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Controversies in parasitology

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

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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.

Keywords: Community ecology; Life-history traits; Parasites

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

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 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 [redacted]

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 [redacted] 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 [redacted]

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 in- [redacted] 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 cuticule [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

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 coexistence 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 re-

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