Opinion

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Are nematodes a missing link in the confounded ecology of the entomopathogen *Bacillus thuringiensis*?

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***Bacillus thuringiensis*, which is well known as an entomopathogen, has been accepted by the public as a safe bioinsecticide. The natural ecology of this bacterium has never been particularly clear, with views ranging from it being an obligate pathogen to an opportunist pathogen that can otherwise exist as a soil saprophyte or a plant endophyte. This confusion has recently led to it being considered as an environmental pathogen that has evolved to occupy a diverse set of environmental niches in which it can thrive without needing a host. A significant driving force behind this classification is the fact that *B. thuringiensis* is found in high numbers in environments that are not occupied by the insect hosts to which it is pathogenic. It is our opinion that the ubiquitous presence of this bacterium in the environment is the result of a variety of vectoring systems, particularly those that include nematodes.**

Controversial status of the ecology of *Bacillus thuringiensis*

Bacillus thuringiensis is widely known and used commercially as an insect pathogen that is ubiquitous in soil environments (Box 1). However, the ecology of *B. thuringiensis* is puzzling. Why is a bacterium that has acquired a diverse set of virulence factors to target different insects (in particular leaf-eating ones) found so ubiquitously in soil, an ecological niche where its target is absent? One train of thought is that the bacterium ends up in the soil through a variety of biotic and abiotic processes, but is largely inactive there until it encounters a susceptible host [1]. Recently, there have been suggestions that *B. thuringiensis* is an environmental pathogen (see Glossary) that has adapted to many different niches and can persist in a variety of environments, including the soil, plants, and even potentially humans [2]. We suggest that the confounded ecology of *B. thuringiensis* can be largely explained through its complex association with vectors such as nematodes (Box 2). Three possible roles of nematodes in the ecology of *B. thuringiensis* are proposed: (i) as a means of dispersal (phoresy); (ii) as a nutrient source after death (necromeny); and (iii) as a host for infection (pathogenesis). Here, we provide supporting evidence for these three routes and discuss how such an association with nematodes can both support a pathogenic lifestyle and explain its presence in the soil.

Are insects the sole host of *B. thuringiensis?*

The insecticidal crystal protein (Cry toxin) is essential for the ability of *B. thuringiensis* to occupy an ecological niche as an entomopathogen. Different strains of *B. thuringiensis* differ in their host range mostly owing to the receptor specificity of these Cry toxins [3,4]. To date, the toxin nomenclature database lists 73 Cry toxin families (http://www.lifesci.sussex.ac.uk/home/Neil_Crickmore/Bt/holo2.html). Toxin nomenclature is based solely on amino acid sequence identity without considering toxicity; thus, toxins that are active against the same organism may be classified to different families [5]. The almost exclusive

Glossary

Endophyte: symbiotically living within a plant for at least part of its lifecycle without causing disease.
Environmental pathogen: a pathogen with metabolically versatile traits that can adapt to different habitats, hosts, and niches comprising different nutrients.
Necromeny: the ability to feed and propagate on a decomposing cadaver (as distinct from humus).
Phoresy: the associated animal is used only as means of transportation. Phoresy is usually defined as a method of dispersal.
Photorhabdus: a genus of bioluminescent, Gram-negative bacilli that live symbiotically within entomopathogenic nematodes. *Photorhabdus* is pathogenic to a range of insects and has been used as a biopesticide in agriculture.
Saprophyte: a heterotroph that obtains nutrition from humus, including decaying pieces of plants or animals.
Paratenic: in which a parasite can colonize a host, but does not trigger disease or cause damage to the host. The host is not necessary for the development of parasite, but nonetheless may serve to maintain its life cycle.
Pan-genome: the pan-genome comprises a ‘core genome’ containing genes present in all strains, and a ‘dispensable genome’ containing genes present in two or more strains and genes unique to single strains [82].

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Box 1. *Bacillus thuringiensis*: insecticidal and nematocidal mechanism

Bacillus thuringiensis, which is well known as an entomopathogen, has been accepted by the public as a safe, topical pesticide. It is toxic to larvae of many insect species and also to nematodes. The crystalline inclusion body that is formed during sporulation acts as the primary pathogenic factor. Protein toxins are proteolytically activated in the midgut upon ingestion by a susceptible larva. The activated toxins form pores in the epithelial cells of the midgut, which can either kill the larva outright or allow the bacterial cells into the hemocoel, where they can cause septicemia [83]. The most characterized nematicidal Cry protein is Cry5B, which binds to glycolipid receptors located on the intestinal cells before forming pores [84].

focus of research on *B. thuringiensis* as an insect pathogen may have resulted in inertial thinking. *Bacillus thuringiensis* was first identified in an insect (by Ishiwata in 1902 in a *Bombyx mori* infection) and research focused on insect pests subsequently thrived [6,7]. The fact that most isolates showed little or no toxicity to the tested insects was generally overlooked. A review of the insecticidal specificity of Cry toxins indicated that 26 of 140 Cry toxins tested had no known pesticidal activity [8,9]. In an attempt to assign activities to isolates with no known insecticidal toxicity, studies in Japan identified six families of Cry toxins that specifically targeted human cancer cell lines [10]. These toxins were named parasporins; however, it seems unlikely that they have evolved to target human cancer cells, although if they have another target it is currently unknown [9]. A taxonomic characterization of 52 strains of *B. thuringiensis* using *csaB* as marker [11] found that soil-isolated strains were split into two major clusters with all but one of the 22 insect-active strains in the same cluster. The activity, if any, of the strains in the other cluster was unknown. Current strategies to identify novel Cry toxins are often based on homology searches [12–14] and, as a result, are biased towards those related to existing insecticidal toxins, particularly those sharing the common three-domain fold [3,15]. Anthropogenic influences could also shape the distribution and discovery of novel strains. *Bacillus thuringiensis* was commercialized as an insecticide in 1938 and the possibility exists that its application as a pesticide has altered the indigenous bacterial population structure [16]. Its application could also alter the evolution and ecology of hosts [3,17], let alone of the pathogen itself. Thus, while most *B. thuringiensis* research has concentrated on insect pests as the host, there is scope for finding strains that target different hosts.

Box 2. Ecology of nematodes in natural soil

Nematodes are one of the most diverse groups of soil organism. The total number of nematode species has been estimated to be approximately 1 million, including free-living and parasitic ones. The concentration of nematodes in soil can exceed 1 million per m^2, belonging to 400 species [85]. Plant-parasitic and free-living nematodes are the dominant nematode fauna in most soil communities [86], with free-living forms comprising 60–80% of the nematode fauna. The free-living nematodes have an essential role in ecosystem structure and function, such as soil nutrient cycling, decomposition, disease suppression, and microbial population regulation [87].

The ecology of *B. thuringiensis*

Aside from the production of the Cry toxins, *B. thuringiensis* is phylogenetically indistinguishable from *Bacillus anthracis*, an obligate mammalian pathogen, and *Bacillus cereus*, an environmental organism and opportunistic human pathogen. However, the lifestyle of *B. thuringiensis* differs from these closely related species because *B. thuringiensis* has acquired diverse virulence factors that enable it to target a variety of insect species [1,18]. *Bacillus thuringiensis* forms stable endospores and, therefore, can persist in the environment, including in extreme regions such as deserts, marine sediments [19], and even Antarctica [20] where insects are sparse or absent. Genomic studies suggest that, unlike *B. anthracis*, *B. thuringiensis* has an open pan-genome [21] enabling it to more easily adapt to new environments. As a result of these observations, Argôlo-Filho and Loguercio [2] recently proposed that *B. thuringiensis* should be considered an environmental pathogen because it is capable of reproducing in many different habitats. Environmental adaption, such as an evolutionary transition towards psychrotolerance, could shape the ecological diversification in the *B. cereus* group [22]. Consideration of habitats other than an insect host is important for understanding the puzzling ecology of *B. thuringiensis*. Although *B. thuringiensis* seems to adapt to different niches, the trophic interactions between it and its hosts are the most likely driving forces for the differentiation of its ecology from that of other organisms in the *B. cereus* group. Crystal-producing *B. thuringiensis* strains are particularly susceptible to competition from Cry toxin null strains that gain a growth advantage by avoiding the cost of crystal protein production [23,24]. How selection maintains the expression of insecticidal toxins in abiotic or plant habitats remain elusive. When the ability of *B. thuringiensis* to reproduce in these habitats is scrutinized closely, it becomes clear that, while the bacterium may be able to persist, reproduction is poor when compared with better-adapted species. *Bacillus thuringiensis* colonizes plant roots, but the rhizosphere is unlikely to represent the preferred ecological niche of the bacterium [25]. In addition, *B. thuringiensis* has been reported as reproducing on plant leaves and even as an endophyte [26–28], with some isolates, such as genotype ST8, proving better than others at endophytic and epiphytic colonization [16]. In one particular study, strains of *B. thuringiensis* were found to be able to complete full colonization of a plant following inoculation of seeds [29]. However, in these environments, the strains grew slowly and were unable to reach high cell densities. Genomic analyses of the *B. cereus* group indicate that these organisms are adapted to a protein-rich diet rather than the carbohydrate-based diet preferred by the saprophytic *Bacillus subtilis* [30]. The requirement for a protein-rich diet is compatible with the necromenic lifestyle of *B. thuringiensis*. Although studies have shown that *B. thuringiensis* can be readily isolated from, and persist for a long in, the soil [31,32], it reproduces poorly in this environment [33]; thus, persistence may be linked to the stable, but metabolically inactive, endospores. Insect activity increased the levels of *B. thuringiensis* in soil [16], although there was no strong correlation between the presence of insects and the presence of *B. thuringiensis*

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