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Phenotypic plasticity and developmental innovations in nematodes

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Developmental plasticity has been implicated as a facilitator for phenotypic diversification, but the molecular mechanisms controlling it are largely unknown. We review recent comparative analyses in non-Caenorhabditis nematodes that display polyphenisms in larval development, mouth morphology and reproductive mode. Some of the challenges ahead will be to connect how these phenotypic traits are linked to each other at the molecular level, and at the ecological level. This will require sampling of several nematode species, the characterization of their ecology and the employment of both classical genetics and recently developed technological advances, such as genome editing.

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Introduction

Natural selection shapes the evolution of populations, communities and ecosystems by acting on phenotypes. It is through the elimination of poorly adapted traits that populations change, diversify, specialize or become extinct. Phenotypic plasticity — i.e., the ability of an organism to produce different phenotypes in response to its environment — offers the possibility for organisms to adapt to varying environments in real time. Plasticity can thus be studied as a trait under selection: organisms unable to respond adaptively to environmental pressures by lack of plasticity or maladaptive plasticity will be eliminated whereas those exhibiting adaptive plasticity will be selected for. How phenotypic plasticity evolves and how it, in turn, influences evolution, are fundamental questions in modern biology.

It has been argued that increased plasticity enables the appearance of new phenotypes and thus promotes diversification, population divergence and speciation [1–4]. Conversely, it has also been put forward that plasticity can prevent diversification. Indeed, if one plastic genotype can result in various phenotypes, the emergence of alternative genotypes becomes unnecessary. Additionally plasticity can hide genetic diversity since one (optimal) phenotype can originate from multiple genotypes (canalization) [2,4].

Despite the ecological and evolutionary importance of plasticity, there is little experimental evidence that explains the underlying molecular and physiological mechanisms controlling such traits or how they evolved. Moreover, the interplay between phenotypic plasticity, ecology and evolution is further complicated by the fact that the plasticity of one trait can influence the phenotype of another, later in the developmental trajectory or in the life cycle of a species [5••,6••]. How plastic traits become linked, and the ecological and evolutionary consequences of such connections remain unclear.

Nematodes are a model of choice to study the mechanisms and evolution of phenotypic plasticity [7]. This widespread species-rich group displays a tremendous array of life-styles and adaptations, which make them ideal for evolutionary, developmental and ecological studies. Moreover, the simplicity of their morphology makes them an easy model to tackle these Eco-Evo-Devo questions at the molecular (genetic) and organismal (physiological) levels.

In this mini-review, we relate recent findings on the development of phenotypic plasticity in nematodes, particularly on the link between dauer polyphenism and ecologically relevant traits such as reproduction and diet. The focus is placed on non-Caenorhabditis nematodes, and especially *Pristionchus*, a model particularly attractive for evo-devo studies, since it is amenable to classical and modern genetics techniques (genome editing with CRISPR/Cas9) [8].

Dauer formation and adult mouth morphology

Pristionchus species have two types of polyphenism, both of which are influenced by environmental cues experienced during larval development. The first type of polyphenism, which can also be found in other nematodes including *Caenorhabditis elegans*, is the facultative formation of a non-feeding larval stage. The second type of polyphenism, which is specific to the diplogasterid clade of nematodes that includes *Pristionchus*, is reflected in the mouth morphology of the last larval stage and the adult. To understand the evolution and adaptive significance of these polyphenisms, and the link between them, it is useful to first consider *Pristionchus* in its ecological context.

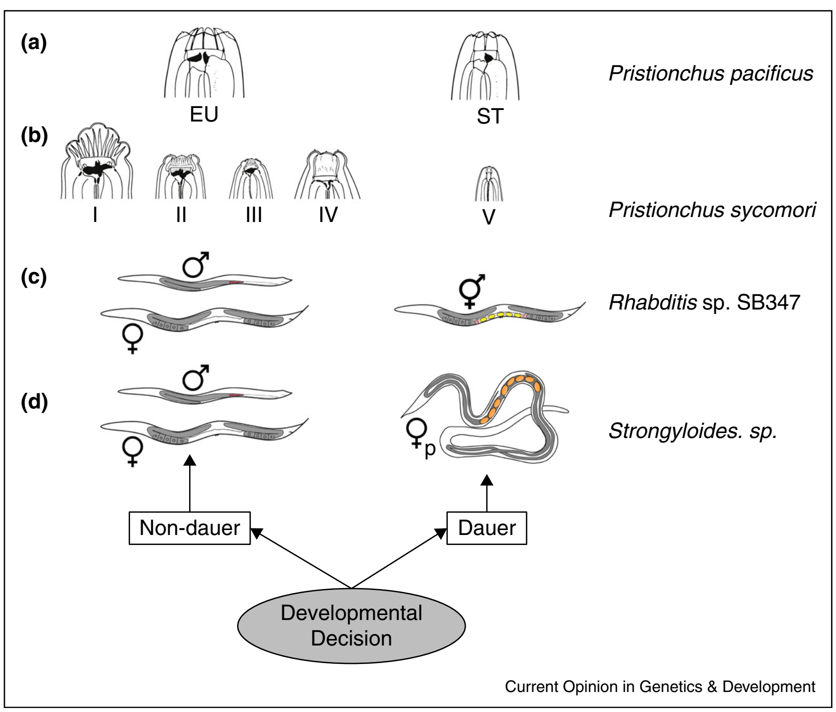
The best-known *Pristionchus* species, *P. pacificus*, is a free-living nematode that associates with scarab beetles. The beetles are used as vectors for dispersal and substrate for the growth of microbial food [9–12]. When on live beetles, *P. pacificus* is typically found in an arrested larval stage named 'dauer', and can remain in this non-feeding stage for up to a year [13]. After the death of the beetle, microbial growth on the carcass triggers *P. pacificus* to resume its larval development to become a reproductive adult [14,15].

Self-fertilizing hermaphrodite adults typically produce over 100 progeny for 4–5 days [13,16], resulting in high population densities in a relatively short period of time. This fast population growth becomes challenging for their own survival, because of competition with other individuals for rapidly depleting food resources. Pheromones present in dense nematode populations guide larvae towards developmental choices that equip *P. pacificus* to cope with these stressful conditions. Larvae may develop either into adults that can efficiently eat additional diets besides bacteria, or arrest development as the starvation-resistant dauers [17]. This developmental choice is highly dependent on the type of pheromone to which the juveniles are exposed [18], maternal phenotype [19•], and the nematode genetic background [20,21].

Larvae exposed to specific pheromones (e.g., part#9, ubas#1 and npar#1) develop into dauers [18,21], which have biochemical and behavioral traits suited for dispersal [22]. After exiting dauer, the resulting *P. pacificus* adults mostly develop a narrow mouth [6••], referred to as stenostomatous (ST) [23,24] (Figure 1a). Larvae that bypass dauer can develop into adults with either a ST mouth or a broader mouth named eurystomatous (EU) [23]. Those EU nematodes have two large teeth that move as scissors to break open fungal spores and nematodes [23,24]. This mouth morph develops more often when the larvae are starved or when exposed to pheromones (e.g., dasc#1, pasc#9 and npar#1) [18]. Thus, *P. pacificus* can become carnivorous and survive on a non-bacterial diet [25].

The link between dauer formation and mouth polyphenism has been recently extended to other *Pristionchus*

Figure 1



Simplified diagram of links between polymorphisms in nematodes. Coupling of polymorphisms can occur between dauer decision and mouth form **(a, b)**, and between dauer decision and sexual morph **(c, d)**. For *Strongyloides* sp. **(d)**, females can be obligate outcrocrossers (♀) or parthenogenetic ($♀_p$). Cross-generational factors, environmental factors and the individual's genetic background can influence the developmental decisions.