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Parasites and ecosystem engineering: what roles could they play?

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In recent years, there has been a growing interest in understanding the ecological importance of ecosystem engineers. In this paper we argue that parasites, through the phenotypic alterations they induce in their hosts, are likely to be involved in engineering processes for at least two reasons. First, when ecosystem engineers are themselves infected, phenotypic alterations induced by parasites can interfere with host traits involved in the engineering processes. Secondly, parasites themselves can be ecosystem engineers since the phenotypic alterations of hosts directly modify the habitat of all the species inhabiting free-living organisms. This new research area at the interface between ecology and parasitology should improve our understanding of the ecological consequences of phenotypic alterations induced by parasites in ecosystems.

Ecosystem engineers are organisms, plants or animals, that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, 1997). These species have strong effects on ecosystem processes in modifying, maintaining or creating new habitats (available ecological niches, Jones et al. 1994). Since evidence suggests that many habitats on Earth support, and are influenced by, ecosystem engineers, increasing attention is now devoted to understand the ecological and evolutionary importance of these species (Jones et al. 1997, Aho et al. 1998, Alper 1998). However, although the literature is rich in examples of habitat modification by organisms, little is known concerning the possible influence of parasites in these processes. Numerous parasites have been shown to alter the phenotype of their host (see Combes 1991, Poulin 1998 for reviews). The reasons behind these phenomena are various, ranging from simple pathological side effects to adaptive changes in the context of parasite transmission or reproductive strategies (see Poulin 1998 for a review). Whatever the exact proximate or ultimate causes of these changes, many of them are substantial

and, consequently, it is plausible to consider that parasites are able to turn living materials from one state to another, shifting the host phenotype from a state A to a state B. Indirect ecological consequences of phenotypic alterations induced by parasites on their hosts remain, however, poorly investigated and understood. Until now, evidence for a key role of parasites in structuring animal communities is based on the idea of a differential susceptibility of closely related host species to infection or its consequences (Park 1948, Minchella and Scott 1991, Thomas et al. 1995, Combes 1996, Yan et al. 1998). Indeed, parasites do not usually infect host species at statistically similar frequencies, and/or virulence differs from one host species to another. Thus, a host species whose fitness is impaired by parasitism is at a selective disadvantage in competition with a closely related but relatively unaffected species (Fig. 1). In this paper, we discuss and illustrate the idea that parasites can directly or indirectly be involved in engineering processes through the phenotypic alterations they induce in their hosts.

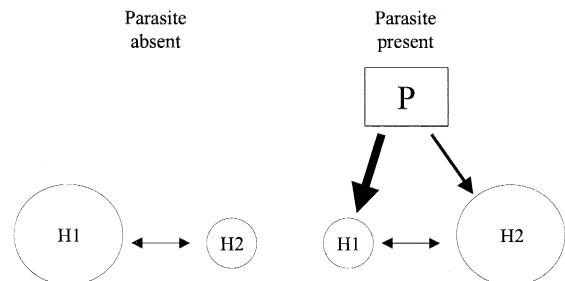


Fig. 1. Direct effect of parasites on communities already documented in the literature and recognized by ecologists. A parasite with differential effects on two or more host species can change the outcome of competition between these species. The thickness of lines represents the relative strength of interspecific effects. The size of circles represents the relative abundance of species in the communities.

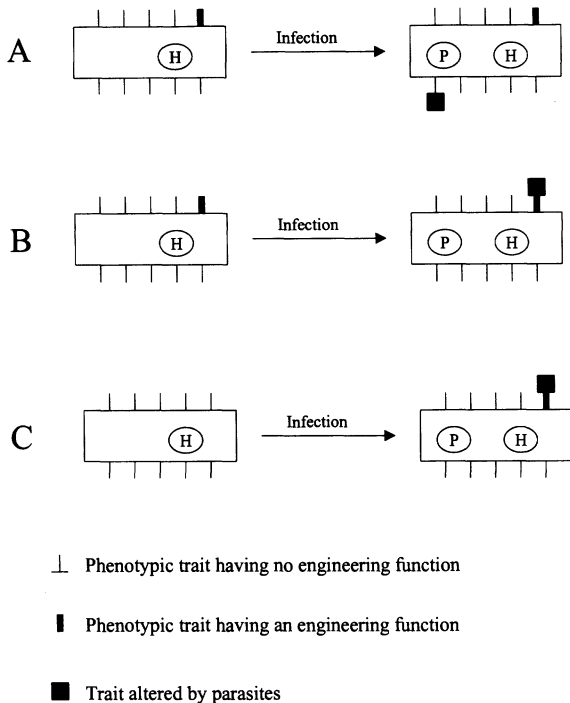


Fig. 2. Interactions between traits altered by parasites and traits involved in engineering processes (see text for explanation).

Infection of ecosystem engineers

All acts of engineering from free-living species in ecosystems directly or indirectly result from traits of their phenotype as for instance their morphology, their behaviour and/or their molecular make-up. Knowing that parasites alter a large variety of phenotypic traits in their hosts (see Poulin 1998 for a review), several cases of interactions can be envisaged between host traits that are altered by parasites and those that are involved in engineering acts.

The simplest situation is the case of non-interference (Fig. 2A) when host traits altered by parasites are not those, or not related to those, involved in an engineering function of the host. This would be for instance the case of parasites altering the colour of host species that play an engineering role because of their behaviour or their size. Although cases of non-interference are probably common, traits altered by parasites can also directly correspond, or be related, to traits involved in an engineering function of the host (Fig. 2B). In these situations, parasites are thus expected to interfere with the engineering processes of their hosts. For instance, numerous free-living species are considered as autogenic engineers because they directly provide living space for other organisms (see Jones et al. 1997). Any parasite altering the growth of such hosts (negatively or positively) should then affect the trait (i.e. host size) involved in the engineering process. Empirical evidence

of such phenomena may come from studies on mollusc first intermediate hosts of trematodes. Indeed, while the shells of molluscs are well known to serve as substrate for a variety of epibionts such as algae and sessile invertebrates (Smith and Newell 1955, Nichols and Wilcox 1997, Thomas et al. 1998), several cases of shell gigantism have also been reported in molluscs infected by trematodes (Minchella 1985, Joose and Van Elk 1986). Since colonisation rates are generally positively influenced by the size of the shell (e.g. Warner 1997, Thomas et al. 1998), trematode infections could positively influence the diversity of invertebrate communities. More generally, engineering acts that result from the engineer's activity are likely to be altered by parasites since a common consequence of numerous pathologies is a reduced activity. This simple effect could theoretically have important ecological consequences. For instance, it has been argued that gastrointestinal nematodes can have an impact on plant communities by altering the appetite of herbivores (Arneberg et al. 1996). The engineering functions of the host and/or their effects are also likely to be modified when parasites induce a major alteration of the host such as a change of microhabitat (e.g. Helluy 1984, Curtis 1987). Indeed, the ecological conditions and the interactions between the host and the other species are likely to be modified in the new habitat. This situation is well illustrated in the association between the cockle *Austrovenus stutchburyi* and the trematode *Curtuteria australis* (Thomas et al. 1998). The cockle *A. stutchburyi* typically lives just under the surface of the mud in many sheltered shores of New Zealand. In the absence of rocky surface in these areas, the shell of *A. stutchburyi* is the only hard substrate where benthic invertebrates such as limpets and sea anemones can attach. In this respect, *A. stutchburyi* itself can be considered as an (autogenic) ecosystem engineer (sensu Jones et al. 1997). However, when infected by *C. australis*, cockles are unable to burrow perfectly under the mud and typically lie at the surface of the sediment. This behavioural alteration renders cockles more vulnerable to predation by oystercatchers, the definitive host of the parasite (Thomas and Poulin 1998). Given the important ecological differences (e.g. light, humidity, temperature) between living under or above the surface of the mud, manipulated cockles constitute clearly a new habitat for invertebrate species. As expected, the structure of the invertebrate community is significantly altered by the effect of *C. australis* on host behaviour. Indeed, while limpets significantly prefer manipulated cockles to uninfected ones, an opposite preference is observed for sea anemones (Thomas et al. 1998). Competition between the two species for attachment space on cockles, and the greater susceptibility of anemones to desiccation during low tides when on surface cockles, suggest that the trematode *C. australis* creates two distinct types of cockles and facilitates the local co-existence of limpets and anemones (Thomas et al. 1998).

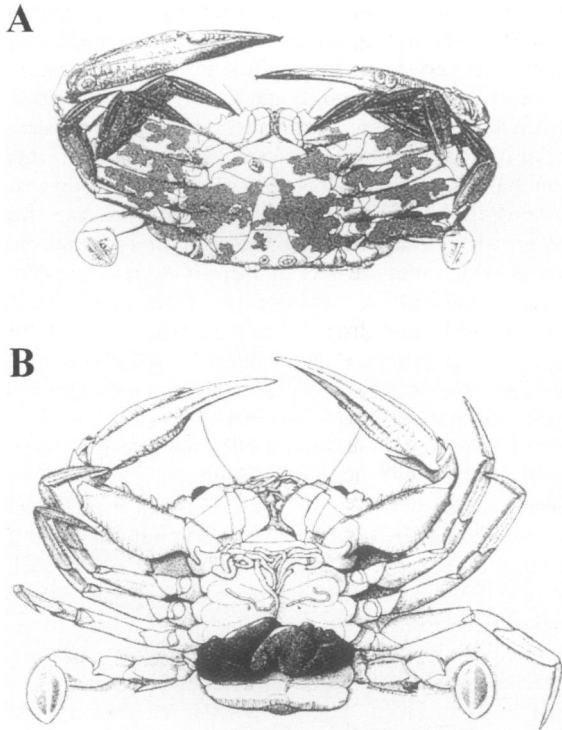


Fig. 3. Crabs infected by Rhizocephalans. A) The colonial rhizocephalan *Thompsonia dollfusi* infecting the ventral side of a mature male *Portunus pelagicus* caught near Tuas, Singapore (drawn by Beyerholm, after Jespersen and Lützen 1992). The artist carefully represented several barnacles on the cuticle. B) Specimens of the sacculinid *Heterosaccus dollfusi* Boschma attached to the abdomen of the swimming crab *Charybdis longicollis* Leene caught along the Israel shores (after Høeg and Lützen 1995). Once again, the artist represented epibionts (serpulid polychaetes) on the cuticle. The presence of these epibionts reveals that moulting events have ceased for crabs.

Parasites as ecosystem engineers

By altering particular traits of their hosts, parasites can also favour the emergence of engineering functions in their host (Fig. 2C). In these cases, parasitic alteration is thus responsible for habitat creation. This situation is for instance illustrated in the association between the crustacean parasite *Sacculina carcini* (Rhizocephala

and its host, the crab *Carcinus maenas*. The parasitic larval stage penetrates into the crab and develops an extensive system of branches extending even into the appendages of the host (Høeg 1995). The physiology of the crab is then completely altered and an important aspect of these alterations is that infected crabs do not moult in most cases (O'Brien and van Wyk 1985). The cuticle of infected *C. maenas* then becomes a more permanent substrate for several invertebrate species than that of non-infected crabs which present a normal moulting cycle. Interestingly, classical illustrations of crabs infected by rhizocephalan parasites mentioned an epibiont community on the cuticle (Fig. 3A, B). This example illustrates that sometimes only one trait (e.g. the inter-moult duration) can prevent one species from having an engineering role and that by altering specifically this trait, parasites can favour the emergence of engineering functions.

Probably the most important role of parasites as ecosystem engineers occurs inside host species since free-living organisms are themselves habitats for numerous parasite species. Thus, by altering their hosts, parasites directly alter some characteristics of the habitat for other parasites. To understand these phenomena, it is, however, necessary to consider the living host as a particular habitat. For instance, one of the most important ecological constraints met by parasites and pathogens to exploit free-living organisms is the defensive systems of host species (e.g. immune response of vertebrates). In this context, parasites responsible for immuno-suppression control the availability of resources for other parasites by modifying the level of environmental adversity. For example, positive effects on abundance and richness of other parasite species (i.e. opportunistic diseases) are well demonstrated in the case of humans infected by HIV (Table 1). Knowing that these secondary infections often reduce the host's survival and subsequently the engineer's fitness, a negative feedback is, however, likely to exist for immuno-suppressor engineers.

Numerous parasite species have complex life cycles, exploiting successively different host species as temporary habitats. Among these parasitic communities, nu-

Table 1. Some of the major opportunistic complications of HIV infection from Moore and Chaisson (1996). Data come from clinical records of 1246 patients with HIV infection: 300 were monitored for the development of opportunistic diseases between 1989 and 1995.

Viral infections	Bacterial infections	Fungal infections	Protozoal infections
Herpes simplex virus	Mycobacterium Avium complex	Candidiasis	Cryptosporidiosis
Varicella zoster virus (HSV)	Tuberculosis	Aspergillosis	Microsporidiosis
Cytomegalovirus retinitis (CMV)	Bacterial respiratory infections	Cryptococcal meningitis	Pneumocystis carinii pneumonia (PCP)
CMV neurological disease	Bacterial enteric infections	Coccidioidomycosis	Toxoplasmosis
Leukoencephalopathy (PML)	Bartenolla	Cryptococcal meningitis	Leishmaniosis

merous species have the potential to alter the phenotype of their intermediate hosts (see Combes 1991 and Poulin 1998 for reviews). Several studies suggest that the exploitation of intermediate hosts by different parasite species is sometimes determined by the new characteristics of modified hosts. For instance, a positive influence has been demonstrated in a trematode community: the non-manipulative trematode *Maritrema subdolum* infects preferentially gammarid hosts that are already modified by the manipulative trematode *Micropophallus papillorobustus* (Thomas et al. 1997). Indeed, compared with non-infected hosts, gammarids harbouring *M. papillorobustus* are strongly photophilic, geophobic and display an aberrant evasive behaviour making them more likely to be predated by aquatic birds, the definitive hosts of both parasites (Helluy 1984). In this case, gammarids manipulated by *M. papillorobustus* have to be considered as a new type of habitat for other parasites, with new characteristics such as a higher predation rate by aquatic birds. Selection pressures exerted in this interaction have also led to evolutionary responses (sensu Miller and Travis 1996) since *M. subdolum* displays a particular adaptation to preferentially infect gammarids harbouring *M. papillorobustus* (Thomas et al. 1997).

Engineering processes can have both positive and negative effects on species richness (Jones et al. 1997). Although modified hosts, because of their new properties, may be easier to exploit by other parasites than other hosts, it is, however, expected that conflict of interests should also exist between manipulative parasites. This situation is realised when several parasite species share the same intermediate host but end their life cycle in different definitive hosts. Lafferty (in press), in a complex association between four parasites sharing a crab as intermediate host, provided evidence that conflicts of interest between manipulative parasites significantly influence the structure of the parasite community. While two of these parasites end their life cycle in the intestine of an aquatic bird, the other species end their life cycle in the intestine of a shark. Parasite species sharing same interests are more often found together in the same crabs than expected by chance. Conversely, avoidance is observed between parasite species that have different destinations. Differential interspecific competition between parasite species could explain these distributions. However, it seems also likely that these patterns of association versus avoidance between parasites directly result from how the intermediate host is modified.

Concluding remarks and future directions

To date, most of the studies illustrating a key role of parasites in structuring animal communities rely on

evidence for a differential susceptibility of closely related host species to infection or its consequences (e.g. Minchella and Scott 1991, Combes 1996). It seems, however, that parasites could have other important effects on communities through their roles in engineering processes. Although the possible evidence for engineer parasites mainly concerns examples from marine systems, we believe that engineer parasites can exist under a wide range of ecological situations. More empirical evidence of indirect and direct roles of parasites (and parasitoids) in engineering processes is clearly needed at the moment. Future studies could for instance investigate how the engineering activity of engineers is altered when they are infected by parasites. Such information, coupled with data on parasitic abundances in populations, should allow us to predict some indirect effects of parasites on community structure. It seems also likely that competition between related engineers could be mediated by parasites in natural communities. Consequences of this phenomenon on diversity in ecosystems remain to be explored. The issues of how engineer parasites may cause changes in hosts are undoubtedly important ones. More particularly, we have a very poor idea of the effect of engineer parasites on their hosts in evolutionary terms. How engineer parasites may interact with the ecological traits of their hosts, e.g. fixation of one character like shell shape and size, which could confer higher colonization capabilities and persistence to parasitised individuals harbouring these features, compared to unparasitised smaller organisms. The role of parasites in ecosystem engineering in evolutionary terms has still not been studied, and we strongly encourage research in this direction. Finally, we also encourage parasitologists to analyse the entire parasitic community inhabiting hosts debilitated by manipulative parasites since these situations are ideal to understand the role of engineer parasites on the structure of the parasitic community. Overall, knowing that most, if not all, free-living organisms harbour parasites and knowing the variety of host traits altered by parasites, this new area of research at the junction of ecology and parasitology appears promising.

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