to microorganisms, it is hard to define what is a node in the interaction-web. This means that ecologists will no longer be able to take it as self-evident that the nodes in the interaction-web are species populations. Groups of species (or cytoplasmic components) will have to be treated as a node when in practice they have very strong interdependence and behave as a unit with respect to biota outside the group. Such groups could include quite large numbers of species populations. Researchers are beginning to develop methods for investigating objectively the compartmental structure of webs (8, 92). The web descriptions to which these methods have been applied so far are not thorough in their coverage of

parasites, so we do not yet know whether these objective methods will allow further progress on the interaction-web program.

The genetic intimacy of intracellular parasites with their hosts may also have consequences for how the structure of interaction webs develops over evolutionary time. Parasites do move between host lineages on occasion, and because of their close contact with host genomes, it is possible that they may occasionally move genetic material between hosts. Arthropods act as vectors of diseases between plant species or animal species; parasites have complex life cycles passing between trophic levels; fungi connect unrelated plants, and bacteria digest plant material, acting as mutualists with herbivores. In such an environment, the possibilities for transfer of genetic material via plasmids, viruses, and other forms span the entire assemblage of organisms in communities and ecosystems. Proponents of this possibility have speculated for many years that much of macroevolution needs to be understood in terms of gene transfer. For example, Anderson (1) argued that "viral translocation is a key mechanism for transporting segments of DNA across species and phylum barriers, and that evolution depends largely on this transfer." As Anderson put it "the evolution of one organism depends on contributions and new ideas from all." Pirozynski & Malloch (93) hypothesize that terrestrial plants are the product of an ancient and continuing symbiosis of semiaquatic green algae and an aquatic fungus. Lamboy (67) suggests that many angiosperm traits may have resulted from fungus-to-host horizontal gene transfer, and similarly, Atsatt (4, 7) argues that the haustorial apparatus of parasitic plants is encoded by genes from microbial pathogens. Teratomas that could result in macroevolution have been implicated in plant evolution for many years (115).

This is a topic where previously untestable speculations are rapidly being tested by molecular evidence. Gene transfer has been demonstrated among prokaryotes; from prokaryotes to eukaryotes in the case of crown gall, and perhaps *Progenitor cryptocides* in some human tumors; and from eukaryotes to prokaryotes (60, 77). A significant proportion of the mouse genome is of viral origin (28). One possible mechanism for acquisition of complex adaptations for dealing with the highly toxic canavanine in legume seeds by a bruchid weevil may involve gene transfer from plant to weevil, or from adapted microorganisms (103). It remains to be seen how important gene transfer between lineages has been in macroevolution.

CONCLUSIONS

The bacteria, fungi, protozoa, and small primitive metazoans all have phylogenetic histories several orders of magnitude longer than the larger organisms from which we tend to develop concepts in ecology. As larger metazoans and plants developed, new substrates for microbial activity

opened, providing in turn new adaptive pathways for radiation onto metazoans and plants. With this perspective, we should expect the ubiquitous interactions between large and small organisms. These interactions have been widely recognized as essential elements of ecosystem function in the cases of nitrogen fixation, and carbon and nutrient cycling through digestion, decomposition, and mycorrhiza. We now argue that parasites affect ecosystem function as profoundly as any other elements in the system. The interactions they mediate are as abundant, complex, subtle, and important as any others.

This review has attempted to categorize an enormous but, until now, unsynthesized literature on such interactions, although our perceptions can be only of a tip of the iceberg awaiting discovery. Parasite-mediated interactions are due much more attention in ecological and evolutionary studies. Experiments with antibiotics, fungicides, and anthelmintics should become routine parts of ecological investigations, as routine as competitor removal and predator exclusion.

The evidence suggests that parasites may modify the ecology and evolution of every kind of interaction, from the evolution of molecules such as hemoglobin and immunoglobulins to the evolution and extinction of biota on a global scale. Wells (118) may be right in anticipating that interplanetary clashes between civilized beings will be decided by differential pathogenicity of parasites.

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