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Two parasites, virulence and immunosuppression: how does the whole thing evolve?

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A recommendation – based on reviews by two anonymous reviewers – of
Kamiya T, Mideo N and Alizon S. 2017. Coevolution of virulence and immunosuppression in multiple infections. bioRxiv, ver. 7 of 15th December 2017 doi: http://dx.doi.org/10.1101/149211

How parasite virulence evolves is arguably the most important question in both the applied and fundamental study of host-parasite interactions. Typically, this research area has been progressing through the formalization of the problem via mathematical modelling. This is because the question is a complex one, as virulence is both affected and affects several aspects of the host-parasite interaction. Moreover, the evolution of virulence is a problem in which ecology (epidemiology) and evolution (changes in trait values through time) are tightly intertwined, generating what is now known as eco-evolutionary dynamics. Therefore, intuition is not sufficient to address how virulence may evolve. In their classical model, Anderson and May (1982)[1] predict that the optimal virulence level results from a trade-off between increasing parasite load within hosts and promoting transmission between hosts. Although very useful and foundational, this model incurs into several simplifying assumptions. One of the most obvious is that it considers that hosts are infected by a single parasite strain/species. Some subsequent models have thus accounted for multiple infections, generally predicting that this will select for higher virulence, because it increases the strength of selection in the within-host compartment. Usually, when attacked, hosts deploy defences to combat their parasites. In many systems, however, parasites can suppress the immune response of their hosts. This leads to prolonged infection, which is beneficial for the parasite. However,

immunosuppressed hosts are also more prone to infection. Thus, multiple infections are more likely in a population of immunosuppressed hosts, leading to higher virulence, hence a shorter infection period. Thus, the consequences of immunosuppression for the evolution of virulence in a system allowing for multiple infections are not straightforward. Kamiya et al. [2] embrace this challenge. They create an epidemiological model in which the probability of co-infection trades off with the rate of recovery from infection, via immunosuppression. They then use adaptive dynamics to study how either immunosuppression or virulence evolve in response to one another, to then establish what happens when they both coevolve. They find that when virulence only evolves, its evolutionary equilibrium increases as immunosuppression levels increase. In the reverse case, that is, when virulence is set to a fixed value, the evolutionarily stable immunosuppression varies non-linearly with virulence, with first a decrease, but then an increase at high levels of virulence. The initial decrease of immunosuppression may be due to (a) a decrease in infection duration and/or (b) a decrease in the proportion of double infections, caused by increased levels of virulence. However, as virulence increases, the probability of double infections decreases even in non-immunosuppressed hosts, hence increased immunosuppression is selected for. The combination of both Evolutionary Stable Strategies (ESSs) yields intermediate levels of virulence and immunosuppression. The authors then address how this co-ESS varies with host mortality and with the shape of the trade-off between the probability of co-infection and the rate of recovery. They find that immunosuppression always decreases with increased host mortality, as it becomes not profitable to invest on this trait. In contrast, virulence peaks at intermediate values of host mortality, unlike the monotonical decrease that is found in absence of immunosuppression. Also, this relationship is predicted to vary with the shape of the trade-off underlying the costs and benefits of immunosuppression. In sum, Kamiya et al. [2] provide a comprehensive analysis of an important problem in the evolution of host-parasite interactions. The model provides clear predictions, and thus can now be tested using the many systems in which immunosuppression has been detected, provided that the traits that compose the model can be measured.

References

[1] Anderson RM and May RM. 1982. Coevolution of hosts and parasites. Parasitology, 1982. 85: 411–426. doi: http://dx.doi.org/10.1017/S0031182000055360

[2] Kamiya T, Mideo N and Alizon S. 2017. Coevolution of virulence and immunosuppression in multiple infections. bioRxiv, ver. 7 of 15th December 2017, 149211. doi: http://dx.doi.org/10.1101/139147

Appendix

Reviews by two anonymous reviewers: http://dx.doi.org/http://dx.doi.org/10.24072/pci.evolbiol.100043