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Application of kin theory to long-standing problem in nematode production for biocontrol

Thomas W. Sappington[1] and Ruth A. Hufbauer[2]

1 Corn Insects and Crop Genetics Research Unit, USDA-Agricultural Research Service -- Ames, Iowa, United States of America
2 Colorado State University -- Fort Collins, United States of America
Correspondence to Tom W. Sappington (tom.sappington@ars.usda.gov)
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Much research effort has been extended toward developing systems for managing soil inhabiting insect pests of crops with entomopathogenic nematodes as biocontrol agents. Although small plot or laboratory experiments may suggest a particular insect pest is vulnerable to management in this way, it is often difficult to scale-up nematode production for application at the field- and farm scale to make such a tactic viable. Part of the problem is that entomopathogenic nematode strains must be propagated by serial passage in vivo, because storage by freezing decreases fitness. At the same time, serial propagation results in loss of virulence (ability to infect) over generations in the laboratory, a phenomenon called attenuation.

To probe the underlying reasons for development of attenuation, as a prerequisite to designing strategies to mitigate it, Shapiro-Ilan and Raymond [1] turned to evolutionary theory of social conflict as a possible explanatory framework. Virulence of entomopathogenic nematodes depends on a combination of virulence factors, like various proteases, secreted by both the nematode and symbiotic bacteria to overcome host defenses. Attenuation is characterized in part by a reduced production of these factors. Invasion of a host involves simultaneous attack by a group of nematodes ("cooperators"), which together neutralize host defenses enough to allow individuals to successfully invade. "Cheaters" in the invading population can avoid the metabolic costs of producing virulence factors while reaping the benefits of infecting the host made vulnerable by the cooperators in the population. The authors hypothesize that an increase in frequency of cheaters may contribute to attenuation of virulence during serial propagation in the laboratory. The evolutionary dynamics of cheater frequency in a population have been explored in many contexts as part of kin selection theory. Cheaters can increase in a population by outcompeting cooperators in a host if overall relatedness within the invading population is low. Conversely, frequency of altruism, or costly cooperation, increases in a population if relatedness is high, which is enhanced by low effective dispersal. However, a population that is too isolated can suffer from inbreeding effects, and competition will occur mainly among relatives, which decreases the fitness benefits of altruism.

Shapiro-Ilan and Raymond [1] tested changes in virulence and reproductive output in a serially propagated entomopathogenic nematode, *Heterorhabditis floridensis*. They compared lines of high or low relatedness, manipulated via multiplicity of infection (MOI) rates (where a low dose of nematodes gives high relatedness and a high dose gives low relatedness); and under global or local competition, manipulated by pooling populations emerging from all or only two host cadavers per generation, respectively. As predicted, treatments of high relatedness (low MOI) and global competition had the greatest level of reproduction, while all lines of low relatedness (high MOI) evolved decreased reproduction and decreased virulence, which led to extinction. The key finding was that lines in the high relatedness (low MOI) and low (local) competition treatment exhibited the most stable virulence through the 12 generations tested. Thus, to minimize attenuation of virulence while maintaining fitness of recently isolated entomopathogenic nematodes, the authors recommend insect hosts be inoculated with low doses of nematodes from inocula pools from as few cadavers as possible.

The application of evolutionary theory, with a clever experimental design, to an important problem in pest management makes this paper particularly noteworthy.

References

[1] Shapiro-Ilan D, Raymond B. 2016. Limiting opportunities for cheating stabilizes virulence in insect parasitic nematodes. *Evolutionary Applications* 9: 462-470. doi: 10.1111/eva.12348