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2 Top-down control of root-feeding nematodes in range-expanding and congeneric native plant
3 species

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21 **Abstract**

22 Climate warming may result in range expansion of species towards previously colder
23 environments, and it has been demonstrated that in the new range successfully range-expanding
24 plant species can be less attacked by aboveground and belowground enemies than congeneric
25 natives. Plant enemies may be controlled naturally by complex bottom-up and top-down
26 interactions with their hosts, however, little is known about how these interactions may operate in
27 the new range. Here, we examine how root-feeding nematodes are controlled in the root zone of
28 successfully range-expanding plant species in comparison with congeneric plant species native to
29 the new range. As range-expanding plant species can have less negative soil feedback than
30 congeneric natives, we tested the hypothesis that top-down control of root-feeding nematodes
31 may be strongest on range-expanding plant species. To test this, we grew 4 pairs of range-
32 expanding plant species and their native congeners in field soil, to which we added soil microbes,
33 nematodes, or microarthropods from the new habitat. Addition of soil microorganisms and
34 microarthropods reduced the numbers of root-feeding nematodes, being strongest when
35 microorganisms were added. Opposite to our expectation, nematode control was not more
36 effective in the root zone of range-expanding than native plant species. We conclude that top-
37 down control of root-feeding nematodes is highly plant species-specific and that top-down
38 control of these nematodes in the root zone of range-expanding plant species can be as effective
39 as in the root zone of congeneric natives.

40

41

42 **Keywords:** Belowground; Indirect defense; Invasive plants; *Meloidogyne chitwoodi*; Multitrophic
43 interactions; Plant-soil interaction.

44 **Introduction**

45 Currently, the ranges of many plant species shift pole-wards (Walther et al., 2002) and such range
46 expansions are supposed to be promoted by climate warming (Parmesan & Yohe, 2003). In the
47 native range, plants interact with a naturally co-evolved multitrophic community of aboveground
48 and belowground enemies, symbionts and their antagonists. However, the active dispersal
49 capacity of many soil organisms has been proposed to be less than that of many aboveground
50 herbivores and their enemies (Berg et al. 2010). Therefore, rapidly range-expanding plant species
51 will encounter novel soil communities in the new range and much is still unknown on
52 multitrophic composition and functioning of these communities. It has been shown that plant-soil
53 feedback interactions in the new range are less negative for range-expanders than for congeneric
54 native plant species (van Grunsven et al., 2007; Engelkes et al., 2008). However, plant-soil
55 feedbacks reveal the net effects of soil communities, but not the underlying interactions
56 (Kulmatiski, Beard, Stevens & Cobbold, 2008). Therefore, in the present study we will move
57 beyond the plant-soil feedback approach and explore from a multitrophic perspective how range-
58 expanding plant species may interact with root-feeding nematodes in the new range.

59
60 One previous study has reported fewer root-feeding nematodes per unit root mass of range-
61 expanding plant species compared to congeneric plant species that are native in the new range
62 (Morriën, Duyts & van der Putten, 2012). In theory, herbivore abundance may be controlled by
63 resources (bottom-up), as well as by enemies (top-down) (Price et al., 1980). It is possible that
64 the traits of range-expanding plant species make them unattractive, toxic or even not recognized
65 as a new food source to the soil-borne enemies in the invasive range, resulting in enhanced
66 bottom-up control. It is also possible that the exotic plant species have better ability to interact
67 with the enemies of their enemies, resulting in enhanced top-down control, but experimental

68 studies on belowground multitrophic interactions are generally rare (Chakraborty, Pangga &
69 Roper, 2012), and absent in the context of range expansion.

70
71 Aboveground studies on range-expanding plant species have shown that these plants had fewer
72 herbivorous insects per unit shoot biomass and more carnivorous insects per unit herbivore
73 biomass than congeneric natives (Engelkes, Wouters, Bezemer, Harvey & van der Putten, 2012),
74 and that butterflies preferred to oviposit on the native plant, due to higher offspring survival and
75 performance (Fortuna et al., 2013). This would suggest that aboveground, both bottom-up and
76 top-down control may be greater on range-expanding plant species than on their congeneric
77 natives. Belowground, the evidence for indirect defense is more limited and mostly focused on
78 entomopathogenic nematodes (EPNs). This indirect defense may be attributed to either
79 improving the EPNs' foraging by, for example, providing a moisture-rich seasonal refuge
80 (Preisser, Dugaw, Dennis & Strong, 2006), or to the release of chemicals that attract EPNs upon
81 attack by insect larvae (van Tol et al., 2001; Rasmann et al., 2005; Ali, Campos-Herrera, Alborn,
82 Duncan & Stelinski, 2013). In addition, these plant volatiles have also been shown to affect not
83 only EPNs, but also bacterial-feeding and plant-parasitic nematodes (Ali et al., 2013). However,
84 these studies did not consider nematode control in the rhizosphere of range-expanding plant
85 species.

86
87 The aim of our study was to make a first step in unraveling top-down control interactions of root
88 herbivores in the rhizosphere of range-expanding plant species compared to their congeners that
89 are native in the new range. By using four such pairs of congeneric plant species, we were able to
90 compare the effect of plant genus versus plant nativeness, as the plant species forming a
91 congeneric pair can be considered more similar than species from different pairs. We considered

92 root-feeding nematodes, which can be soil-borne enemies of cultivated, as well as of wild plant
93 species. Our main hypothesis was (1) that range-expanding plant species are more capable of
94 using top-down control agents than the native plant species, which would explain the lower
95 abundance of root-feeding nematodes on range expanders (Morriën et al., 2012). We also
96 hypothesized (2) that microbes are better antagonists to root-feeding nematodes than
97 microarthropods (Piśkiewicz, Duyts, Berg, Costa & van der Putten, 2007; Piśkiewicz, Duyts &
98 van der Putten, 2008), and (3) that root-hair feeders and ectoparasites are more subjected to top-
99 down control than endoparasites (Piśkiewicz et al., 2008), as they occur in the rhizosphere soil
100 during their complete life-cycle, therefore being exposed more intensively to antagonists in the
101 rhizosphere.

102

103 **Material and methods**

104 Soil and plants

105 In December 2008, soil was collected from the riparian area Millingerwaard, the Netherlands
106 (51°52' N, 6°0' E). This area houses many range-expanding plant species and native congeners,
107 amongst others, because of its connectedness to southern and south-eastern Europe through the
108 Rhine and the Rhine-Danube canal. The soil was stored in plastic bags under ambient winter
109 temperature in order to mimic field conditions. Storage took place in a glasshouse that was kept
110 frost free only, with an average storage temperature of approximately 2-4 °C. In April 2009, the
111 soil was then sieved (0.5 cm mesh size) and homogenized. Soil for the extraction of
112 microarthropods was not sieved.

113

114 We used 4 range-expanding plant species (3 originating from Eurasia and 1 originally from South
115 Africa) and 4 congeneric native plant species (Table 1). The range-expanding plant species were

116 first recorded in the Netherlands in the 20th century and have shown a 10-fold increase in the last
117 decade (Engelkes et al., 2008). The plant species were grown from seeds collected from sites in
118 the riparian area (*Artemisia vulgaris*; *A. biennis*; *Senecio inaequidens*; *Jacobaea vulgaris*; the
119 latter two are from the *Senecio* group and contain similar metabolites, but *Jacobaea* has been
120 renamed recently), obtained from local seed suppliers that collect seeds from natural populations
121 (*Centaurea stoebe*, Rieger-Hofmann GmbH; *C. jacea*, KNNV natuurinfocentrum De
122 Hoornbloem), or grown from 1-1.5 cm root fragments collected from the field (*Rorippa*
123 *austriaca*; *R. sylvestris*). The seeds were surface-sterilized with bleach (10%) for 3 minutes
124 (*Artemisia* 30 seconds), and the root fragments with bleach and ethanol (30 seconds each). Most
125 seeds were germinated on moist glass beads, but the seeds of *Artemisia* were germinated on and
126 the root fragments planted in sterilized soil (>25 KGray gamma irradiation). Both seeds and root
127 fragments were germinated at alternating 16/8 hrs light/dark regime at 23/15 °C to mimic long
128 day growth conditions.

129
130 In order to start the experiment, seedlings and root cuttings were transplanted to plastic 1.1-L pots
131 filled with 1000 g dry weight of non-sterile soil with 16% w w⁻¹ soil moisture. The reasons for
132 using non-sterile soil were to leave the soil communities intact to mimic more natural conditions
133 and to avoid confounding effects on plant biomass production of co-introduction of microbes
134 together with the nematodes in only some treatments. We planted 2 seedlings of the same plant
135 species per pot. The soil surface was covered with tin foil to protect the surface from desiccation
136 and prevent spreading of microarthropods. The soil moisture was maintained by weighing the
137 pots twice a week and re-setting the initial weight by adding demineralised water. Once a week,
138 full-strength Hoagland nutrient solution was added; first 6 weeks 12.5 ml pot⁻¹ and later 25 ml

139 pot⁻¹. The experiment was carried out in a greenhouse with a day/night cycle of 16L/8D and
140 21/16 °C.

141

142 Nematodes and potential antagonists

143 A full nematode community, microorganisms and microarthropods were extracted from field soil.
144 For each pot, nematodes were extracted from 250 g soil by Cobb's decanting method and
145 inoculated as a suspension of 10 ml pot⁻¹. This gives 7000 nematodes per kg uninoculated soil
146 and 9000 nematodes per kg soil with additional inocula. The nematode community present in the
147 unsterilized soil used to fill the pots at the set-up of the experiment and in the inoculum was
148 analysed microscopically (magnification 200x) and consisted of root-feeders (56%), fungivores
149 (5%), bacterivores (37%), omnivores (1%) and carnivores (1%). The microorganisms were
150 obtained by shaking 1500 g of soil with demineralised water (1:1 w w⁻¹) for 20 min and filtering
151 the supernatant through a 20 µm mesh. The pots were inoculated with 10 ml of the filtrate, so that
152 microbes from 30 g of soil were inoculated to every pot. Microarthropods were extracted from
153 250 g of soil by Tullgren funnels. The jars contained a thin layer of water and were emptied daily
154 for three consecutive days, and the microarthropods were inoculated into the pots in 10 ml of tap
155 water. The microarthropod community present in the unsterilized soil used to fill the pots and in
156 the inoculum consisted of equal numbers of collembolans and mites.

157

158 Experimental set-up

159 The experiment included three treatments that were obtained by inoculating a full nematode
160 community, a full nematode community plus microorganisms, or a full nematode community
161 plus microarthropods to the pots. The inocula were applied 4 weeks after the planting of the
162 seedlings. To monitor the development in the non-sterile soil, there was a fourth treatment that

163 received no additional inocula of nematodes and potential antagonists (not further considered
164 here), giving 24 pots for each plant species (4 treatments x 6 replicates).

165
166 The pots were harvested 12 weeks after inoculation to allow at least one reproductive cycle of the
167 majority of the root-feeding nematodes (Singh, Hodda, Ash & Banks 2013). At harvest, the
168 nematodes were extracted from soil using Oostenbrink elutriators and from roots using mistifiers.
169 The nematodes were counted and identified using a reverse light microscope (magnification
170 200x) and their numbers were expressed as numbers per pot. The nematodes were divided into
171 different feeding groups based on oesophageal characteristics and known feeding habitats
172 (Yeates, Bongers, de Goede, Freckman & Georgieva, 1993). The roots and shoots of the different
173 plant species were dried for 48 h at 75 °C and weighed.

174
175 Data analyses

176 Three-way ANOVAs with plant genus, origin and treatment as main effects and all possible
177 interactions were performed using PROC MIXED in SAS for Windows 9.2 (SAS Institute Inc.,
178 Cary, NC, USA). Plant genus, origin and treatment were all handled as fixed factors. If
179 significant interactions existed, these interactions were examined with LSMEANS. This analysis
180 was performed separately for root-feeding nematodes as a group, as well as for root-hair feeders,
181 ectoparasites and endoparasites. Abundances were $\ln(x+1)$ -transformed to meet the assumptions
182 for ANOVA. To examine the potential antagonistic effect of omnivorous/predacious nematodes
183 on the root-feeding nematodes, Spearman rank correlations were performed between these
184 feeding groups in the nematode treatment for each plant species individually. Correlations were
185 also performed with the most abundant root-feeding nematode taxa (present in more than half of
186 the pots).

187
188 To examine the potential antagonistic effect of microorganisms and microarthropods on the most
189 abundant individual root-feeding nematode taxa, Mann-Whitney U-tests were used to compare
190 the abundance of these taxa in the presence of either antagonist and abundance in the nematodes-
191 only treatment. In addition, the population change in nematode abundances was calculated as
192 $\ln(N_t/N_c)$ (Brinkman, van der Putten, Bakker & Verhoeven, 2010), with a negative value
193 reflecting top-down control of the antagonists. N_t is the abundance when the antagonist is present
194 and N_c when it is absent. If the abundance of a taxon was zero for all replicates in one or more of
195 the treatments, the population change was not calculated for this taxon.

196
197 **Results**

198 Plant biomass production

199 The biomass production of the plant species differed (Fig. 1), but there were no effects of inocula
200 on either aboveground or belowground biomass (Table 2). Therefore, expressing the nematode
201 abundances as numbers per gram root biomass (Appendix A: Table A1-A4) did not change our
202 results.

203
204 Top-down control of root-feeding nematodes

205 We did not find general effects of adding microbes, nematodes and microarthropods, but the
206 significant interaction between genus, origin and treatment indicated that the effects of the
207 potential nematode antagonists were dependent on the identity of the plant species (Table 3; Fig.
208 2). Among the range-expanders, microarthropods were able to suppress root-feeding nematodes
209 in pots with *A. biennis* (Fig. 2A). In the case of *S. inaequidens*, there were fewer root-feeding
210 nematodes in pots with additional microorganisms than with microarthropods, but there was no

211 significant difference between both these treatments and the one with only nematodes (Fig. 2D).
212 Among the native plant species, both microorganisms and microarthropods were able to suppress
213 root-feeding nematodes in the case of *R. sylvestris* (Fig. 2C). In pots with *C. jacea*, there were
214 more root-feeding nematodes when extra microorganisms were added compared to only
215 nematodes (Fig. 2B). No antagonistic effect of adding nematodes could be detected as all
216 correlations between root-feeding nematodes and the omnivorous/predacious nematodes were
217 non-significant (data not shown).

218
219 Top-down control of different groups of root-feeding nematodes
220 Even though the individual feeding groups of root-feeding nematodes were not affected by
221 treatment, they were affected by plant genus and origin (Table 3). In all plant genera except
222 *Centaurea*, there were more endoparasites in pots with range-expanders. Ectoparasitic nematodes
223 reached higher abundances in pots with range-expanding *Centaurea* and *Senecio*, but in soils of
224 *Rorippa* there were more ectoparasites in pots with the native plant. Root-hair feeders were less
225 abundant in soil of *Centaurea*, while they were most numerous in pots with the native plant
226 species.

227
228 Some effect of nematode addition could be detected for the individual feeding groups of root-
229 feeding nematodes. For the range-expanding *Artemisia*, the abundance of omnivores/predators
230 was negatively correlated with the abundance of root-hair feeders ($\rho = -0.87$, $p = 0.02$), while for
231 the range-expanding *Rorippa* the abundance of omnivores/predators was positively correlated
232 with the abundance of root-hair feeders ($\rho = 0.94$, $p = 0.005$).

233
234 Top-down control of individual root-feeding nematode taxa

235 Individual nematode taxa reacted differently to the potential antagonists, however only a handful
236 of the differences recorded were statistically significant (Fig. 3). The root-hair feeding
237 Tylenchidae, responded negatively to microorganisms in pots with the range-expanding *Rorippa*
238 (Fig. 3A), but positively to microarthropods in pots with the native *Artemisia* (Fig. 3B). The
239 ectoparasite *Paratylenchus* was suppressed by microorganisms in pots with the native *Centaurea*
240 (Fig. 3A), but another family of ectoparasites, Dolichodoridae, responded positively to both
241 microorganism and microarthropod additions in case of the native *Senecio* (Fig. 3). The sedentary
242 endoparasite *Meloidogyne chitwoodi*, which establishes a permanent feeding site inside the root,
243 responded negatively to adding microarthropods in pots with the range-expanding *Artemisia* and
244 both to microorganisms and microarthropods in pots with the native *Rorippa*, but positively to
245 microorganisms in pots with the native *Centaurea* (Fig. 3).

246
247 An effect of nematode addition could also be detected for the individual root-feeding nematode
248 taxa. For the native *Rorippa*, the abundance of omnivores/predators was negatively correlated
249 with the abundance of the ectoparasite *Paratylenchus* ($\rho = -0.88$, $p = 0.02$).

250

251 **Discussion**

252 We found that the effects of the potential nematode antagonists were dependent on the identity of
253 the plant species, but not whether plant species were range expanders or not. These results do not
254 support our first hypothesis that top-down control is more effective in range-expanders. In
255 support of our second hypothesis, the addition of microorganisms had a greater control effect
256 than addition of microarthropods. However, ectoparasites and root-hair feeders were not more
257 subjected to top-down control than endoparasites, contrary to our third hypothesis. Instead, the

258 root-knot nematode *M. chitwoodi*, a highly polyphagous sedentary endoparasite, was controlled
259 by both microbes and microarthropods in pots with both native and exotic plant species.

260
261 The strength of the effects of our antagonist additions should be considered in relation to the fact
262 that we made the inoculations to non-sterilized field soil, which will already have some nematode
263 control potential (De Rooij-van der Goes, 1995). This design was used to mimic natural field
264 conditions with intact soil communities, and to avoid confounding effects of co-introduction of
265 microbes together with the nematodes. The chosen design gives strength to our results as there
266 were still significant effects on the abundance of root-feeding nematodes after adding nematodes
267 and antagonists to non-sterilized soil. Enhancing the potential of nematode antagonists in field
268 soil might provide more realistic results than creating extreme positive *versus* negative treatment
269 effects in previously sterilized soil, as also has been established for plant-soil feedback studies
270 (Kulmatiski et al., 2008). However, even with the present design our findings may be biased as
271 the data are heavily skewed towards a highly specialized, single endoparasitic species *M.*
272 *chitwoodi*.

273
274 Results of adding microorganisms may have depended on plant species-specific effects on the
275 rhizosphere communities and/or microbial induction of plant defenses (Doornbos, van Loon &
276 Bakker, 2012). However, as the inoculations were done to field soil and therefore all plant
277 species were subjected to the same microflora and possible induction of plant defenses, results of
278 the addition were more likely caused by enhanced top-down control, rather than by enhanced
279 induction of plant defense chemicals, unless induction is density-dependent. Our nutrient
280 additions may have affected plant-herbivore relations (Erb & Lu, 2013), however, adding
281 nutrients avoided stressed plants and increased root defenses due to low nutrient conditions.

282 Nevertheless, similar experiments with different levels of nutrient availability could yield
283 important information about top-down control in the natural environment.

284
285 In the study of Morriën et al. (2012), in general root-feeding nematodes had lower numbers per
286 unit of root mass in the root zone of range-expanding plant species than of natives. This was not
287 the case in the present study. However, Morriën et al. (2012) included more plant species in their
288 study. Considering the plant species pairs common to both studies the patterns are actually the
289 same: more root-feeding nematodes on *A. biennis* than *A. vulgaris* and similar levels on *C. jacea*
290 and *C. stoebe*. For *Senecio inaequidens*, different native congeners were chosen by Morriën et al.
291 (2012) than in the present study; namely *S. vulgaris* and *S. viscosus*. These natives contain fewer
292 types of pyrrolizidine alkaloids than *J. vulgaris* (Smith & Culvenor, 1981), which could be the
293 reason why Morriën et al. (2012) found more root-feeding nematodes on natives than on *S.*
294 *inaequidens*. This suggests that plant species identity could be important when analyzing
295 differences between the effects of native and non-native plant species on root-feeding nematode
296 community composition.

297
298 Although effects of adding potential antagonists were variable, our results show that both
299 microorganisms and microarthropods have some potential for controlling root-feeding nematode
300 numbers in the rhizosphere of both native and range-expanding plant species (Figs. 2 and 3). In
301 agreement with previous studies (Piśkiewicz et al., 2007; 2008), the addition of microorganisms
302 had a greater control effect than addition of microarthropods. Piśkiewicz et al. (2008) also found
303 that ectoparasites were more strongly controlled than the endoparasites. However, in the present
304 study the sedentary endoparasite *M. chitwoodi* was controlled by both microbes and
305 microarthropods in the rhizospheres of both native and exotic plant species (Fig. 3). Secondary

306 metabolites in plants are usually stored in relatively high concentrations (Wink, 2010). The
307 feeding mode of *Meloidogyne*, draining the phloem through specialized feeding sites, might make
308 them avoiding the high concentrations of the toxic compounds present in the plant cells, and only
309 encounter the compounds transported in the phloem. This could explain why sedentary
310 endoparasitic nematodes were less sensitive to exotics than other feeding types of root feeders
311 (Müller-Schärer, Schaffner & Steinger, 2004). Biological control research has shown that root-
312 knot nematodes can be controlled by the microbes *Pochonia chlamydosporia* and *Pasteuria*
313 *penetrans* both in crop (Wesemael, Viaene & Moens, 2011) and in natural systems (Costa, Kerry,
314 Bardgett & Davies, 2012).

315
316 In the present study, we did not see an effect of adding microbes, nematodes, or microarthropods
317 on biomass production of the plant species (Fig. 1). However, it is possible that these effects
318 would show up in the next generation of plants growing in these soils, and this may be due to
319 plant-soil feedback effects (Kulmatiski et al., 2008). In soil conditioned by the different plant
320 species with regulating effect on the root-feeding nematodes, germinating seedlings may benefit
321 reduced herbivore pressure, which may result in increased growth, however, such studies have
322 not yet been performed.

323 324 **Conclusions**

325 In our study using four plant pairs, differences between nematode control in the root zone of
326 range-expanding plant species and congeneric natives appeared to be due to bottom-up, rather
327 than top-down control factors. Effects of microbes, nematodes, or microarthropod addition on
328 nematode abundances were dependent on plant species, but not on plant origin. This variability in
329 top-down control of root-feeding nematodes in the rhizospheres of range-shifting plant species

330 may, at least in part, explain variability among plant species in becoming disproportionately
331 abundant in their new range.

332

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338

339 **Appendix A. Supplementary data**

340 Supplementary data associated with this article can be found, in the online version, at XXXXX.

341

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421 **Fig. 1.** Shoot and root biomass (mean \pm SE) for plant species pairs of range-expanding plants
422 (grey bars) and their native congeners (white bars) in a greenhouse experiment investigating top-
423 down control of root-feeding nematodes. Treatments: left bar - nematodes; middle bar –
424 nematodes + microorganisms; right bar – nematodes + microarthropods.

425
426 **Fig. 2.** Numbers of root-feeding nematodes (per pot; mean \pm SE), divided into different feeding
427 types (endoparasites - grey; ectoparasites – white; epidermis/root-hair feeders - black), in a
428 greenhouse experiment with 4 plant species pairs of range-expanders and their native congeners
429 investigating top-down control of root-feeding nematodes. Nematodes were extracted both from
430 soil (Oostenbrink elutriators) and from roots (mistifiers). Treatment codes: N – nematodes; B –
431 nematodes + microorganisms; M – nematodes + microarthropods.

432
433 **Fig. 3.** Population change of four root-feeding nematode taxa in plant species pairs of range-
434 expanding plants and their native congeners subjected to top-down control of (A)
435 microorganisms and (B) microarthropods. N_t is the abundance when the antagonist is present and
436 N_c when it is absent. (* $p < 0.05$, Mann-Whitney U test abundance in pots with vs without
437 antagonist)

438

439

Table 1. Investigated plant species pairs of range-expanding plants in the Netherlands (in bold) and their congeners native to the Netherlands.

Plant species	Geographical origin	Time of first introduction ^a
<i>Artemisia biennis</i> Willd.	Eurasian (North Asia)	1950-75
<i>Artemisia vulgaris</i> L.	Native	
<i>Centaurea stoebe</i> L.	Eurasian (Mid-Europe)	1950-75
<i>Centaurea jacea</i> L.	Native	
<i>Rorippa austriaca</i> (Crantz) Besser	Eurasian (East Europe)	1900-25
<i>Rorippa sylvestris</i> (L.) Besser	Native	
<i>Senecio inaequidens</i> De Candolle	South Africa	1925-50
<i>Jacobaea vulgaris</i> P. Gaertn (syn. <i>Senecio jacobaea</i> L.)	Native	

^a Tamis et al., 2005

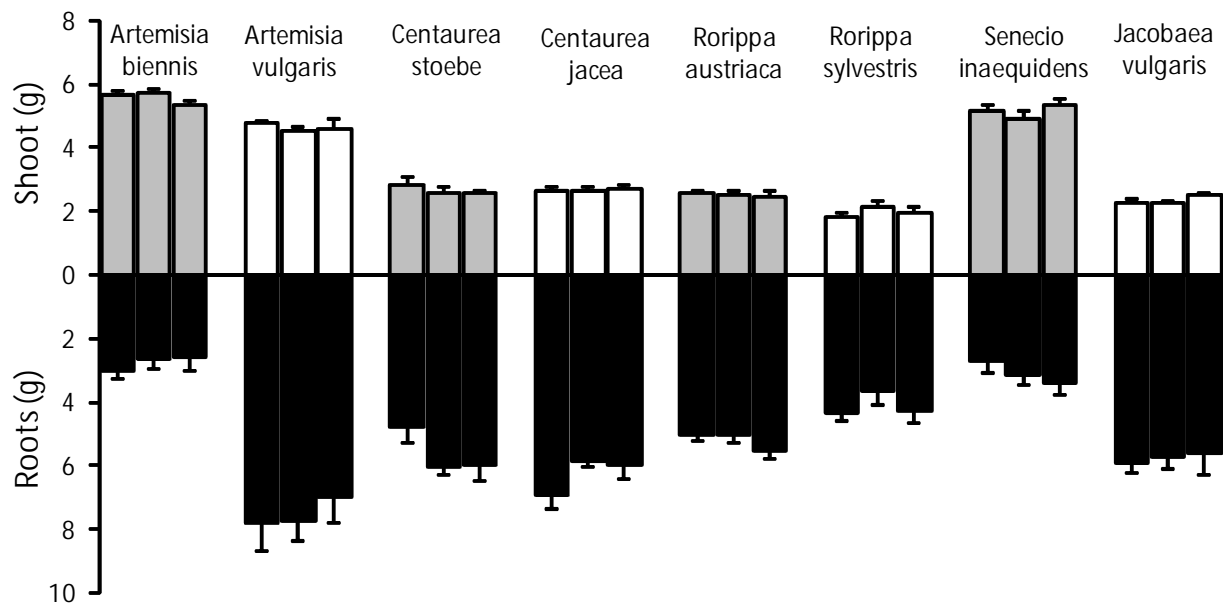
Table 2. Results from three-way ANOVAs investigating the effect of plant genus, plant origin and nematode antagonist treatment and their interactions on the shoot and root biomass of plant species pairs of range-expanders and their native congeners. The treatment with no additional inocula is included in the analyses.

	Shoot biomass		Root biomass	
	F	P	F	P
Genus (G)	50.02	<0.0001	9.89	<0.0001
Origin (O)	26.43	<0.0001	43.72	<0.0001
Treatment (T)	1.14	0.33	0.14	0.93
G x O	14.58	<0.0001	15.69	<0.0001
G x T	0.99	0.45	0.59	0.80
O x T	0.48	0.70	2.02	0.11
G x O x T	0.79	0.62	0.52	0.86

Table 3. Results from three-way ANOVAs investigating the effect of plant genus, plant origin and nematode antagonist treatment and their interactions on the abundance of root-feeding nematodes.

	Total root-feeding nematodes		Root-hair feeders		Ectoparasites		Endoparasites	
	F	P	F	P	F	P	F	P
	Genus (G)	240	<0.0001	11.3	<0.0001	23.6	<0.0001	370
Origin (O)	219	<0.0001	9.39	0.0027	6.97	0.0094	121	<0.0001
Treatment (T)	1.44	0.24	1.79	0.17	0.46	0.63	0.47	0.63
G x O	38.8	<0.0001	1.42	0.24	23.4	<0.0001	22.8	<0.0001
G x T	2.60	0.02	1.71	0.12	1.89	0.09	1.01	0.43
O x T	0.91	0.40	0.05	0.96	1.81	0.17	0.27	0.76
G x O x T	3.07	0.0078	1.49	0.19	1.70	0.13	1.42	0.21

Figure 1



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Figure 2

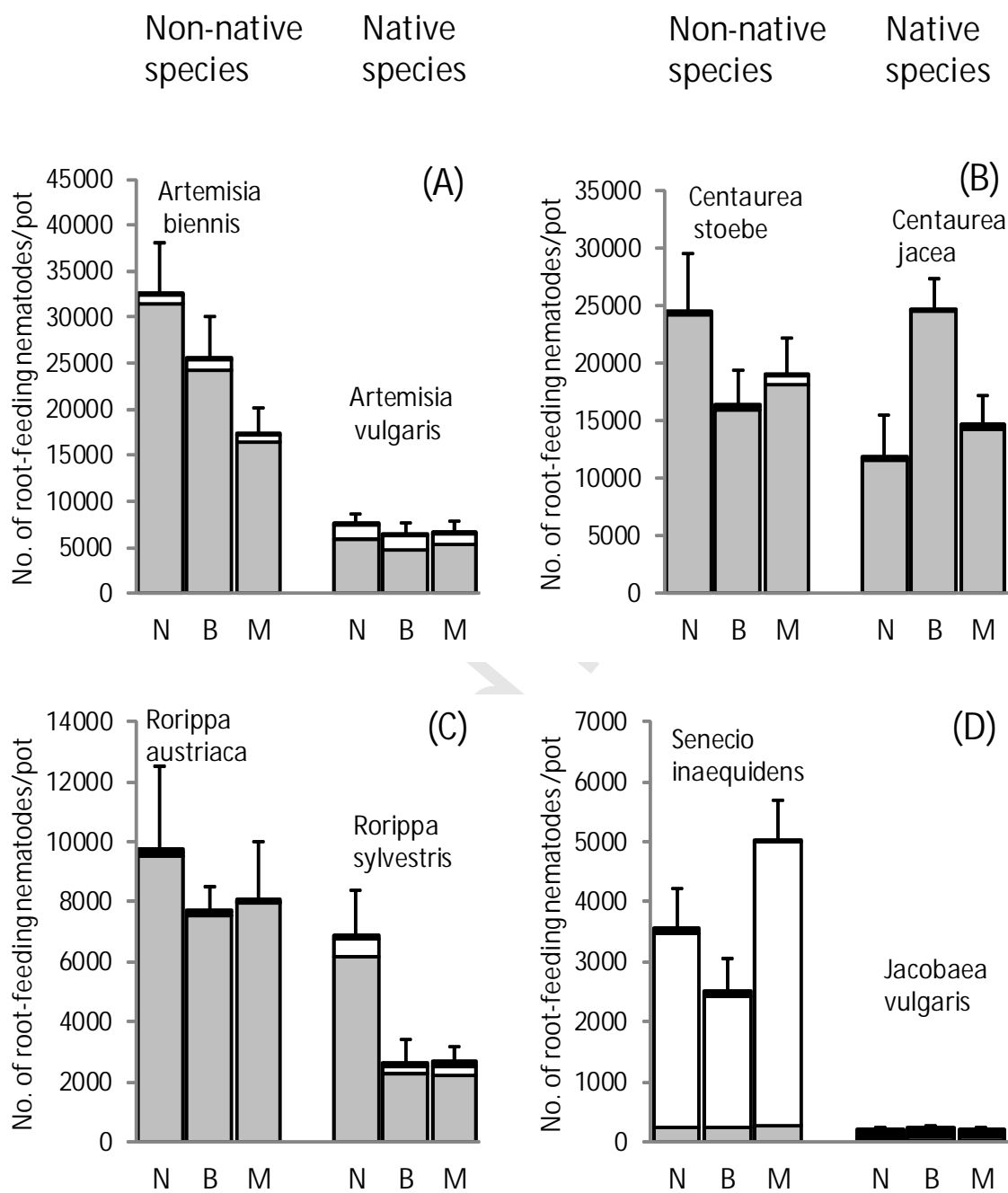
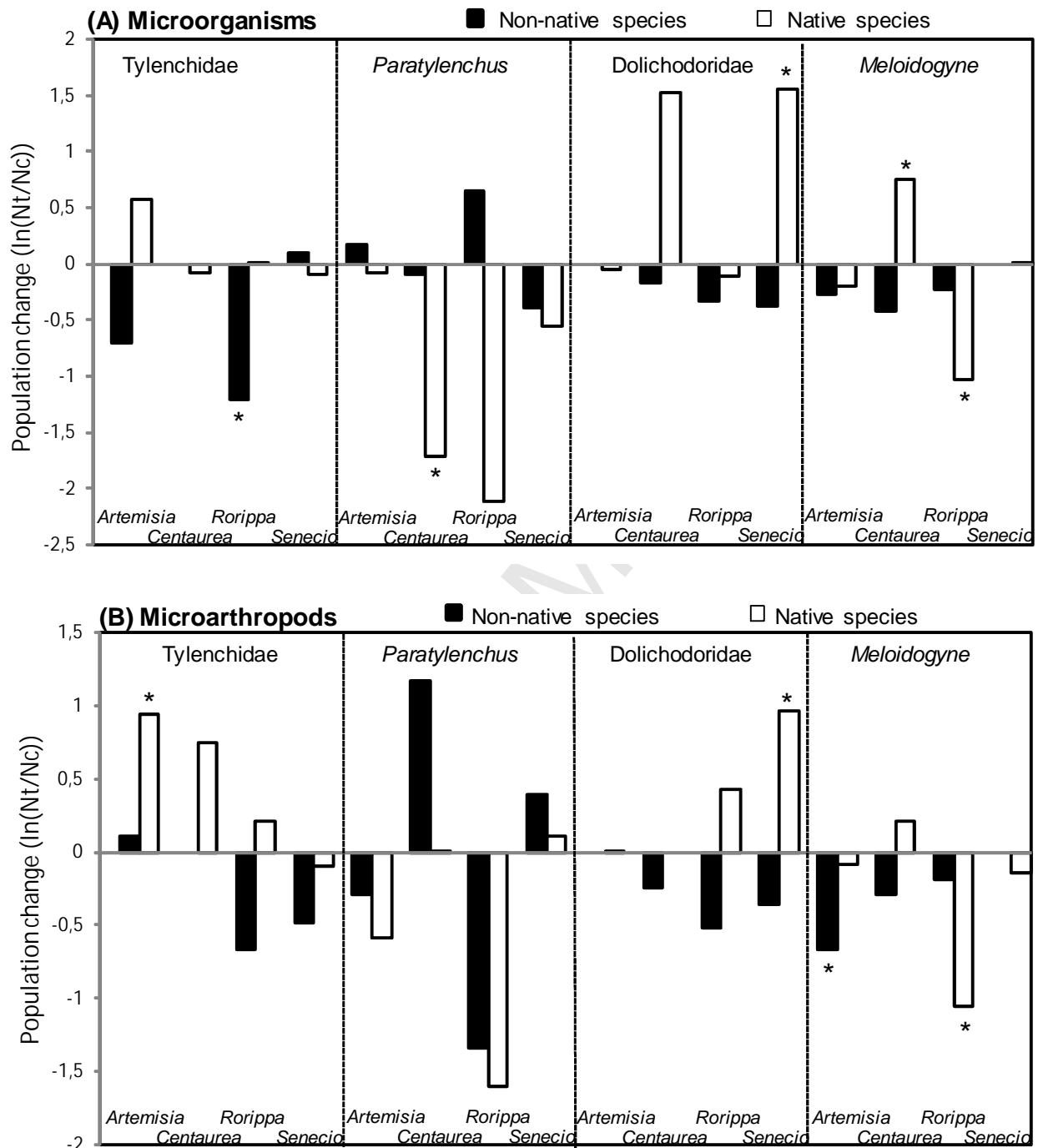


Figure 3



Zusammenfassung

Die Klimaerwärmung könnte zu einer Erweiterung des Verbreitungsgebietes von Arten hin zu früher kühleren Gebieten führen. Es konnte gezeigt werden, dass im neuen Siedlungsgebiet erfolgreich expandierende Pflanzenarten weniger stark von ober-

Zusammenfassung

Die Klimaerwärmung könnte zu einer Erweiterung des Verbreitungsgebietes von Arten hin zu früher kühleren Gebieten führen. Es konnte gezeigt werden, dass im neuen Siedlungsgebiet erfolgreich expandierende Pflanzenarten weniger stark von ober- oder unterirdischen Feinden attackiert werden können als einheimische Arten aus derselben Gattung. Feinde können natürlicherweise durch komplexe bottom-up- oder top-down-Interaktionen mit ihren Wirtspflanzen kontrolliert werden, es ist aber wenig darüber bekannt, wie diese Interaktionen im neuen Verbreitungsgebiet wirken. Wir untersuchen hier wie wurzelfressende Nematoden in der Wurzelzone von erfolgreich expandierenden Pflanzen im Vergleich zu der von kongenerischen einheimischen Arten kontrolliert werden. Da expandierende Pflanzenarten ein geringeres negatives Boden-Feedback als die einheimischen Schwesterarten aufweisen können, überprüften wir die Hypothese, dass die top-down-Kontrolle der wurzelfressenden Nematoden am stärksten bei den expandierenden Pflanzen wirken könnte. Um diese zu testen, kultivierten wir vier Paare von expandierenden und einheimischen Schwesterarten in Freilanderde, zu der wir Bodenmikroben, Nematoden oder Mikroarthropoden aus dem neuen Habitat hinzufügten. Die Hinzugabe von Mikroorganismen und Mikroarthropoden reduzierte die Anzahl wurzelfressender Nematoden, insbesondere wenn Mikroorganismen zugesetzt wurden. Entgegen unserer Erwartung war die Kontrolle der Nematoden in der Wurzelzone der expandierenden Pflanzenarten nicht stärker als bei den einheimischen Schwesterarten. Wir schließen, dass die top-down-Kontrolle der wurzelfressenden Nematoden sehr stark von der Pflanzenart abhängt und dass die top-down-Kontrolle dieser Nematoden in der Wurzelzone von expandierenden Pflanzenarten ebenso effektiv sein kann wie in der Wurzelzone ihrer einheimischen Schwesterarten.