

Biodiversity and evolution in host–parasite associations

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Evolutionary relationships in heterospecific associations (parasitoidism, parasitism, commensalism and mutualism) are analysed through a game theory model defined in terms of fitness of hosts and parasites. In front of the game solutions (i.e. ESS) which present a great diversity of evolutionary patterns, we envisage co-evolution between hosts and parasites through the evolution of its two fundamental parameters (i.e. host's resistance and parasite's virulence). We then discuss the reciprocal influence of hosts and parasites on their respective biodiversity.

Keywords: parasitism; evolution; biodiversity.

Introduction

Even though our knowledge of biological diversity is still limited, biologists agree that parasites represent a large proportion of known species.

Parasites exploit a living and therefore temporary habitat. This necessitates that they encounter compatible hosts which will assure their persistence from one generation to the next. The evolution of parasite genomes depends to a large extent on the environment(s) of their host(s) (Renaud *et al.*, 1992). While it is the biological characteristics of host populations that define the parameters essential for parasite ecological niches, parasite populations can, in turn, impose constraints on their living biotopes (hosts).

Thus, parasitism is of particular interest, since the evolution of parasites and their hosts may be linked, each partner in a host–parasite association potentially exerting a selective pressure on the other. Reciprocal selection is, of course, also to be found in other heterospecific interactions such as between mutualists.

We have two main aims. First, we present the range of possible forms of host–parasite association, following an evolutionary model based on the relative costs-and-benefits of different systems, and proposed by Renaud and De Meeüs (1991). Second, we consider

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this model in the analysis and discussion of the characteristics of evolution in heterospecific associations. We then analyse the reciprocal influence of hosts and parasites on their respective diversity. We stress throughout the relevance of our findings with the help of different biological models.

Diversity in heterospecific associations

In order to envisage the different types of relationship between the heterospecific partners we have used the widely accepted definition proposed by Price (1977); 'an organism in or on another living organism obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modification, and causing some degree of real damage to its host.'

Thus, in this paper, we will consider parasitism in terms of potential damage caused to the host. In order to analyse the diversity of heterospecific interactions, however, we must consider parasitism in the framework of evolutionary biology. The damage caused to the host, as defined by Price (1977), alters the fitness of the host. In this context, Renaud and De Meeüs (1991), using the game theory, have proposed a simple cost/benefit model to investigate which kinds of interaction can lead to an ESS (evolutionary stable strategy) (Maynard-Smith and Price, 1973). The game consists of two symmetrical strategies (aggressive versus non-aggressive), and two players (parasites and hosts), each of which use one strategy during a confrontation. This game is known as 'The Killer and the Diplomat' and is summarized in Table 1.

Depending on the balance between costs (i.e. (R_h, V_p) versus (G_h, G_p) , Table 1), two ESSs can exist. One, (Killer/Killer), based on conflict, is always evolutionarily stable whatever the relationships between parameters. The other (Diplomat/Diplomat), based on compromise, constitutes an ESS if $R_h > G_h$ and $V_p > G_p$. These two ESSs can

Table 1. Utility functions of the two players in terms of fitness (W)

Parasite		
Host	Killer	Diplomat
Killer	$W_h = P_h(W_{hmax} - R_h)$ $W_p = P_p(W_{pmax} - V_p)$	$W_h = W_{hmax} - R_h$ $W_p = 0$
Diplomat	$W_h = 0$ $W_p = W_{pmax} - V_p$	$W_h = W_{hmax} - G_h$ $W_p = W_{pmax} - G_p$

Killer and Diplomat are the two game strategies of both host and parasite.

W_h and W_p are expected fitness in the different types of confrontation for host and parasite respectively.

W_{hmax} and W_{pmax} are the maximum fitness that individuals can obtain.

P_h and $P_p (= 1 - P_h)$ represent the chances of winning for the host and the parasite respectively.

R_h is the selective cost of evolving resistance genes.

V_p is the cost of virulence, corresponding to a reduction in parasite fitness as a result of premature host death and/or the cost of avoidance mechanisms needed to escape increasing host resistance.

G is the 'gift' to partner, corresponding to the energy given by the host to the parasite (G_h) or to available energy not exploited by the parasite and left to the host (G_p).

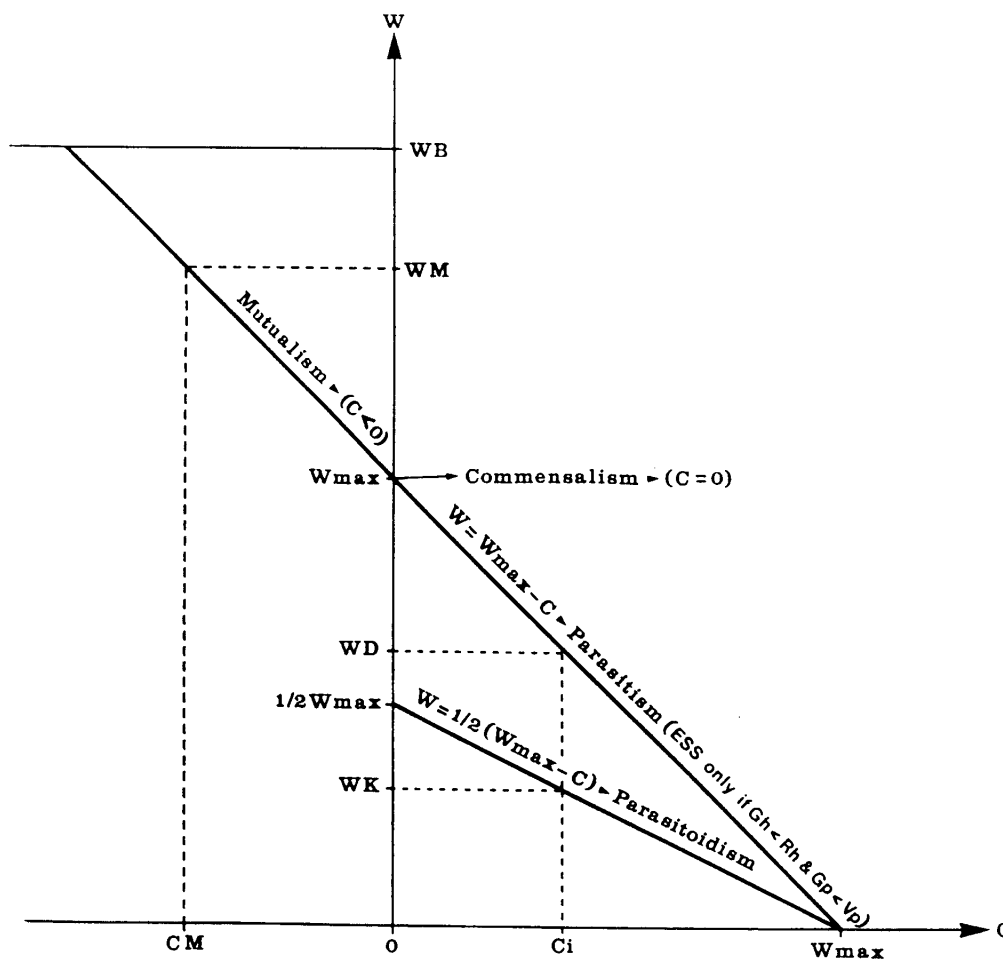


Figure 1. Graphic representation of the relations between costs (C) and fitnesses (W) of hosts or parasites for systems at the ESS. Classification of the types of relations are from Renaud and De Meeüs (1991). For the same cost C_i , the fitness of a Killer (W_K) is always smaller than that of a diplomat (W_D). The fitness $W_M > W_{max}$ can be envisaged only in the case of mutualism. It is noted that mutualism represents a particularly effective Diplomat–Diplomat relationship. W_B = maximum biotic capacity of the system in question.

respectively correspond to the models of ‘mutual aggression’ and ‘prudent parasitism’ proposed, but not formalized, by Holmes (1983), and thus represent the overall diversity of interactions existing in the world of heterospecific associations (Fig. 1). Figure 1, which represents the relationships between cost and fitness, suggests that evolution towards a lesser virulence is possible only in the case of parasitism (versus parasitoidism). Thus, mutualism can evolve only from parasitic-type relationships. To the best of our knowledge the only case of mutualism which seems to have evolved from a form of parasitoidism is that of fig wasps (e.g. Kjellberg *et al.*, 1987).

Evolution of resistance/virulence and co-evolution

According to the costs and benefits inside these systems, we should now consider the evolution of resistance and virulence in heterospecific interactions depending on the situation encountered. It might appear that over a period of time parasites should evolve towards a lesser virulence, but the generalization of this point of view remains controversial (May and Anderson, 1983; Toft and Aeschlimann, 1991). There are two basic paradigms concerning the co-evolution of the hosts and their parasites (Levin and Lenski, 1985). According to the conflict paradigm, selection favours evolutionary arm races between hosts and parasites (van Valen, 1973, Dawkins and Krebs, 1979), while according to the compromise paradigm, selection favours evolution of host's tolerance and parasite's avirulence (Burnet and White, 1972).

The best example of the evolution towards reduced virulence is the interaction between the myxomatosis virus rabbit interaction (Fenner and Ratcliffe, 1965; Ross, 1982; Dwyer *et al.*, 1990). In this instance we know the relationship between parasite and host at the beginning of the confrontation. The myxomatosis virus was extremely virulent to rabbit populations when first introduced into Australia (1950), France (1953) and the UK (1953); the evolution of virulence has been monitored in these three geographical areas for several decades (Ross, 1982). Microbiologists have carried out tests on inbred strains of laboratory rabbits to characterize the virulence of the parasite, and at the same time tested the susceptibility of wild rabbits by infecting them with laboratory strains of the virus (Fenner and Ratcliffe, 1965). A decrease in the degree of parasite virulence was observed, with a simultaneous increase in host resistance. This evolution towards lesser virulence could be explained by the transmission and dispersion of the parasite in the host population via a biting insect vector (i.e. mosquito or flea). The more virulent the strain, the quicker the death of the host, and therefore the less the likelihood of an encounter with the vector. This would result in a lower transmission rate of virulent strains (cost of virulence), and therefore the higher fitness of less virulent strains.

This type of evolution can also reflect the constraints of the environment and the evolutionary history of the interaction. Bouma and Lenski (1988) have shown that a bacterial plasmid can pass from the parasite state, costly for the host cell in the absence of an antibiotic, to a mutualist state, beneficial for the host cell in the presence of the molecule. It is thus remarkable to observe that mutualism persists if one suppresses, after 500 generations of interaction between virus and bacteria, the selective constraint contributed by the antibiotic.

The biology of certain parasites necessitates, however, a high cost inflicted on the host. This is particularly true for trematodes (helminths), which castrate the first intermediate host mollusc. Michalakis *et al.*, (1991) propose that a pleiotropic parasitic effect could reduce the costs on the host population. Indeed, if the parasite increases initially the survival or fecundity of the host, and afterwards diminishes them, then it acts in way similar to that of a senescent gene (according to the definition of Williams (1957). For example, the trematode *Schistosoma mansoni* castrates its host mollusc 4–6 weeks after infestation (Etges and Gresso, 1965). Thornill *et al.* (1986) studied the number of eggs emitted by these infected molluscs during the first 35 days following infestation. Uninfected molluscs, of the same age, and reared in the same conditions, emitted significantly fewer eggs than parasitized molluscs 16 and 28 days after infestation. Thereafter, parasitized molluscs produced fewer and fewer eggs, and eventually became

completely sterile. Minchella and Loverde (1981) came to the same conclusions in a similar experiment.

In host–insect parasitoid interactions the host invariably dies before reproducing as a consequence of the parasitoid lifecycle. In this type of interaction, the host population may ‘fight’ against that of the parasite by evolving mechanisms of resistance. The parasite population can, in its turn, circumvent this resistance through mechanisms of increased virulence (Rosenzweig, 1973). The outcome is a situation where each genetic system of resistance in the host corresponds to one genetic system of virulence in the parasite (similar to the concept of ‘gene for gene’ interactions (Flor, 1955, 1971; Mode, 1958; Person, 1966). This situation is found in plant fungal parasites (Mode, 1958; Person, 1966; Flor, 1971; Barrett 1983), phytophagous insects (Panda, 1979; Kaneda and Kisomoto, 1979), and parasitoid insects (Price, 1980). For example, Carton (1984) experimentally analysed the levels of interactions of host–parasitoid systems and showed that associations that have interacted for the greatest period of time are the most co-adapted.

Other co-evolutionary strategies can be cited. Hochberg *et al.* (1992), for example, suggest that where there is increasing virulence of the parasite, the host can evolve resistance by decreasing its generation time, and thus its size. They conclude that in order to have a long pre-reproductive period, the host needs to develop other resistance mechanisms to cope with the invasion and internal proliferation of virulent parasites.

The evolution of cost/benefit relationships has been investigated in two biological models, one in a bacterium–virus interaction, and the other in a fig wasp–nematode interaction. Bull *et al.* (1991) were the first rigorously to test the evolution of cost/benefit interactions by infesting *Escherichia coli* with a bacterial virus. When the virus was permitted to infect only the offspring of those it had already infected, it rapidly evolved towards a lesser pathogenicity by producing fewer toxins. By contrast, if the same virus had the opportunity to infest new bacteria, it once again became pathogenic. It would appear that it is the alternation of vertical (to the offspring of its host) and horizontal transmission (to new hosts) which defines the level of aggression. This was also found in fig wasp parasitic nematodes (Herre, 1993). Parasite species attacking solitary female wasp species and their descendants reduce the fitness of their hosts significantly less than those wasp species where the females are gregarious.

In terms of adaptive strategies, there is thus a great diversity of evolutionary patterns found in heterospecific associations, and it is hence interesting to explore further the biodiversities that both parasites and hosts can generate.

Hosts, source of parasite diversity

Pronounced co-adaptation is a logical consequence of strong interactions (i.e. parasitoidism, mutualism), since the host and the ‘parasite’ are, by definition, among the principal selective pressures of the system. In the case of obligate mutualism, the survival of one individual depends necessarily on the survival of others, whereas, with parasitoidism, the death of one is a consequence of the survival of the other.

It is difficult to imagine the occurrence of plurispecific systems in mutualisms, and there is, as far as we know, a low diversity of host symbiont in these associations. For example, each of the 750 known species of fig depends on only one specific species of mutualist wasp (Kjellberg *et al.*, 1987). This also holds for parasitoidism, where the demography and evolution of the host can be considerably affected by the presence of a parasitoid. As

reported by May and Hassell (1981), the density of a host population always decreases when the number of parasitoid species increases. Tallamy (1983) demonstrated a strong limitation on the number of parasitoid species which can be established in a host population. May (1982) made the point that the diversity of parasite species in host populations is generally higher than that of parasitoids. However, things might change in cases of protection of hosts due to the existence of refuges and/or to the heterogeneity of the environment (Hochberg and Hawkins, 1993). Interestingly, these authors showed that the parasitoid species richness tends to be dome-shaped as a function of host accessibility, with maximums observed for intermediate values. Consequently, it may be considered that parasitoid species richness is negatively correlated with the direct impact displayed by parasitoids on the population of their hosts.

Thus, in the case of true parasites (as opposed to castrators, parasitoids and mutualists), where the selection pressure on the host is weaker, parasite diversity obtains greater levels. The literature on this subject is vast, and we restrict ourselves to the presentation of only a few relevant examples. In studying metazoan parasites, Renaud *et al.* (1980) documented the co-existence of at least 14 species of parasites belonging to very different zoological groups for a population of a small teleost fish in the Gulf-of-Lions (France, Fig. 2). Birgi and Lambert (1987) reported the presence of seven congeneric species of gill parasites belonging to the genus *Dactylogyrus* (helminths) of a *Barbus* (teleost fish) of South Cameroon. As far as birds are concerned, the species *Ibis falcinellus* harbours seven species of specific mallophagous insects (Dogiel, 1964). In humans, at least 21 host-specific species of parasites, belonging to very diverse zoological groups, are known.

In conclusion, the example of trematodes, castrators of their first intermediate host, and often commensal (Bartoli, 1987) in the digestive tube of their definitive host, illustrates the possibility of a negative correlation between the degree of interaction (more or less strong) and parasite richness per host species. For example, three sibling species of *Helicometra* are found in the lagoon Etang-de-Thau (France). All are specific, and only attack one mollusc species (Trochidae), but all three can be found in the intestine of *Gobius niger* (a teleost fish) (Reversat *et al.*, (1991).

Parasites as sources of host diversity

Parasites have been directly or indirectly involved in (i) the geographical limitation of host communities, (ii) the regulation of densities and dynamics of host populations, (iii) the outcome of competition between their host and other organisms, (iv) the maintenance of genetic host polymorphisms, and (v) the evolution of sexual reproduction (Hamilton and Zuk, 1982; Rice, 1983; Seger and Hamilton, 1988; Toft, 1991). Here we illustrate the role that parasites may play in the evolution and maintenance of biological diversity.

The theoretical role of parasites in the coexistence of different host species has been established (Holt and Pickering, 1985). Some experimental studies support this theory. Boulétreau *et al.* (1991) have shown that the presence of a parasite seems to alter the competitive outcome between two species of *Drosophila*. *Drosophila melanogaster* and *D. simulans* compete for their resource (Opuntia fruits), and co-exist in different biotopes where they are subjected to parasitism by the Cypinid wasp *Leptopilina boulardi*. *D. melanogaster*, however, is far more susceptible to the parasite than is *D. simulans*, and the number of adults emerging is negatively correlated with the degree of parasite prevalence. In the field, *D. simulans* shows higher frequencies than *D. melanogaster*. Furthermore,

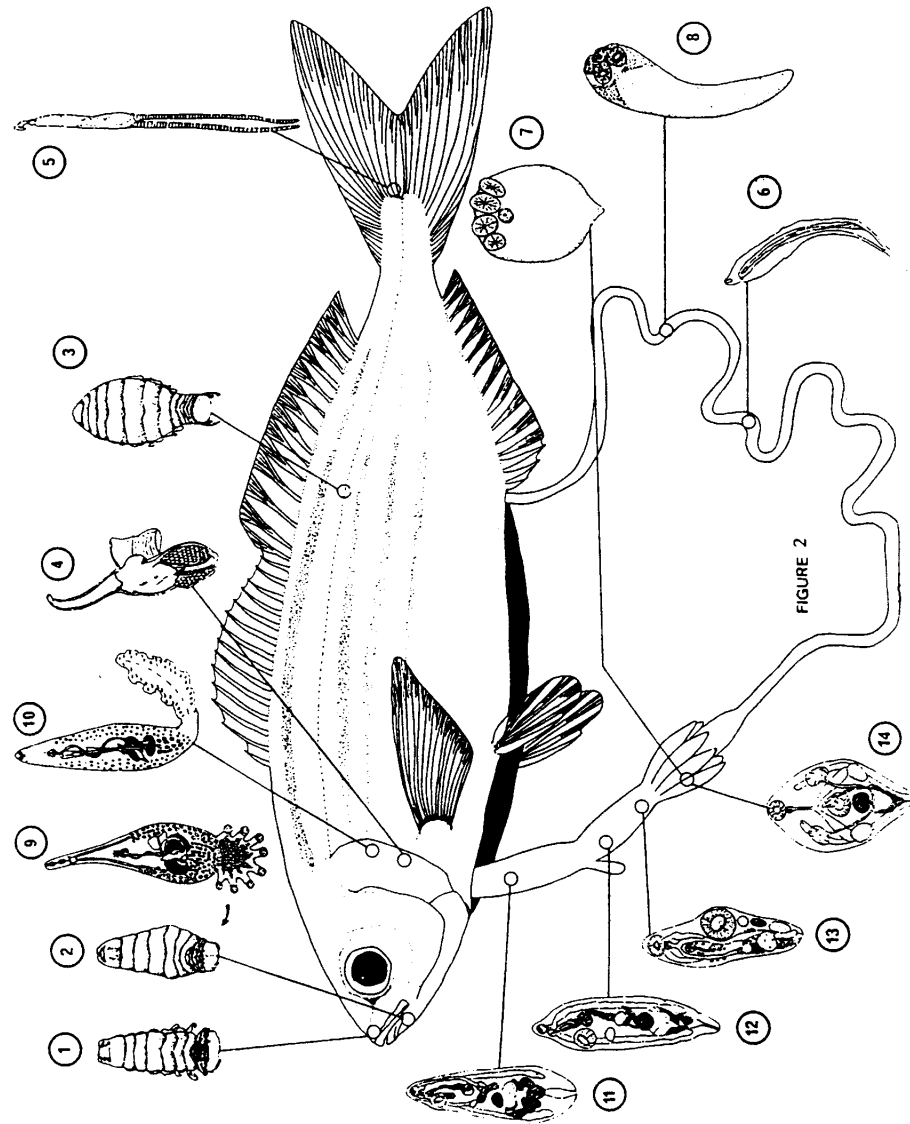


Figure 2. Metazoan parasites of *Boops boops* (Teleostean) in the Gulf-of-Lions (France) (from Renaud *et al.*, 1980). Crustaceans: 1-3: Isopoda; 4-5: Copepoda. Helminths: 6: Nematoda; 7-8: Cestoda; 9-10: Monogenea; 11-14: Trematoda.

competitive tests carried out in the absence of the parasite have shown that *D. melanogaster* always eliminates *D. simulans*. When the parasitoid is introduced into laboratory cultures, depending on the temperature, either the two fruit flies co-exist or *D. melanogaster* is eliminated by *D. simulans*. Similar results have been observed in plants. Burdon and Chilvers (1977) analysed the competitive relationship in natural populations between barley and wheat. Barley is the best competitor except in the presence of a pathogen which is specific to it (the barley mildew *Erysiphe graminis*) which stunts its development and reduces its superiority with respect to wheat. As both species have very similar ecological niches, the authors attribute an important role to the parasite in the coexistence of these two plants.

Whereas parasite-mediated host co-existence has been well studied in both the animal kingdom with parasitoid insects, and in that of plants with fungi, the same cannot be said for helminths and their hosts. The problem here is that in most cases it is difficult to define the intensities of confrontation between hosts and parasites. In the case of host hybrid zone, the parasites are confronted with two parental host genomes and a series of recombinant genomes with different degrees of introgression. It is thus possible to test *in situ* a certain number of hypotheses concerning the ecological and genetical processes which link the partners in each host/parasite association. The understanding of the limits of parasite specificity and host susceptibility, given by the variability of genomes present in the populations, enables the analysis and interpretation of the role of the parasite (i.e. selective constraints) in the evolution of host biodiversity. In the following, we present two biological models of helminths involved in hosts hybrid zones that we have studied in our laboratory.

Two taxons of European mussel (*Mytilus edulis* and *M. galloprovincialis*) co-exist on the French Atlantic coast. These bivalves are infected by the larval stages (sporocysts) of the trematode *Proserhynchus squamatus*. In a mussel-farming station situated on the Island of Groix (France), we have observed a pronounced difference in infestations between the mussels (*Mytilus edulis*) reared on ropes and those coming from the local population found attached to the structures of the station. The cultivated mussels display higher parasite prevalences compared to 'local mussels' (Coustau *et al.*, 1990). It was found that a hybridization between the two bivalve taxons existed at all sites where environmental conditions were suitable. Hybrid zones consisted of 'local environmental structures' (sheltered versus open environments) (Coustau *et al.*, 1991a). The analysis of those hybrid zones revealed that individuals of *M. edulis* genotypes are more susceptible to infection than *M. galloprovincialis* genotypes. In other words, the differential specificity of *P. squamatus* depends on the physiological and biochemical characteristics of *M. edulis* that are compatible with the settlement and development of the parasite (Coustau *et al.*, 1991b). Given the marked pathogenic effect of this trematode, which causes the castration and death of its host, its presence in sympatric sites constitutes a source of differential selective pressure acting against *M. edulis*. Selective pressures against *M. edulis* had already been demonstrated in studies concerning the evolution of the genetic and demographic structure of hybrid populations on the British coast (Skibinski *et al.*, 1978). However, only the abiotic factors were invoked to explain the selection against *M. edulis* genomes. Coustau *et al.* (1991b) noticed that the 'parasitic' factor, like abiotic factors, should be taken into account in the study of interactions between *M. edulis* and *M. galloprovincialis*. In this example, the parasite can influence the genetic structure of natural host populations in

favour of a parasite-resistant competitor (*M. galloprovincialis*) in environments where abiotic factors would have favoured the parasite-sensitive *M. edulis*.

The analysis of gut parasitic nematodes (Oxyurids) in mice (*Mus musculus domesticus* and *M. m. musculus*) in a hybrid zone reveals a somewhat different case. In the example just presented (*P. squamatus* and bivalves), one parental type is more susceptible to parasitism than the other. Here, it is the hybrid mice, i.e. those displaying recombinant genotypes, that are the most heavily infected (Mouliia *et al.*, 1991). The genetic determinism of this high susceptibility to nematodes is confirmed by an experimental analysis (Mouliia *et al.*, 1993). These studies suggest that hybrid mice (recombinant genotypes) no longer possess co-adapted genetic systems which permit the regulation of within-host helminth populations. Even though the impact of these parasites on the fitness of 'over-infected' individuals has not been quantified, these high parasite infections are actually the only phenotype revealing a disgenesis in hybrid mice, and the possibility of their counter selection in the hybrid zone. The parasites may thereby contribute to the genetic barrier between host genomes, and to the maintenance of the hybrid zone between the two mouse sub-populations.

Concluding remarks

There are different points which would help us better to understand the genesis and maintenance of biological diversity in the world of heterospecific associations (e.g. host-parasite associations). These points are important for the development of 'evolutionary parasitology' research, and should form the basis of a reflection concerning biodiversity and its functioning in host-parasite interactions.

All analyses on host-parasite systems need a precise characterization of the taxa present. Numerous errors are the result of a poor knowledge of the organization of parasites and their hosts as genetic entities (species richness). It is crucial to integrate into parasitology new methods of molecular biology and population genetics.

In host-parasite systems, the cost/benefit relationships represent, as we have seen, the basis for the evolutionary patterns of interactions. If biologists essentially focus on the associations where the costs are maximum (parasitoidism and mutualism), we must in the future bring our attention to 'discrete' parasites, i.e. the majority of parasites, where it is difficult to quantify the impact on host populations (such as the mouse-nematode association described above).

At the intraspecific level, the analysis of genetic variability between and within populations or demes would provide essential information on the functioning of natural populations (levels of gene flow, reproductive units delimitations, migration, local adaptations) and the divergence between the observed entities. This information would help to locate the source of parasite infection, the patterns of their transmission and their evolutionary potential. As mentioned previously, the host will generate strong selective pressures on parasites, and has numerous potential, hierarchical and well defined levels of population structuring: the individual, genotype, population, species, and classes of age and sex. This means that parasites represent very efficient tools in the study of the processes governing the structuring of natural populations. In return, the parasites represent constraints able to influence the dynamics and genetic components of host populations and can consequently strongly alter the patterns of host diversity. Thus, the

comparison of levels of population structuring in both hosts and their parasites appears to be a fundamental research perspective which has focused little attention at this time.

The aim of the studies in parasite ecology is to describe and understand the evolution of demographic structures of parasite and host populations. However, nearly all work in progress on this topic considers, in the system studied, the individuals as genetic clones. Geneticists work mostly on constant-sized populations. Nevertheless, the reality is quite different since host and parasite are genetically and demographically variable. In the future it will be necessary for ecologists and geneticists to carry out their research in direct collaboration on the genotypic/environmental relationships which govern the evolutionary ecology of parasitism. This future collaboration now appears essential for the development of a synthetic analysis and for improving our understanding of the patterns and diversities observed in heterospecific associations.

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