



# Interspecific differences in nematode control between range-expanding plant species and their congeneric natives



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## ABSTRACT

Climate change enables range expansions of plants, animals and microbes to higher altitudes and latitudes. Plants may benefit from range expansion when they escape from natural enemies. However, range expansion becomes a disadvantage when plants become disconnected from organisms that control enemies in the new range. Here, we examined nematode control in the root zone of range-expanding plant species and congeneric natives. In a greenhouse, we determined bottom-up (by the plants) and top-down (by natural enemies of the nematodes) control of two root-feeding nematode species (*Helicotylenchus pseudorobustus* and *Meloidogyne hapla*) in the rhizospheres of two range-expanding plant species, *Centaurea stoebe* and *Geranium pyrenaicum*, and two congeneric natives, *Centaurea jacea* and *Geranium molle*. Pots with plants growing in sterilized soil were inoculated with either a microbial soil community from the newly colonized natural habitat, a mixture of native microbial nematode antagonists, or a combination of these two communities. We tested the hypotheses that bottom-up control of root-feeding nematodes would be strongest in the root zone of range expanders and that top-down control would be strongest in the root zone of native plant species. We observed profound intra- and interspecific differences in bottom-up and top-down control among all four plant species. Bottom-up control by the range-expanding plant species was either strong or weak. Top-down control by microbes was strongest in native *Centaurea*. The addition of a mixture of both microbial communities reduced control of *M. hapla* in the root zones of the native plant species, and enhanced its control in the root zones of range-expanding plant species. We conclude that there was species-specific bottom-up and top-down control of root-feeding nematodes among the four plant species tested. Range-expanding plant species influenced their microbial rhizosphere community differently compared to native plant species, but top-down control in the root zone of natives was not systematically superior to that of range-shifting plant species.

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## 1. Introduction

Recent climate warming has enabled altitudinal and latitudinal range expansions of many animal and plant species (Parmesan, 2006; Chen et al., 2011). Such range expansions can lead to disruptions of co-evolved biotic interactions, as individual species shift range at contrasting rates (Berg et al., 2010). While some plant species, aboveground vertebrate and invertebrate species may be able to shift range relatively quickly, belowground organisms are likely to lag behind (Berg et al., 2010). Eventually, such complex

interactions might become re-established in the new range, when slower range-expanding species colonize the new areas. However, it is currently unknown what happens in the initial phases of range-expansion, when plant species are colonizing new areas and encounter novel enemies and their antagonists, which are both non-adapted to the introduced plant species.

Some recent studies have shown that climate warming-induced range-expanding plant species or populations can be less strongly affected by belowground enemies in their new range than in their old range (van Grunsven et al., 2010; De Frenne et al., 2014). Moreover, these range expanders may experience less negative effects of soil organisms in their new range than congeneric natives (van Grunsven et al., 2007; Engelkes et al., 2008). This suggests that range shifts result in a release from natural enemies, which has

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been proposed as an important cause of invasiveness of introduced exotic species (Keane and Crawley, 2002; Mitchell and Power, 2003). However, compared to exotic species introduced from geographically isolated areas, plant species expanding their range within a continent are less likely to be completely released from natural enemies as some of these enemies might be widespread in a larger geographical area.

Despite the presence of natural enemies, successful range-expanding plant species might have a benefit over native plants, as range expanders have been shown to be more strongly defended against naïve aboveground herbivores than congeneric natives (Engelkes et al., 2008). This stronger defense against generalists by the range-expanding plant species could be due to increased resource allocation to general defense mechanisms in response to reduced specialist herbivore and pathogen pressure (Müller-Schärer et al., 2004; Joshi and Vrieling, 2005; Oduor et al., 2011; Lin et al., 2015). Additionally, range expanders might possess certain allelochemicals in roots or shoots, to which the native soil community is not well adapted (Cappuccino and Arnason, 2006; Schaffner et al., 2011). Indeed, range expanders produce more unique metabolites than related natives (Macel et al., 2014). Together, these defense mechanisms may provide the range-expanding plant species with a competitive benefit over native plant species, as they suffer less from specialist herbivores and their generalist enemies are not well adapted to their novel defense mechanisms (Bossdorf, 2013; Uesugi and Kessler, 2013).

Also belowground range-expanding plants may be better defended against generalist herbivores from the new range than their native congeners. In soil from the new range, range expanders indeed were shown to accumulate fewer root-feeding nematodes per unit root mass than congeneric species that are native in the new range (Morrien et al., 2012). Such reduced densities of root-feeding nematodes might be due to either enhanced control by the plant roots (also named bottom-up, or resource control) or control by natural enemies (also named top-down or predator control), or a combination of both mechanisms. Previous studies in other systems have shown that bottom-up control by direct plant defense mechanisms (van der Stoep et al., 2006) and top-down control by fungi, bacteria, micro-arthropods and protists are all possible (Kerry, 2000; Piskiewicz et al., 2008; Costa et al., 2012; Geisen et al., 2015). These control mechanisms can operate on nematodes in species-specific ways (Piskiewicz et al., 2008). Range-expanding plant species have been shown to accumulate different microbial communities in their rhizospheres compared to closely related natives (Morrien and van der Putten, 2013). However, it is unknown whether these community differences have consequences for root-feeding nematode control, for example due to longer shared co-evolutionary histories of microbial nematode antagonists with native than with range-expanding plant species.

Here, we quantify and compare effects of top-down and bottom-up control of root-feeding nematodes in the rhizosphere of range-expanding plant species and congeneric natives. We tested the hypotheses that 1) if top-down control of nematodes by soil microbes is plant-species specific, we expect this control within congeneric pairs to be stronger in the native than in the range expander and 2) range-expanding plant species exert stronger bottom-up control on root-feeding nematodes than congeneric natives. In order to test the hypotheses, we conducted a greenhouse experiment to examine the microbial control of two native generalist root-feeding nematode species, *Meloidogyne hapla* and *Helicotylenchus pseudorobustus*, in the rhizospheres of two range-expanding plant species and their native congeners. This experiment will provide insights in how complex multi-trophic interactions may function in the rhizospheres of climate-driven range-expanding plant species in their new range, and how these

interactions differ from those of related native plant species. The experimental results will contribute to enhanced insights in how multi-trophic interactions of non-native plant species may become assembled in their new range.

## 2. Methods

### 2.1. Plant species and seed collection

We tested our hypotheses using two range-expanding plant species that originate from southern Europe, *Centaurea stoebe* L. and *Geranium pyrenaicum* Burm. f., and two congeneric species that are native in the newly colonized range in north-western Europe, *Centaurea jacea* L. and *Geranium molle* L.. *Centaurea stoebe* originates from the Danube area and since the late 1990's invaded the Rhine valley and some suitable habitats in The Netherlands (FLORON, 2014). *Geranium pyrenaicum* originally has a more widespread south-European distribution and although it colonized Northwestern Europe already in the 19th century, it only showed a strong expansion in the Netherlands since the 1980's, where it now is common (FLORON, 2014). Both congeneric native species *C. jacea* and *G. molle* are common throughout northern and southern Europe.

All seeds used for the present study originated from plant populations from the Netherlands. Seeds of *C. stoebe* and *G. molle* were collected directly from the field. Seeds of *C. jacea* originated from an experimental garden in Wageningen. They were collected from first generation plants grown from seeds of plants growing in Dutch field sites. Seeds of *G. pyrenaicum* were delivered by the seed production company Cruydhoeck (Nijberkoop, The Netherlands), where plant species are cultured from seeds collected in Dutch field sites. Seeds of all plant species were surface-sterilized by washing them for 3 min in 10% bleach solution, after which they were rinsed with demineralized water, and germinated on glass beads in a growth cabinet (20/10 °C; 16 h light/8 h dark).

### 2.2. Nematode cultures

Two generalist root-feeding nematodes that commonly occur throughout Europe were extracted from cultures originating from Dutch field sites. An inoculum of the sedentary endoparasite *Meloidogyne hapla* Chitwood (hereafter referred to as *Meloidogyne*) was collected from a field near Bovensmilde (Drenthe, The Netherlands), subsequently cultured on tomato (*Solanum lycopersicum* L.) at PPO-AGV (Lelystad, The Netherlands) and extracted using a mistifier (Funnel-spray method; Oostenbrink, 1960). A population of the ectoparasite *Helicotylenchus pseudorobustus* Steiner (hereafter referred to as *Helicotylenchus*), originating from coastal sand dunes, was cultured on Marram grass (*Ammophila arenaria* L.) at NIOO-KNAW (Wageningen, the Netherlands) and extracted using an Oostenbrink elutriator (Oostenbrink, 1960).

### 2.3. Microbial inocula

We prepared three different microbial inocula and tested their effects on root-feeding nematode abundance on range expanders and congeneric natives: a general microbial inoculum obtained from field soil, a specific nematode antagonist inoculum and a combination of the two. The used field soil was collected from riverine grasslands where most of the plant species used in the present study are present in the immediate surroundings. To obtain the general microbial inoculum, we used a serial wet-sieving approach to establish a community of predominantly microbes <20 µm (see: van de Voorde et al., 2012). We used nine batches of 2 kg top soil collected from 3 sites (6 kg per site) in a riverine

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