

Controversies in parasitology

Parasites and host life-history traits: implications for community ecology and species co-existence

Frédéric Thomas*, Jean-François Guégan, Yannis Michalakis, Francois Renaud

CEPM, UMR CNRS-IRD 9926, 911 Avenue Agropolis B.P. 5045, Equipe 'Evolution des Systèmes Symbiotiques', 34032 Montpellier cedex 1, France

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Abstract

Most of the evidence for a key role of parasites in structuring communities is based on the idea of a differential susceptibility of host species to infection and its consequences. Recent advances in community ecology suggest that life-history traits of free-living species can be an important determinant of their co-existence within communities. On the other hand, parasites have the potential to indirectly alter the life-history traits of their hosts, such as developmental time or dispersal. We discuss the idea that these indirect effects could influence the structure of free-living and parasite communities. We explore this idea in relation to related concepts including 'parasitic arbitration' and engineering processes. © 2000 Australian Society for Parasitology Inc. Published by Elsevier Science Ltd. All rights reserved.

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One major goal of community ecology is to identify the ecological and evolutionary processes which generate, maintain and erode biological diversity in ecosystems [1,2]. For decades the major biotic determinants of community structure were assumed to be competition and predation. Since the pioneering work of Park [3], however, showing that one parasite with differential effects on two host species can change the outcome of competition between these species, ecologists acknowledged the importance of parasites as a factor structuring interacting populations within communities [4–10]. Mainly because few other ideas have been really explored, it is also generally accepted that this 'parasitic arbitration' [8] in ecosystems is the main process through which parasites influence the structure of communities.

In this paper, we generalise the idea that parasites could play an important ecological and evolutionary

role in community ecology beyond arbitration. Our argument is based on three steps: (i) that life-history traits of species are important determinants of co-existence, (ii) that hosts compensate for the negative effects of infection by altering life-history traits, other than those directly affected by the parasites (e.g. developmental rate or dispersal), and (iii) that through their potential to alter the life-history traits of their hosts, parasites can influence and significantly alter the structure of free-living communities. This process is much more general than arbitration. In arbitration, parasites differentially affect the growth of competing host species. The compensatory modifications of life-history traits, however, potentially allow infected hosts to exploit niches unavailable to uninfected hosts thus allowing co-existence. First, we briefly review the evidence on the first two steps since extensive reviews on these topics can be found elsewhere. We then discuss cases where the third step could be observed, and its consequences on the community structure of both hosts and parasites. Such new insights offer useful ideas and predictions on the influence of parasites on

* Corresponding author. Tel.: +33-467-41-6232; fax: +33-467-41-6299.

E-mail address: thomas@cepm.mpl.ird.fr (F. Thomas).



species co-existence within communities, and thus deserve consideration both from an ecological and evolutionary perspective.

1. Life-history traits and species co-existence

Increasingly, ecologists recognise that, in addition to ecosystem traits (e.g. productivity, complexity, stability...), organismal traits (e.g. body size, dispersal ability, fecundity, timing of reproduction...) have a strong influence on the co-existence of species [2]. Evidence indeed suggests that species with certain life-history traits are more likely to co-exist than others. A simple reason for this phenomenon is that different life-history traits may favour resource specialisation, and then co-existence based on resource partitioning. For instance, morphological differences such as body size among a set of closely related species often constitute the causal basis for the utilisation of different types of resources which in turn facilitates the co-existence between these species [11–14]. Similarly, sequential reproductive periods within a group of species (i.e. temporal segregation) can reduce the possibility and magnitude of resource competition [15,16]. Dispersal is another important organismal trait in terms of its potential to influence species co-existence in both evolutionary and ecological contexts. Whether a species can successfully colonise new habitats and the potential for local adaptation largely depend on its dispersal [17–22]. In addition, dispersal has often been identified as an important factor which influences the genetic diversity and the structure of populations, and the probability of regional/global extinction [13,23,24].

2. Parasites and host life-history traits

Parasites have been hypothesised to play an important role in the evolution of host life-history traits because they often impose important selective pressures on them. Parasites remove resources from their hosts that could otherwise be used for host growth, maintenance or reproduction [25]. Direct costs resulting from this exploitation are the first cause of between-individual or between-population variation in the life-history traits such as fecundity, growth or survival.

Alternatively, changes in host life-history traits may be an adaptive response to parasitism [26]. For instance, one solution developed by many animal species against biotic aggressors (such as parasites) is the adjustment of life-history traits in order to compensate for their negative effects on fitness [27–30]. Hosts unable to resist infection by other means (e.g. immunological resistance or inducible defences) are

theoretically favoured by selection if they partly compensate the losses due to the parasite by reproducing earlier [27,28]. In doing so, infected individuals may increase their reproductive activities before dying or being castrated by parasites [31–35]. Parasites also have the potential to impose selective pressure on other life-history traits such as growth [36], dispersal [37–39] or reproductive effort [40,41]. In addition, when the risk of parasitism is significantly correlated within families across generations, and when mothers can alter the phenotype of their offspring, there is also evidence for inter-generational modifications of life-history traits, i.e. influence of the parental parasite load on the life-history traits of offspring [37].

Finally, when the trade-offs between life-history traits and parasite resistance have a genetic basis, parasite pressure can lead to an evolutionary change in the host population. For instance, hosts living in an environment where the risk of future infection is high may reduce their age of sexual maturity in order to reproduce before becoming infected [42,43].

Thus, parasites are responsible for changes in their host life-history traits by directly manipulating them to enhance their fitness and/or by inducing adaptive response from their host.

3. Parasites, host life-history traits and species co-existence

Several cases of interactions between host life-history traits involved in the co-existence of host species and those altered by parasites can be conceived. The simplest situation is the case of non-interference when traits altered by parasites do not correspond, or are not related, to the life-history traits involved in host species co-existence. Although cases of non interference are probably common, life-history traits altered by parasites can also correspond directly with, or may be related to, life-history traits involved in the co-existence of species. Several situations previously assigned to 'parasitic arbitration' fall within the scope of the ideas presented here. For instance, numerous parasites have the potential to decrease the fecundity and/or the survival of their hosts. By altering these two life-history traits (through direct effects), parasites can also alter the population dynamics of their hosts and indirectly the community structure (see references in introduction).

However, the alteration of these two life-history traits (i.e. survival and fecundity) by parasites can also correspond with negative genetic correlations among life-history traits (i.e. evolutionary trade-offs) [44,45]. For instance Poiani [46] has shown in a comparative study that parasitism is associated with small clutch size in birds. The interpretation of this relationship is

that since parasitism selects for less investment in each reproductive event, parasitised species should spread their reproductive activities over a large number of breeding seasons. A similar phenomenon has been observed among North American passerines parasitised in many areas by cowbirds: these species invest relatively less in current reproduction than their European counterparts, while survival rates are generally higher [30]. Unfortunately, little is known on how different life-history trade-offs (mediated by parasites) may lead to different ways of using resources which in turn could influence the diversification and maintenance of co-existing species.

3.1. Temporal segregation through effects on developmental rate

Another situation of interference between host life-history traits altered by parasites and those involved in species co-existence may occur when parasites select for early investment in reproduction. In many plant and insect species, the occurrence of non-overlapping reproductive periods (i.e. temporal segregation) is often viewed as a mechanism reducing the possibility and magnitude of resource competition [47–49]. Irrespective of whether or not such patterns evolved as a result of past competitive interactions, they undoubtedly contribute positively to maintaining species co-

existence [2]. Parasites selecting for early reproduction in their host populations are likely to alter positively or negatively the magnitude of the temporal segregation between species, for instance during a breeding season. Depending on which species is mainly affected by the parasitic pressure, the resulting competitive interactions may contribute, positively or negatively, to species co-existence (Fig. 1). Similarly, a temporal segregation between species in a community may result from differential selective pressures exerted by parasites on host species. The disappearance of such parasites from the ecosystem would then result in an increase of the magnitude of the competition between co-existing species.

3.2. Dispersal

One classical consequence of pathological change is a reduced activity, making hosts probably less able to disperse over large geographical distances [39,50]. Consequently, dispersal and gene flow between more or less infected populations is likely to depend on their respective levels of infection. If individuals from heavily infected populations exhibit lower dispersal rates than those from other populations, parasitism could generate or favour geographical isolation and, over evolutionary time, favour taxonomic diversification. In other situations, a high risk of infection in a given

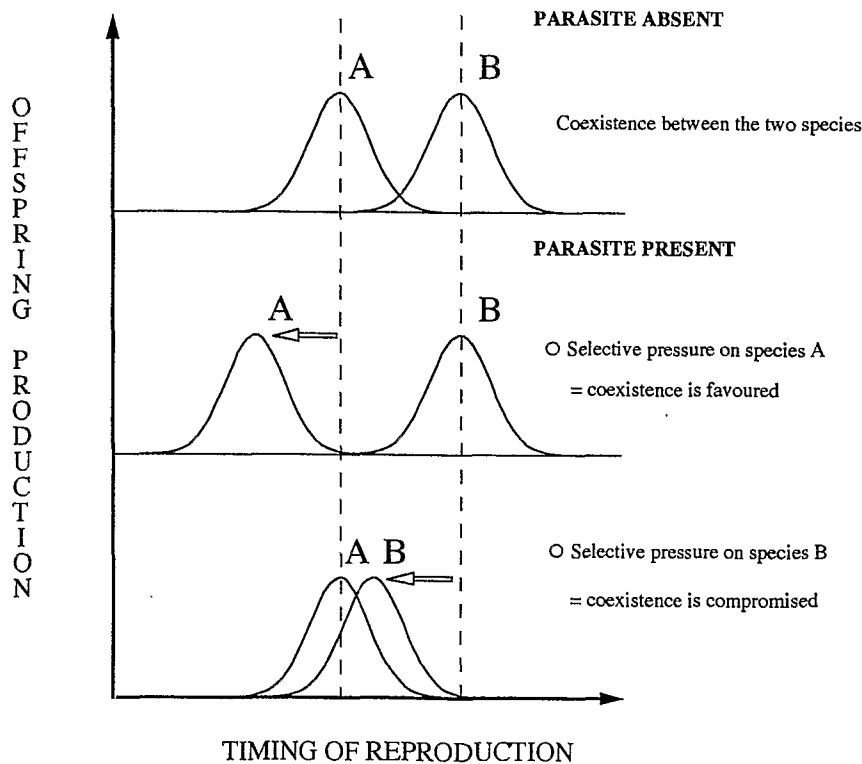


Fig. 1. Effect of parasites selecting for early reproductive investment in their hosts and consequences for species (A and B) co-existence.

habitat may select for increased dispersal to avoid future infection [37]. In such cases, parasites would on the contrary favour gene flow between host populations.

3.3. Effects on parasitic communities

If parasites exert selective pressures on their host life-history traits, the latter also have the potential to influence the structure of parasite communities. Particular life-history traits indeed, render host species more susceptible to parasitism [30]. For instance, high investment in current reproduction, as in semelparous species, has traditionally been assumed to result in elevated risks of parasitism [45]. By altering the trade-off between current vs. future reproduction, parasites then may influence the entire parasitic community. This situation can be viewed as a particular case of engineering [51–54] since parasites modify host life-history traits from a state A to a state B. Such engineering may subsequently alter both the availability and the quality of the habitat for other organisms. A simple example of this phenomenon would be the case of a parasite having a development time similar to its host's life expectancy. Any increase of host mortality due to another parasite will decrease the first parasite's transmission success. Currently, several studies support the idea that changes of life-history traits in a given host species can have substantial consequences on the performance of its parasites [55,56].

3.4. Engineering through effects on morphology

Not only parasites but also epibiont communities may be affected by these processes. For instance, parasites altering positively or negatively the growth and the size of their hosts are likely to subsequently influence the structure of the epibiont community living on this host. For example, by altering the moulting processes of their host crabs, crustacean parasites from the genus *Sacculina* strongly alter the epibiont community living on its cuticle [54,57]. Although infected crabs remain smaller than uninfected ones because the moulting processes have ceased, their cuticle becomes a more permanent substrate for invertebrate species (serpulid polychaetes, barnacles...) than that of non-infected crabs. A similar, although indirect, effect is expected when parasites alter the host adult size through the alteration of its age at maturity.

3.5. Effect on both host and parasite communities

Finally, it is also possible that within ecosystems only a limited number of parasites altering host life-history traits influence both the structure of parasite and host communities. A nice illustration of this

double effect is for instance the case of the trematode *Microphallus papillorobustus* and its effect on gammarid survival. Gammarids harbouring cerebral metacercariae of *M. papillorobustus* display an aberrant behaviour making them more likely to be preyed upon by aquatic birds, the definitive host of the parasite [58]. *Microphallus papillorobustus* promotes the co-existence of the sympatric species *Gammarus insensibilis* and *Gammarus aequicauda* since the species with the highest fecundity and the highest rate of population growth (i.e. *G. insensibilis*) is also the species which suffers the most from parasite induced mortality [59]. In addition, *M. papillorobustus* has a positive influence on the trematode community harboured by *G. insensibilis*: the trematode *Maritrema subdolum* favours its transmission to definitive hosts by preferentially infecting gammarids already infected by *M. papillorobustus* (i.e. hitch-hiking strategy) [60].

4. Concluding remarks and future directions

Compared with the huge effort that ecologists and parasitologists have devoted to the study of parasite and host fitness, community consequences remain an under-investigated area. Examples of indirect consequences of parasites on community ecology through the alteration of host life-history traits are still very few, but probably only because of a lack of appropriate studies. Cases of 'parasitic arbitration' when parasites differentially alter fecundity or survival of their hosts (through direct effects) are in our opinion only particular cases of the general idea presented here and would consequently deserve to be considered in a broader perspective, from both an ecological and evolutionary point of view. Parasite community webs could provide valuable situations to analyse the effects of parasites on the composition, the form and the nature of the relationships between host species within communities. At the moment, we clearly need empirical data from comparative and experimental studies, models and conceptual integration. We also need to understand the relative importance of parasites as a determinant of life histories compared to factors such as predation and phylogenetic inertia. Furthermore, we should explore the net effect for diversity at regional or landscape scales of the selective pressures exerted by parasites on host life-history traits. Similar remarks apply to the effects of parasites on communities through evolutionary time. In conclusion, we strongly encourage researchers analysing costs of parasites and/or host evolutionary responses to parasites to also examine all the community implications of their findings.

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