

# The ecological significance of manipulative parasites

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**The diversity of ways in which host manipulation by parasites interferes with ecological and evolutionary processes governing biotic interactions has been recently documented, and indicates that manipulative parasites are full participants in the functioning of ecosystems. Phenotypic alterations in parasitised hosts modify host population ecology, apparent competition processes, food web structure and energy and nutrient flow between habitats, as well as favouring habitat creation. As is usually the case in ecology, these phenomena can be greatly amplified by a series of secondary consequences (cascade effects). Here we review the ecological relevance of manipulative parasites in ecosystems and propose directions for further research.**

## Ecology of ecosystems and parasites: a recent story

Although parasites were virtually ignored for decades by ecologists, considerable efforts have been made over the past 15 years to understand their functional importance in ecosystems [1–5]. Although easy to overlook, parasites can sometimes account for a significant portion of total biomass in natural ecosystems [6]. Most, if not all, ecologists and conservation biologists are now aware that the introduction or elimination of a parasite in an ecosystem can strongly affect the interactions between a diverse range of species in the community, and hence affect biodiversity [7]. Most studies concern apparent competition phenomena—that is, how shared parasites impact on diversity by mediating competition between different host species (Box 1)—and food webs [8,9].

Very recently, interest in the relationship between ecosystem functioning and parasites has stimulated exploration in other directions, focussing in particular on the so-called category of manipulative parasites (see Glossary). A wide range of protozoan and metazoan parasites indeed manipulates the phenotype (e.g. behaviour, morphology and/or physiology) of their hosts in a way that favours their own transmission (Figure 1). These alterations can vary greatly in their magnitude, from slight shifts in the percentage of time spent performing a given activity (e.g. biting rate in *Leishmania*-infected sandflies [10]) to the production of complex and spectacular behaviours (e.g. Figure 1e) [11,12].

Although manipulative parasites have been traditionally approached from the viewpoint of parasitology, they now constitute a common research area of interest to both parasitologists and ecologists. Understanding their importance significantly contributes to expanding our knowledge of the pivotal role of parasites in ecosystems. Manipulated hosts can be seen as complex organisms because they keep some of the properties and attributes of uninfected individuals but also display new characteristics, involving them in novel direct and indirect interactions with other species and/or conspecifics. Because of this singularity, manipulative parasites have unusual ecological effects compared with ‘regular’ parasites (i.e. parasites that do not manipulate their host). Our primary purpose is to review evidence for these original consequences. We also outline future research needs to advance our understanding of this emerging topic.

## Ecology of parasitically modified populations

When the shift in phenotype caused by parasites is large, and when prevalence in the host population is less than 100%, the distribution of trait values is likely to become bimodal, with parasitised and unparasitised individuals forming distinct groups [11,13]. For instance, the ecology of

## Glossary

**Functional response:** the effect of prey abundance on the predator's consumption rate. There are three main types of functional response.

- Type 1: consumption rate rises linearly with prey density.
- Type 2: consumption rate rises with prey density until a plateau at which it remains constant irrespective of prey density.
- Type 3: this response is sigmoidal: at high prey densities, consumption rate is similar to type 2, and at low densities, the response has an accelerating phase where an increase in prey density leads to a more than linear (e.g. exponential) increase in consumption rate.

**Manipulative parasite:** parasite-inducing phenotypic (morphology, behaviour, physiology, etc.) changes in their hosts that increase the probability of their transmission from one host to another, and/or ensure that propagules will be released in an appropriate location.

**Niche:** term describing the ways in which tolerances and requirements interact to define the conditions and resources needed by an individual or a species in order to practise its way of life.

**Parasite abundance:** number of individuals of a particular parasite in or on a single host regardless of whether or not the host is infected.

**Parasite prevalence:** number of hosts infected with one or more individuals of a particular parasite species divided by the number of hosts examined for that parasite species [58].

**Reproductive success:** defined as the passing of genes on to the next generation. In practise, this is often the number of offspring produced by an individual (or species) per time unit.

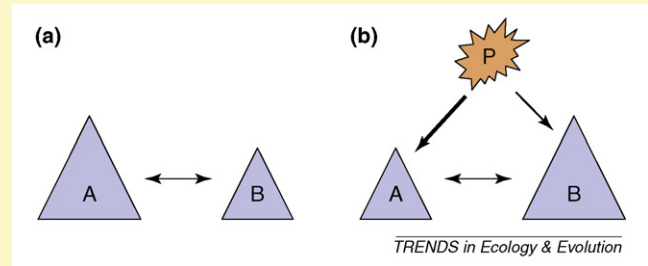
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### Box 1. Parasite-mediated apparent competition

Like most natural enemies, parasites are capable of having profound impacts on the demography and the population dynamics of their hosts when they decrease host fecundity and/or survival in a density-dependent fashion (see, for instance, Refs [16,63–66]). Frequency of infection and level of virulence of a parasite usually differ between two or more host species. The species whose fitness is the most impaired by the infection is therefore at a selective disadvantage in competition with less-affected species (apparent competition; Figure 1). Park, in 1948 [67], was the first to show experimentally that parasites could maintain biodiversity through the effects of shared enemies and apparent competition. When the two flour beetles *Tribolium castaneum* and *Tribolium confusum* were kept together in the same containers, *T. castaneum* usually drove *T. confusum* to extinction. However, when the sporezoan parasite *Adelina tribolii* was also present in the mixed cultures, the reverse pattern was observed. The parasite *A. tribolii* was simply more deleterious to *T. castaneum* than to *T. confusum*, and its presence shifted the outcome of competitive interactions between the two beetle species. Following the pioneering work of Park, there are now many theoretical and empirical studies on parasites and apparent competition [68–74] (see Ref. [75] for a review). It is now well recognised

that parasite-mediated apparent competition might be as important as direct competition or predation.



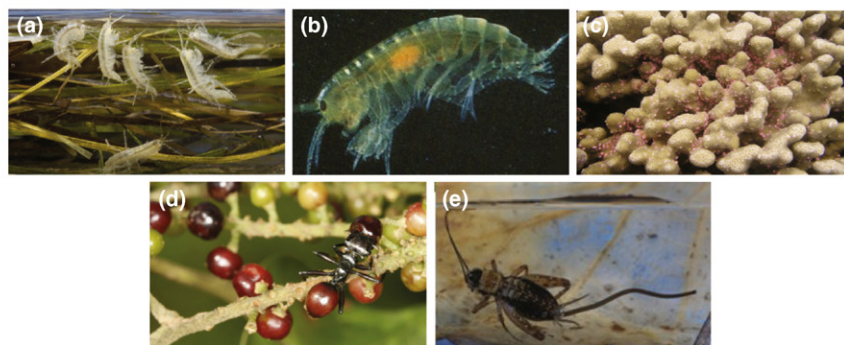
**Figure 1.** Apparent competition via a shared parasite. When the parasite (P) is absent from the ecosystem (a), host species A is more competitive than host species B. Species A is, however, more susceptible to infection than species B and, thus, in the presence of the parasite (b), the outcome of the competition between the two hosts is changed. The size of the triangles represents the abundance of each host in the ecosystem, and the arrow width indicates the intensity of the interactions between the two species.

*Gammarus insensibilis* (Figure 1a) populations could not be fully understood without acknowledging the fact that a fraction of the population harbours the manipulative parasite *Microphallus papillorobustus* [14]. Not only does this parasite split its host population into two discrete subunits (one at the water surface and one near the bottom), but several differences also exist between the characteristics of individuals from the two subunits (differences in body size, intermoult duration, fecundity, physiology, density of individuals, etc.). The pattern of mating is also deeply influenced, with paired individuals being matched for the presence or absence of the parasite.

Infection by the trematode *Cercaria batillariae* causes a large portion of the Asian mud snail (*Batillaria cumingi*) population to move lower in the intertidal zone [15]. Infected snails thereby increase their submergence time, which increases access of cercariae to their secondary host,

a fish. This parasite also induces gigantism in the mollusc. These shifts in habitat and size change resource utilisation within the snail population. The movement of infected snails away from uninfected snails alleviates competition with the remaining reproductive snails. Interestingly in this case, we can no longer speak of intraspecific competition because infected snails are castrated and produce only larval trematodes, so that it becomes more a case of interspecific competition between uninfected snails and trematodes with a similar (snail) phenotype [15].

Thus, just because of a manipulative parasite, a given host population in a given ecosystem consists of at least two groups with different ecological traits. Even though the examples described above [14,15] focussed on spatial segregation between infected and uninfected individuals, sources of phenotypic heterogeneity between infected and uninfected subunits are potentially numerous (e.g.



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**Figure 1.** Examples of manipulative parasites. (a) The crustacean amphipod *Gammarus insensibilis* manipulated by the trematode *Microphallus papillorobustus* (photo by P. Goetgheluck); infected gammarids display a positive phototaxis, a negative geotaxis and an aberrant evasive behaviour. Indeed, instead of hiding under stones, they swim toward the surface, and are preferentially eaten by aquatic birds (definitive hosts) [59]. (b) Cystacanth of *Polymorphus minutus* (Acanthocephalan) encysted in the body cavity of *Gammarus pulex* [49] (photo by F. Cezilly). Unlike *M. papillorobustus*, which is encysted in the brain of the gammarid (in (a)), the acanthocephalan is encysted in the body cavity in (b). Remarkably, this acanthocephalan also ends its life cycle in an aquatic bird and induces similar behavioural changes in the gammarid. Because trematodes and acanthocephalans are phylogenetically distant, this illustrates a case of evolutionary convergence in the manipulative process. (c) Coral polyps infected with a trematode (*Podocotyloides stenometra*). The parasite induces pink, swollen nodules on the coral colony and impairs their retraction ability. Infected polyps are, therefore, both conspicuous and vulnerable to predation by the coral-feeding butterflyfish *Chaetodon multicinctus* (the parasite's definitive host) [60] (photo by G. Aeby). (d) An ant (*Cephalotes atratus*) parasitised by a nematode (*Myrmeconema neotropicum*). The parasite induces fruit mimicry and modifies the ants' behaviour, making them more likely to be ingested by fruit-eating birds (final hosts) [61] (photo by S.P. Yanoviak). (e) The Gordian worm (*Paragordius tricuspidatus*) exiting the body of a cricket (*Nemobius sylvestris*) (photo by P. Goetgheluck). Mature worms manipulate cricket behaviour, causing them to jump into water. Once emerged, the parasite swims away to find a mate [62].

body size, physiology, life-history traits). These effects not only influence host population biology, they also affect biotic interactions and thus result in profound ecological consequences.

### Apparent competition

With few exceptions, parasitic manipulation dramatically reduces host fitness. Not surprisingly, manipulative parasites have been shown to be involved in apparent competition processes (see Box 1), like other kinds of parasites. For instance, although the bird trematode *M. papillorobustus* equally infects the two gammarids *Gammarus insensibilis* and *Gammarus aequicauda* as (second) intermediate hosts, it does not alter their behaviour with the same ease [16]. Infected *G. insensibilis* are always manipulated, displaying a suicidal behaviour which increases their probability of predation by aquatic birds. By contrast, in *G. aequicauda*, host manipulation is observed only when infection occurs in juvenile gammarids; in adults, *M. papillorobustus* has no significant effect on the crustacean's behaviour. In the field, populations of the two host species exhibit strongly contrasting patterns of parasite-induced mortality, indicating that *M. papillorobustus* acts as an important mechanism regulating the density of *G. insensibilis* populations only. Interestingly, the latter gammarid species is also known to possess a greater reproductive success than *G. aequicauda*. The manipulative parasite *M. papillorobustus* can thus favour the coexistence of the two gammarids when in sympatry [16].

Along the same lines, a study analysed the effects of bird acanthocephalans (*Proflicollis antarcticus* and *Proflicollis novaezelandensis*) on two intertidal shore crabs, *Macrophthalmus hirtipes* and *Hemigrapsus crenulatus*, both species serving as intermediate hosts [17]. The two crab species are common inhabitants of sheltered mudflats in New Zealand and are frequently found coexisting. It is typical for these two crab species to avoid predation by burrowing into the sediments at low tide; however, many individuals of both species are also found totally exposed even when the tide is at its lowest. Exposed individuals of *M. hirtipes* (i.e. those still active at low tide), but not *H. crenulatus*, have significantly higher infection levels than do hidden conspecifics. This result suggests that *Proflicollis* cystacanths, by altering hiding behaviour, can increase the vulnerability of their intermediate host *M. hirtipes* to predation [17]. In this case, the preferential manipulation of one intermediate host species over another can directly influence the population dynamics of *M. hirtipes* and also the relative abundances of other crab species occurring in the same habitat.

The role of manipulative parasites in apparent competition phenomena has also been documented in the context of invading species. Bauer *et al.* [18] compared the behavioural influence of a fish acanthocephalan parasite, *Pomphorhynchus laevis*, on two species of amphipods: *Gammarus pulex*, a resident species, and *Gammarus roeseli*, a recent coloniser present in the same river. Infected *G. pulex* are strongly photophilic compared with uninfected conspecifics and to both infected and uninfected *G. roeseli*. Host manipulation is thus observed for the resident species but not for the invasive ones. A field-based study [19] has

additionally demonstrated an increased predation mortality of *P. laevis*-infected individuals compared with uninfected amphipods in the indigenous gammarid host but not in the invasive one. Knowing that the two gammarids are sympatric and share the same trophic niche, this inequality in the face of the same manipulative parasite probably contributes to local invertebrate community structure. Thus, although manipulative parasites alter a different repertoire of phenotypic traits in their hosts compared with 'regular' parasites, they also have the potential to mediate interspecific competition processes in communities. Although this influence is important, manipulative parasites also strongly influence biotic interactions by altering trophic links between species.

### Food webs and energy flow

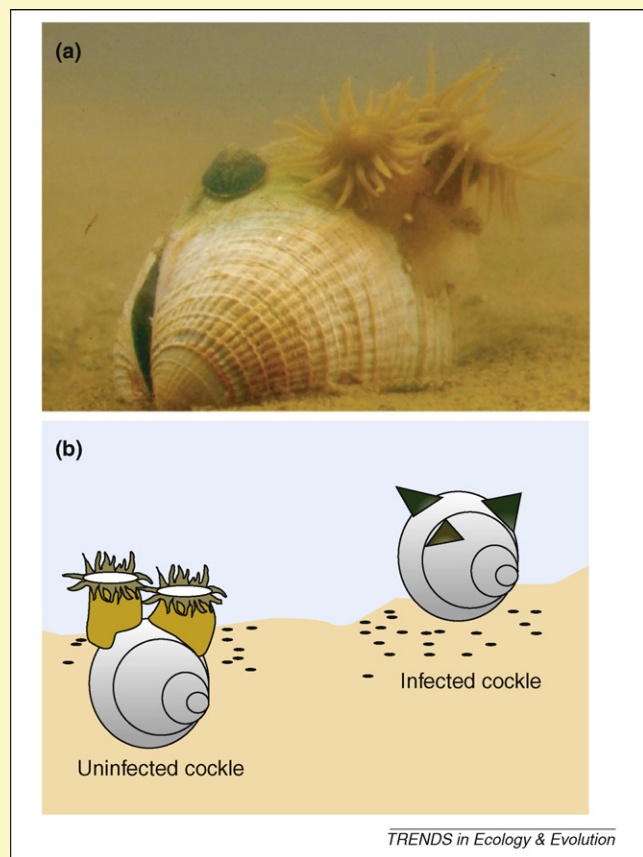
The basic structure of a food web consists of the web's architecture, or topology, and of the relative amounts of matter and energy flowing along the different trophic chains making up the topological network. Manipulative parasites can affect food webs in many ways ([20,21] and references therein). First, manipulative parasites can modulate the flow of energy throughout the web by strengthening the trophic links involved in their transmission. Numerous trophically transmitted parasites alter the behaviour of prey hosts in ways that increase their rates of consumption by predators (e.g. Figure 1a,d). Field experiments used to quantify these rates for both parasitised and unparasitised prey (see, for example, Refs [22,23]) have shown that parasites inducing relatively small host modifications can nevertheless increase rates of energy flow from prey to predator disproportionately.

Second, manipulative parasites can affect the strength of other trophic links, that is, trophic links not directly involved in parasite transmission. For example, the isopod *Caecidotea communis* is a major consumer of detritus in New Jersey streams. When infected by the manipulative parasite *Acanthocephalus tahlequahensis*, however, its consumption rates decrease significantly [24]. The impact of the parasite is greatest in autumn, when the bulk of leaf detritus enters the streams, thus affecting the input of an important basal resource to the ecosystem. Similarly, non-lethal effects of trematodes on the intertidal mud snails *B. cumingi* (see earlier section) are likely to alter energy transfer in littoral food webs by shifting host population size structure, as well as habitat and resource use [15].

Third, manipulative parasites can create completely novel trophic interactions, and the exclusion of parasites from a community would affect food web structure more profoundly by removing other links as well. For example, cockles stranded on the sediment surface of New Zealand intertidal mudflats because of heavy trematode infections in their foot (see Box 2) experience nonlethal predation from wrasses: the fish crop the foot of surfaced cockles that try in vain to burrow at high tide [25]. This particular trophic relationship exists exclusively because of parasites: unparasitised cockles are unaffected and remain buried under the sediments out of the fish's reach. Surface-stranded cockles are also exploited by other opportunistic predators such as whelks, adding to the total cockle biomass diverted to other members of the food web solely

### Box 2. Manipulative parasites and habitat creation: the cockle–trematode association

Figure 1a shows the cockle *Austrovenus stutchburyi* with the two most common invertebrate species living on its shell, the limpet *Notoacmea helmsi* and the anemone *Anthopleura aureodiata*. When the foot of the cockle is heavily parasitised by metacercariae, the mollusc cannot burrow under the mud and lies at the sediment surface. This behavioural alteration facilitates the parasites' transmission to the definitive host by making cockles more susceptible to avian predators (e.g. oystercatchers) [23,76,77]. A study demonstrated that the echinostome parasites facilitate the local coexistence of limpets and anemones [40]. Surfaced cockles indeed represent a new niche for the limpets that are normally outcompeted for space on burrowed cockles by sea anemones (Figure 1b). By manipulating the parasite load of buried cockles and the density of surfaced ones during a long-term field experiment, Mouritsen and Poulin [41] showed that the echinostomes boost benthic biodiversity. First, high parasite loads significantly reduced the cockle's mobility and hence its bioturbation potential. This resulted in an increase of the density of no less than 18 macrofaunal species as well as an increase of total and average species richness. Second, the experimental manipulation of the surfaced cockle density modified the near-seabed hydrodynamics and sedimentary conditions, resulting in a profound impact on the structure of the benthic community. On average, species belonging, for instance, to taxa such as polychaetes, gastropods and nemertines increased in diversity and abundance with increasing density of cockles on the surface [41]. In addition to increasing species density and diversity on small scales, it has been shown that the parasites influence the intertidal zonation of the cockle host as well as that of four other non-host organisms associated with cockles [42]. Figure 1 modified from Ref. [7]. Manipulative parasites thus have the potential to modify and create habitats for other species.



**Figure 1.** Interactions between cockles, trematodes and sessile invertebrates. (a) The cockle *Austrovenus stutchburyi* with the two most common invertebrate species living on its shell, the limpet *Notoacmea helmsi* and the anemone *Anthopleura aureodiata*. (b) Schematic representation of habitat creation by manipulative parasites.

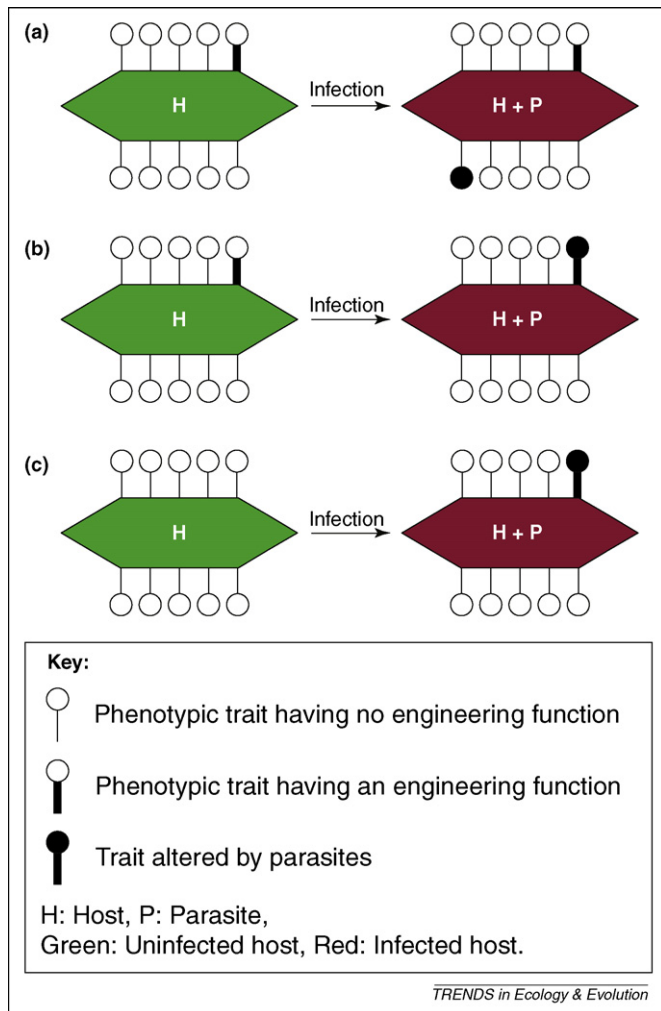
because of manipulative parasites. By increasing the accessibility to prey that are normally difficult to capture, manipulative trophically transmitted parasites are likely to enhance the trophic potential of ecosystems. In Cooking Lake and Hastings Lake in Alberta, most birds (and probably mammals) feed on invertebrates that are at the water surface (those infected by the acanthocephalan *Polymorphus paradoxus*), but relatively few predators are suitable hosts [26]. Similarly, in French rivers, infection with acanthocephalans increases the vulnerability of *Gammarus pulex* (Crustacea, Amphipoda) to non-host invertebrate predators [27]. Manipulative parasites are likely to locally influence the levels of both intra- and interspecific competition between predators, and hence their local community structure.

Novel trophic relationships can even be initiated between different compartments of the ecosystem. Hairworms which make their arthropod hosts (crickets and grasshoppers) jump into water (reproductive habitat of the parasite; see Figure 1e) cause an allochthonous resource input (nutrient transfer between habitats [28]) at the forest–river interface. Indeed, this parasitic manipulation brings terrestrial arthropods into the diet of salmonid fish [29].

Theoretical approaches also support the idea that manipulative parasites can have important impacts on the structure, and possibly the stability, of natural food webs [30–33]. For instance, Fenton and Rands [33] recently showed that the degree of manipulation can greatly alter the dynamic and stability of predator–prey communities. However, the precise outcome of the interaction depends on both the form of the manipulation and the nature of the predator's functional response. The presence of manipulative parasites and the degree of manipulation do not directly affect the persistence of the predator and prey populations, but they can greatly alter the quantitative dynamics of the community, potentially resulting in high-amplitude oscillations in abundance. Another aspect to consider is that the life histories of the predators and their prey are also of importance in determining the persistence of the parasite and the optimal level of host manipulation. Manipulative parasites can drive host population sizes down to levels where environmental stochasticity could render the host (and therefore the parasite) extinct. Host–manipulative parasite interactions and predator–prey interactions are intricately linked because host manipulation can affect predator–prey interactions and vice versa.

### Habitat creation

Some organisms create habitats for other species by modifying the environment through a myriad of activities such as, for instance, nest or dam building. How species change their own niche (niche construction [34]) and physically change the environment in ways that facilitate the production of niches for other species (i.e. ecosystem engineering [35,36]) have received growing attention in the past decade [37,38]. Manipulative parasites, by altering the phenotype of their host, can interfere with these processes and thus potentially have important repercussions on the whole community [7,39] (Figure 2). We can distinguish two main types of interference resulting in habitat creation.



**Figure 2.** Interactions between traits altered by parasites and traits involved in engineering function. (a) Noninterference: host traits altered by parasites are not those involved in an engineering function of the host. (b) Traits altered by parasites are those involved in engineering function. (c) Emergence of an engineering function in the infected host that did not previously exist (modified from Ref. [39]).

First, manipulative parasites can create new habitats by altering a host trait involved in the modification of resource availability to other species (Figure 2b). Second, manipulative parasites can act directly as ecosystem engineers when, for instance, they give rise to an engineering function in the host that did not previously exist (Figure 2c).

The first situation is well illustrated by the association between the New Zealand cockle *Austrovenus stuchburyi* and two echinostome (Trematoda) species, *Curtuteria australis* and *Acanthoparyphium* sp. (Box 2). Given the important ecological differences (e.g. light, humidity, temperature) between living under (uninfected) or above (infected) the surface of the mud, manipulated cockles clearly constitute a new habitat for sessile species. As a result, echinostomes increase the diversity of the invertebrate community by providing habitats for species such as limpets and anemones that would normally be absent from the soft-sediment habitat [40–42] (Box 2).

Probably the most important role of parasites as ecosystem engineers takes place inside host species, because living organisms are themselves an ecosystem for numerous parasite species [43]. Depending on their life cycle and

transmission routes, shared interests or, conversely, conflicts of interests can occur within parasite communities. For instance, behavioural alterations induced by *M. papillorobustus* (Figure 1a) are not neutral for the other parasites co-occurring inside *G. insensibilis*. In field gammarids, there is a positive association between *M. papillorobustus* and another trematode, *Maritrema subdolum*, which does not manipulate the behaviour of the amphipod but has the same definitive hosts as the manipulative *M. papillorobustus* [44]. Because the infective stages of *M. subdolum* swim closer to the water's surface compared to those of *M. papillorobustus*, they more frequently encounter and infect manipulated gammarids than uninfected ones (i.e. the 'hitch-hiking' strategy [44]). Leung and Poulin [45] recently investigated how the presence of manipulative echinostomes in New Zealand cockles impacts the whole community of parasites and symbionts co-occurring in these bivalves. They found a novel potential case of a hitch-hiker parasite: another trematode (a gymnophallid) that shares the same transmission route as echinostomes but is not capable of manipulation preferentially infects manipulated cockles (but see Ref. [46]). These examples illustrate well how manipulative parasites, by modifying their living habitats (i.e. the intermediate host), can change the selective pressures acting on other species and consequently influence the structure of communities.

Just as shared interests exist between manipulative parasites and other parasites exploiting the same host species, conflicts are also likely to occur. The nematode *Gammarinema gammari* (Figure 3) uses *G. insensibilis* as a habitat and source of nutrition, not as a 'vehicle' for transmission to birds. There is evidence that this nematode prefers nonmanipulated gammarids and seems also able to reverse the manipulation induced by *M. papillor-*



**Figure 3.** The nematode *Gammarinema gammari* (arrows) escaping from the head of *Gammarus insensibilis* (photo by P. Goetgheluck).

*obustus*, changing gammarids from an altered behaviour back to a normal behaviour [47]. A similar situation has been reported in the gammarid *G. roeseli* between the bird acanthocephalan *Polymorphus minutus* and microsporidia that are vertically transmitted. Apparently, microsporidia are also capable of sabotage: the behavioural manipulation induced by *P. minutus* to reach aquatic birds is weaker in hosts also infected by microsporidia [48]. Several other potentially conflicting situations exist in nature, for instance between trophically transmitted parasites sharing the same intermediate host but with different definitive hosts [49,50]. Thus, by turning their host from a phenotype A (uninfected) to a phenotype B (infected), manipulative parasites directly and/or indirectly control the habitat characteristics for other parasites and symbionts.

### Future directions

The ecological consequences presented here are generally not associated with 'regular' parasites, suggesting that manipulative parasites deserve special attention from ecologists. Compared to the important effort invested in the study of host manipulations by parasites (reviewed in Ref. [12]), relatively few studies have considered the ecological context in which they occur. This is unfortunate, as it compromises our understanding of many aspects related both to the evolution of manipulation itself and to its ecological consequences within ecosystems [51]. Thus, at the moment, more research linking host manipulation and ecosystem ecology is clearly needed to correctly assess the functional importance of manipulative parasites in ecosystems. Future studies should also determine whether or not ecological generalisations are possible. Do similar manipulative changes exerted by different parasite species result in the same ecological consequences? For instance, New Zealand trematodes are not alone with respect to their ability to impair the burrowing capacities of their bivalve hosts: the same phenomenon is induced by several other trematode species in Europe [23]. However, it is not known whether or not whole intertidal communities of free-living invertebrates and of symbionts are influenced in a similar way.

Generalisations about the ecological importance of manipulative parasites would also require the study of a greater diversity of biological models and ecosystems (particularly terrestrial ones). Ultimately, such data will help to assess which variables, if any, on a large scale explain the magnitude of the ecological consequences due to the presence of manipulative parasites (e.g. host and/or parasite taxonomy, type of ecosystems, levels of interactions between species, types of phenotypic traits that are altered, proportion of manipulative parasites in the parasitic community, etc.). Exploring the idea that ecosystem dynamics and food web complexity contribute in return to the evolution of manipulation by parasites is another exciting direction.

A full understanding of the roles played by manipulative parasites in ecosystems would additionally require detailed investigations of the complexity of manipulated hosts, focussing in particular on phenotypic traits other than those that are the most obviously altered. Parasitically modified hosts are not simply normal hosts with one

(more or less strong) trait alteration (e.g. behaviour); instead they are deeply modified organisms displaying a range of subtle changes [14,51,52]. Certain of these trait alterations, although not spectacular, might be quite relevant in terms of ecosystem consequences. For instance, certain acanthocephalans have recently been shown to increase salinity tolerance in crustacean amphipods [53]. Although this physiological change might be less spectacular than the behavioural changes generally induced by these parasites (e.g. Figure 1b), it can be highly relevant from an ecological viewpoint because salinity tolerance is a key determinant of the invasion potential of amphipod species [54]. Similarly, for reasons that still need to be determined, several studies suggest that aquatic crustaceans whose behaviour is manipulated by helminths of aquatic birds concomitantly display significantly higher levels of lipids and glycogen than uninfected conspecifics (trematodes [14]; acanthocephalans [55]; cestodes [56]). Manipulated hosts are therefore not only easier to capture, they might also represent prey of higher nutritive value for foraging predators [57]. Whatever the exact proximate and ultimate reasons for higher lipid reserves in manipulated hosts, the implications at the ecosystem level and for conservation are undoubtedly important, particularly when variation in parasite prevalence exists between habitats. We thus encourage other researchers to examine a broader range of phenotypic traits in manipulated hosts than the ones of immediate relevance to transmission.

Furthermore, research into this area would benefit greatly from an emphasis on quantitative measurements of the impact of manipulators on ecological processes (e.g. predation rates, competition, energy flow along food chains). The study of host manipulation has its roots in a natural history approach that did not encourage rigorous quantitative analyses beyond those directly linked to the manipulation itself. Indeed, for some of the textbook examples of manipulation (e.g. the spectacular impact of the trematodes *Dicrocoelium* and *Leucochloridium* on ants and snails, respectively), we have no estimate at all of the effects on predation rates by definitive hosts. There is little doubt that manipulative parasites change the strength of numerous links within the web of interactions making up an ecosystem, even links that do not directly involve their hosts. A shift toward these broader impacts is the logical next step in the study of parasite manipulation within an ecosystem context. Such data will also be essential for building theoretical models exploring the evolution of life-history strategies within predator-prey-manipulative parasite communities. Unless we improve our understanding of the ecological significance of the whole biodiversity, including that of manipulative parasites, we have an insufficient understanding of the functioning of ecosystems.

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