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Temporal dynamics of range expander and congeneric native plant responses during and after extreme drought events

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Abstract

Climate change is causing range shifts of many species to higher latitudes and altitudes and increasing their exposure to extreme weather events. It has been shown that range-shifting plant species may perform differently in new soil than related natives; however, little is known about how extreme weather events affect range-expanding plants compared to related natives. In this study we used outdoor mesocosms to study how range-expanding plant species responded to extreme drought in live soil from a habitat in a new range with and without live soil from a habitat in the original range (Hungary). During summer drought, the shoot biomass of the range-expanding plant community declined. In spite of this, in the mixed community, range expanders produced more shoot biomass than congeneric natives. In mesocosms with a history of range expanders in the previous year, native plants produced less biomass. Plant legacy or soil origin effects did not change the response of natives or range expanders to summer drought. During rewetting, range expanders had less biomass than congeneric natives but higher drought resilience (survival) in soils from the new range where in the previous year native plant species had grown. The biomass patterns of the mixed plant communities were dominated by *Centaurea* spp.; however, not all plant species within the groups of natives and of range expanders showed the general pattern. Drought reduced the litter decomposition, microbial biomass, and abundances of bacterivorous, fungivorous, and carnivorous nematodes. Their abundances recovered during rewetting. There was less microbial and fungal biomass, and there were fewer fungivorous nematodes in soils from the original range where range expanders had grown in the previous year. We concluded that in mixed plant communities of range expanders and congeneric natives, range expanders performed better, under both ambient and drought conditions, than congeneric natives.

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However, when considering the responses of individual species, we observed variations among pairs of congenerics, so that under the present mixed-community conditions there was no uniformity in responses to drought of range expanders versus congeneric natives. Range-expanding plant species reduced soil fungal biomass and the numbers of soil fungivorous nematodes, suggesting that the effects of range-expanding plant species can trickle up in the soil food web.

KEYWORDS
climate change, global warming, legacy effects, litter decomposition, mesocosms, plant communities, range shifts, resilience, resistance, soil microbial community, soil nematode community, soil nitrogen mineralization

INTRODUCTION

Current rapid climate warming is enabling range expansions and range shifts of microbes, plants, and animals to previously colder areas (Parmesan & Yohe, 2003, Parmesan, 2006, Pecl et al., 2017), mostly at higher latitudes and altitudes (Alexander et al., 2015; Chen et al., 2011; Grabherr et al., 1994; Parmesan, 2006; Parmesan & Yohe, 2003; Walther, 2010; Walther et al., 2002). As species move individually and not as communities, range shifts likely result in decoupling of original communities and novel community interactions in the new range. For example, different migration rates of plants and their associated above- and belowground microbes and invertebrates (Berg et al., 2010; Van der Putten, 2012) will lead to novel interactions between plants and aboveground and belowground organisms in the expansion range with the potential to influence plant abundance (Van der Putten et al., 2010). Ecological consequences of such community reorganizations are, however, poorly understood.

Besides enabling range shifts, climate change also enhances the frequency and severity of extreme weather events, such as heat waves, extreme flooding, and extreme droughts (Dai, 2011; Easterling et al., 2000; EEA, 2016; IPCC, 2014; KNMI, 2015; Putnam & Broecker, 2017; Smith et al., 2009). It is entirely possible that plant species that shift range from continental or Mediterranean climate regions to temperate (Atlantic) climate regions, as is happening in northwestern Europe, are preadapted to the increasing droughts in their novel range (Hawkes et al., 2011, 2017). Different sensitivities to extreme drought between range expanders and the native residents (Meisner et al., 2013) may influence plant biomass production and plant community composition (Hacket-Pain et al., 2017; Sletvold & Agren, 2015). However, little is known about the outcome of interacting effects of range shifts and extreme weather events on productivity, plant community composition, and ecosystem processes. For example, range expanders might show different levels of resistance (the capacity to withstand) and resilience (the capacity to recover) to extreme weather conditions (Averill et al., 2016; Hawkes et al., 2011, 2017; Hawkes & Keitt, 2015) compared to native species from the expanded range. This represents a gap in our knowledge of the ecological consequences of combined responses to these different aspects of climate change.

In this study, we investigated the effects of extreme summer drought since the incidence of extreme drought is increasing rapidly. In soil, extreme drought generally reduces microbial activity and causes shifts in microbial composition (Barnard et al., 2013; Hawkes et al., 2011; Sheik et al., 2011) because fungi and bacteria differ in their responses to drought (Barnard et al., 2013; De Vries et al., 2012, 2018; Meisner et al., 2018). Drought may also affect higher trophic levels in the soil community, for example, soil nematodes (Franco et al., 2019). As a result, crucial soil ecosystem functions, such as carbon cycling (e.g., litter decomposition, soil respiration; Averill et al., 2016; Hawkes et al., 2017) and nutrient cycling (e.g., soil nitrogen mineralization; Meisner et al., 2013; Ashton et al., 2019; Fuchslueger et al., 2019) may slow down during drought. Plant performance and vegetation composition may be influenced by altered nutrient availability (Fry et al., 2018; Kaisermann et al., 2017; Meisner et al., 2013), as well as by changed abundances of soil pathogens and mutualistic symbionts and the relative composition of soil nematodes (Franco et al., 2019). All these factors may affect community composition and ecosystem functioning during rewetting.

In the new range, range-shifting plant species are less exposed to growth-reducing soil biota than closely related native species (Engelkes et al., 2008; Van Grunsven et al., 2010). Little is known about the consequences of soil biota comigration (Koorem et al., 2018, 2020). Some analyses have been conducted on microbial community composition (Ramirez et al., 2019) and nematodes

(Wilschut et al., 2019) along range expansion gradients, but these studies do not make it possible to formulate specific scenarios of species that do shift range, as has been the basis for choosing plant species for latitudinal range shift studies (Engelkes et al., 2008). Experiments with range-shifting soil biota, such as those that have been carried out with range-shifting plant species, would require isolation and culturing of specific soil biota, which would be highly challenging since most soil microbes are difficult to culture. Therefore, a more practical, although not entirely realistic, approach is to introduce whole soil from the original to the new range and test the combined effects of all soil biota. Results are difficult to predict because possible responses include enhanced exposure to soil-borne enemies (Van Grunsven et al., 2010), enhanced plant resistance or resilience to extreme weather events (De Vries et al., 2020), and enhanced resistance to drought of soil microbes from the original range (Manzoni et al., 2012). Outcomes may not necessarily be intuitive, as a recent study showed that soil microbes from Atlantic climate conditions were more responsive to rewetting after drought than soil microbes from continental climate conditions (Manrubia et al., 2019).

Plant responses to soil biota can be affected by historical factors that have influenced the community composition of soil biota. Both plant species (Heinen et al., 2020) and short-term (Meisner et al., 2013, 2021) or long-term droughts (Averill et al., 2016; Hawkes et al., 2017; Hawkes & Keitt, 2015) can influence soil community composition with consequences for feedback effects on plant performance. Despite the expanding knowledge gained from individual studies, the gap in our knowledge remains understanding how all these factors together may affect plant resistance and resilience under drought (Fry et al., 2018; Kaisermann et al., 2017) or other extreme weather events. Several possible outcomes are imaginable because plants may condition the soil biota such that both positive and negative interactions result. The net effects of such plant–soil feedbacks determine the outcome of plant production and plant community composition (Van der Putten et al., 2013). It is also possible that plant–soil feedback effects are influenced by the selection of specific microbial populations that impact plant responses to drought via regulation of carbon allocation (Hasibeder et al., 2015; Preece & Penuelas, 2016). Though there is a theoretical basis for making predictions, unknown outcomes of such multiple legacy effects complicate forecasting the responses of plant communities invaded by range-shifting plant species under new extreme weather conditions.

Examining the responses of novel plant species requires careful designing controls because plant comparisons may depend on their traits and their degree of relatedness (Liang et al., 2019; Schroeder et al., 2019; Wilschut et al., 2019). Therefore, in studies on the effects of introduced exotic plant species on ecosystem processes, tests have been conducted in a phylogenetically controlled manner by comparing exotics to closely related natives (Agrawal et al., 2005; Funk & Vitousek, 2007). A similar approach has been adopted for climate-change-induced range shifts (Engelkes et al., 2008; Koorem et al., 2018), where range-shifting plant species were compared with closely related congener plant species that occur in the same (invaded) habitat (Dostálek et al., 2016; Engelkes et al., 2008; Koorem et al., 2020; Ramirez et al., 2019; Smith et al., 2019; Tomiolo & Ward, 2018; Wilschut et al., 2019). Despite these approaches that controlled for relatedness, most studies have been carried out under highly controlled indoor conditions, whereas only few studies have examined plant community responses under seminatural outdoor conditions (Manrubia et al., 2019).

To fill these knowledge gaps, we performed an outdoor mesocosm experiment to test how mixed plant communities of range-shifting and congeneric native plant species respond to summer drought. In spring, we tested the interannual responses of plant communities to previous years' drought, whereas the intra-annual responses to the current year's drought were a combination of the recent drought effect and the effect of the drought in the preceding year. The outdoor mesocosm experiment was carried out in a factorial design, where we could also account for the effects of soil origin (individually replicated samples from a habitat in the original and from one in the novel range), as well as for effects of native versus range-expanding plant species that have conditioned the soils. By establishing new plant communities every year of testing, we ensured that possible legacy effects were carried over by the soil properties and not by carryover effects through the plants themselves (Meisner et al., 2013).

We tested the hypothesis that range expanders would be less affected than congeneric native plant species by summer drought and subsequent rewetting. The plants that we used are called range expanding because we know that they expand their range, but we do not know whether the southern range edge is moving up the latitudinal gradient as well, which would make them range shifting. We examined whether the responses of range expanders and congeneric natives depended on the legacies of a previous year's drought or soil conditioning by a previous plant community consisting of natives versus range expanders. In addition, we tested whether these responses differed between soils inoculated with soil samples from habitats in the novel or from the original range. We determined responses to the experimental treatments of plant shoot biomass, plant survival, soil functions (litter decomposition and soil nitrogen availability), soil bacterial and fungal biomass, and the amounts of microbivorous and root-feeding nematodes. To create experimental conditions as close as possible to those in nature, all plant species were grown in mixed species communities.

MATERIALS AND METHODS

We carried out an outdoor mesocosm experiment consisting of a 5-year conditioning phase by either communities of range expanders or congeneric species that occur naturally in the habitat where the range expanders become established. In the year previous to our study, half of the mesocosms had been exposed to a summer drought, whereas the other half received ambient rainfall as it had during the past 30 years (excluding the years that were officially designated by meteorologists as extremely dry years). The experimental treatments also included a comparison between northern soils without and with inoculation with live southern soil (see details in Figure 1). This enabled us to examine the effect of range expansion of all belowground biota in addition to plant range expansion.

Plant species

We selected four range-expanding plant species and for each range expander a native congener plant species (range expanders: *Centaurea stoebe* L. [*C. stoebe*], *Geranium pyrenaicum* (Brum. F.) [*G. pyrena*], *Tragopogon dubius* (Scop.) [*T. dubius*], and *Rorippa austriaca* [Crantz] Besser [*R. austri*] and congeneric native plants: *Centaurea jacea* L. [*C. jacea*], *Geranium molle* L. [*G. molle*], *Tragopogon pratensis* L. [*T. praten*], and *Rorippa sylvestris* (L.) [*R. sylves*]). Selection criteria were based on the premise that all plant species currently co-occur in riverine areas in the expansion range, the native plant species for many centuries, and the range expanders only for a number of decades (Engelkes et al., 2008; Koorem et al., 2020; Manrubia et al., 2019). Moreover, the range expanders should have increased in abundance disproportionately (Engelkes et al., 2008). These selection criteria limit the search, but four range expanders and four congeneric natives met the criteria. The four selected congeneric plant pairs represented different families (Appendix S1: Table S1).

Seeds of all (native and range-expanding) plant species were collected from the expansion range, in the Netherlands. We collected some species ourselves or purchased them from an external supplier (Cruydt Hoeck, Nijeberkoop, the Netherlands) that collects plant seeds from natural habitats, occasionally followed by multiplication in a plant nursery. All seeds were surface-sterilized with 0.5% hypochlorite solution, placed on glass beads, moistened with demineralized water, and germinated in a germination cabinet. Prior to planting, the seedlings

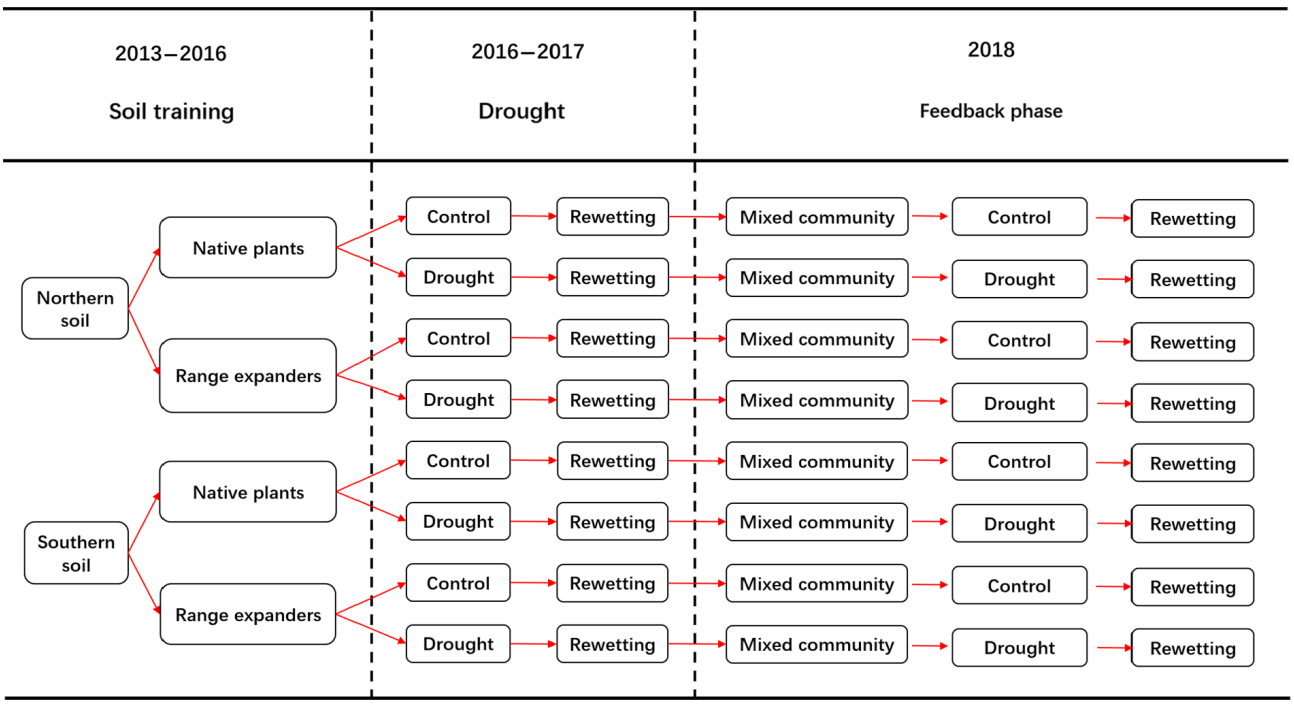

FIGURE 1 Experimental outline of mesocosm experiment. In 2013, we established 40 mesocosms with soil from the north; 20 mesocosms received an inoculum soil from the south (Hungary), whereas the other 20 mesocosms received an inoculum of soil from the north (the Netherlands) of Europe. From 2013 to 2016, soils were conditioned either by a mixture of native plant species or by a mixture of range expanders. In 2016 and 2017, half of the mesocosms (20 in total) were exposed to drought and the other 20 mesocosms were watered. In 2018, mixed plant communities of natives and range expanders were planted in each mesocosm, and half of all mesocosms were again exposed to summer drought.

were transferred to a half-open greenhouse to promote accommodation to outdoor conditions. After 2 weeks, equal-sized seedlings of each plant species were transplanted to the outdoor mesocosms.

Soils

The outdoor mesocosms (1 × 1 × 0.7 m) were established in 2012 by collecting subsurface soil from a floodplain area in the expansion range along one of the branches of the Rhine River. We inoculated the topsoil (around 20 cm deep) of half the mesocosms with 20% of field soil inoculum originating from a riparian area along one of the branches of the Rhine River in the Netherlands, which is part of the expansion range (henceforth called north soil). The other half of the mesocosms was inoculated with soil collected from Hungary, which is part of the original range where the range-expanding plants are native (henceforth called south soil). This treatment in fact exemplified a scenario where all soil organisms from the original range expand their range, and not a subset. We chose this approach because of a lack of information about which soil organisms were expanding their range and because of technical limitations of isolating and culturing such soil organisms. The southern soil was collected from a floodplain area near Solt in Hungary (46°47′58.95″, 18°57′30.97″), and collection took place in March 2013. In the same time period, northern soil was collected from the Millingerwaard area in the Netherlands (51°51′56.97″, 5°59′33.60″). All inoculation soils were collected from five independent locations in the field (minimally 60 m apart) and were kept separately to act as independent replicates in this experiment. After sampling, the inoculation soil of each replicate site was homogenized separately and sieved through a 10-mm mesh to remove coarse fragments and plant material before inoculation to the outdoor mesocosms. In the *Discussion* section, we will further elaborate on the consequences of the soil inoculation procedure using whole soil inoculation and soil collection from a subset of the southern and northern ranges.

Experimental design

During the 5-year conditioning phase, from 2013 to 2017, plant communities of native or range-expanding species were grown in soils with a northern (Netherlands) or southern (Hungary) inoculum in a full-factorial design (Figure 1, see Appendix S1: Table S1 for details on plant species composition). Each year in spring (April or May), we replanted annual plants and perennial plants that had died off, and we removed weedy plant species that had spontaneously colonized the mesocosms either from the seed bank or from the surroundings. In summer 2016 and 2017, we installed transparent rain shelters above all mesocosms. Then half of the mesocosms were artificially watered twice a week to ensure a rainfall regime representative of the seasonal average precipitation in the area of the last 5 years (2011–2015, 34 L/week; source: Royal Netherlands Meteorological Institute [KNMI]). The remaining half of the mesocosms received no artificial watering during a period of 6 weeks in order to mimic an extreme summer drought event that lasted from late June to early August. When the drought phase ended, all rain shelters were removed, and we artificially watered the mesocosms to ensure a minimum water input of 34 L/week for the next 12 weeks, which is when the last measurements were collected (Manrubia et al., 2019).

In May 2018, we grew mixed plant communities consisting of the four range expanders (*Centaurea stoebe* L., *Geranium pyrenaicum* [Brum. F.], *Tragopogon dubius* [Scop.], and *Rorippa austriaca* [Crantz] Besser) and the four congeneric natives (*Centaurea jacea* L., *Geranium molle* L., *Tragopogon pratensis* L., and *Rorippa sylvestris* [L.]) in all mesocosms (see Appendix S1: Table S1 for details on plant species composition). Prior to planting, we divided each mesocosm into four subplots. In each section, we planted one seedling of four range-expanding and four congeneric native plant species, so that there was a total of eight plant species planted according to a random design in each of the four subplots in every mesocosm. For this study, we only used the data from two subplots.

In summer 2018 (all the measurements are presented in Figure 2), we installed rain shelters and performed a 7-week summer drought treatment from 13 July to 29 August. Half of the mesocosms were artificially watered twice a week to ensure a rainfall regime representative of the seasonal average precipitation in the area of the last 5 years (34 L/week, source: KNMI). The other half of the mesocosms received 7 L water per week during a period of 7 weeks in order to mimic an extreme summer drought event (source KNMI). Ambient and drought treatments were given to the same mesocosms as in 2016 and 2017, so that the water treatments in the end had lasted three successive years. After the drought phase, we removed the rain shelters and rewetted the mesocosms, so that they all received 34 L water per week for 7 weeks (Appendix S1: Table S2; see Manrubia et al., 2019).

Plant measurements

Immediately after ending the summer drought, we clipped the shoot biomass of the plant community in one subplot in each mesocosm to determine plant resistance

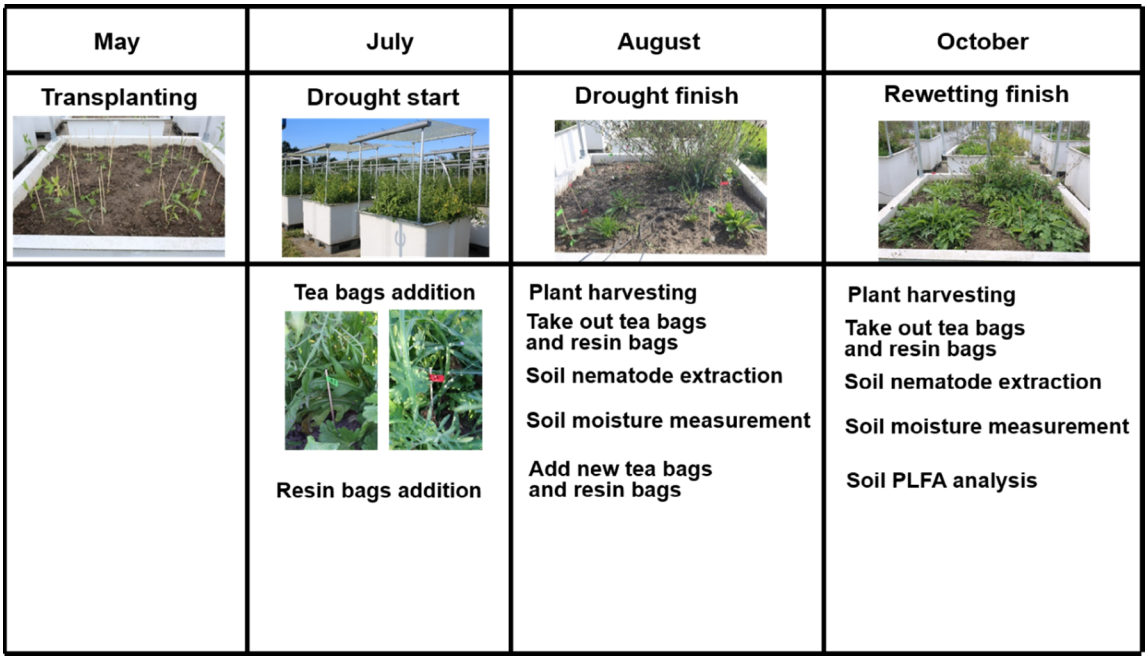

FIGURE 2 The timing of treatments and measurements used for the present study were taken from the mesocosm experiment in 2018.

to drought (Hoover et al., 2014; Pimm, 1984). After 7 weeks of recovery during rewetting, we collected plant survival and biomass in these previously clipped plots to measure plant regrowth. These data were compared to determine plant resilience (Pfisterer & Schmid, 2002; Tilman, 1996; Van Ruijven & Berendse, 2010). For all biomass samples we separated leaf and stem biomass for each plant species and dried the biomass at 45°C for 72 h before weighing. As mentioned earlier, for this study we only used the data from two subplots; the other two subplots were used for a herbivore addition study, which was outside the scope of the present study.

Soil nitrogen availability

Soil nitrogen (N) availability was measured using in situ ion-exchange free resin bags (Binkley et al., 1992) buried in the soil of each mesocosm during both drought and rewetting periods of 7 weeks each. Ion-exchange resins provide a relative measure of soil N availability by adsorbing N in the soil solution to the resin surfaces. Resin bags were made of nylon material with a mesh size of 50 μm (Top7even, Haarlem, the Netherlands). They contained 2 g of cation/anion exchange resin beads (Binkley & Matson, 1983) and were prerinsed in 2 M KCl. In each mesocosm and in both the drought and rewetting phases, the resin bags were placed in the mesocosm soil at 10 cm below the soil surface. At the end of both the drought and rewetting phases, we retrieved the resin bags from the soil, and stored them at 4°C until further analysis. The resin bags were rinsed with demineralized water to remove soil that had adhered to the outside of the bag. The bags were extracted in 25 ml of 1 M KCl by shaking for 2 h (250 rpm). Samples were stored at −20°C until analysis for NH_4^+-N and NO_3^--N content using an autoanalyzer (Quattro, Seal Analytical GmbH, Norderstedt, Germany).

Litter decomposition

We measured litter mass loss during both the drought and rewetting phases using a modified version of the Tea Bag Index method, which is a standardized protocol to assess the decomposition of substrates of contrasting chemical complexity (Keuskamp et al., 2013). At the start of both the drought and rewetting phases, in each mesocosm we buried preweighed green (representing easily decomposable organic matter) and rooibos (representing recalcitrant organic matter) tea bags at 10 cm below the soil surface. In this way, the chemical composition of the substrates was standardized at the beginning of both the drought and rewetting phases. The tea bags were buried at random locations in the center of the mesocosms, avoiding potential edge effects. At the end of both the drought and rewetting phases, we retrieved the teabags from the soil, removed the roots, oven-dried the remaining tea material (70°C for 48 h), dry sieved it to 0.4 mm to remove soil particles, and weighed the dry tea to determine mass loss.

Soil nematode community

At the end of each 7-week—both drought and rewetting—phases, we collected soil samples that were stored at 4°C, until we prepared samples for nematode extraction. Nematodes were extracted from soil using Oostenbrink elutriators (Oostenbrink, 1960). The suspensions with nematodes were then led through one 75-µm sieve and three 45-µm sieves. The material, including the nematodes collected from the 75- and 45-µm sieves, was transferred to a double cotton filter on a sieve in a dish with a layer of tap water (Oostenbrink, 1960). The nematodes were allowed to migrate through the filter into the water for 24 h at room temperature, which resulted in relatively clean suspensions for nematode counting. Suspensions were stored at 4°C until they were fixated with hot formalin. The total numbers of nematodes in the soil samples were counted and identified to the genus or family level using a reverse light microscope and categorized into feeding guilds according to Bongers and Yeates (1988) and Yeates, Bongers, et al. (1993). The root feeders were further subdivided into four feeding types: ectoparasites, semi-endoparasites, migratory endoparasites, and sedentary endoparasites (Yeates, Bongers, et al., 1993). Epidermis or root hair feeders were classified as plant-associated nematodes (Yeates, Wardle, & Watson, 1993). Total numbers of nematodes were expressed as numbers per 100 g dry soil.

We compared the relative abundance of the different feeding groups (root feeders, fungal feeders, and bacterial feeders, omnivores and carnivores). Each nematode family was also assigned to a colonizer-persister value (*c-p*), which indicates their life strategy, ranging from 1 (r-strategist species, colonizers) to 5 (K-strategist species, persisters) (Bongers, 1990). C-p 1 nematodes (only bacterial feeders) have a high fecundity and are relatively resistant to pollutants owing to their nonpermeable cuticle. Only c-p 1 nematodes are able to form dauer larvae to overcome unfavorable conditions, such as resource depletion. Combining the c-p class of the nematode family with the respective feeding type allowed sorting nematodes according to functional guilds (bacterial feeder [Ba_x], fungal feeder [Fu_x], omnivore [Om_x], predators (Pr_x), where x = c-p class) (Ferris et al., 2001). We excluded plant-root-feeding nematodes for the calculation of the nematode indices following Bongers (1990). The functional diversity of the nematode community was analyzed by diversity indices developed for nematode community studies (Ferris et al., 2001). Different nematode indices were calculated based on c-p values and functional guilds.

The Structure Index (SI) reflects the stability and structure of the soil food web and the stability of trophic links. An ecosystem with a high SI means that it has many trophic links and that it is highly structured,

$$\mathrm{SI} = 100 \times \left[\frac{s}{s+b}\right],$$

with s (structure food web component) calculated as the weighted frequencies of Ba_3–Ba_5, Fu_3-Fu_5, Pr_3–Pr_5, and Om_3-Om_5, and b (basal food web component) as the weighted frequencies of Ba_2 and Fu_2 (Ferris et al., 2001).

The Channel Index (CI) indicates the main decomposition channel (bacterial- or fungal-dominated). High CI values indicate a more fungal-dominated system, while low values indicate a more bacterial-dominated system

$$\mathrm{CI} = 100 \times \left[\frac{\mathrm{Fu}_2}{3.2 \times \mathrm{Ba}_1 + 0.8 \times \mathrm{Fu}_2}\right],$$

where 0.8 and 3.2 are coefficients of enrichment weightings for Fu_2 and Ba_1, respectively (Ferris et al., 2001).

Soil microbial community

Phospholipid fatty acids (PLFAs) were extracted from 3 g freeze-dried soil (Frostegård & Bååth, 1996). The PLFAs 15:0, i15:0, a15:0, i16:0, 16:0ω9, i17:0, a17:0, cy17:0, 18:1ω7, and cy19:0 were used as markers of bacterial biomass (Frostegård & Bååth, 1996). Extracted fatty acid methyl esters were analyzed on an Agilent Technologies 7890B gas chromatograph with an Agilent DB-5 ms column. The amount of PLFA 18:2ω6 was used as a marker of nonmycorrhizal fungal biomass, and the neutral lipid fatty acid (NLFA) 16:1ω5 was used as a marker for arbuscular mycorrhizal fungi (AMF) (Olsson et al., 1995).

Drought resilience

Drought resilience was calculated at the end of the rewetting phase as $\mathrm{survival}_{\mathrm{drought}}/\mathrm{survival}_{\mathrm{control}}$ using plant survival from the plots that had been clipped as well at the end of the drought phase.

Statistical analysis

To test whether range expanders differed consistently from natives in their responses to experimental treatments, we first used general linear mixed-effect model (Procedure [PROC] mixed in SAS 9.4, SAS Institute Inc., Cary, NC, USA) to test how the total plant aboveground biomass of four range expanders and of four congeneric native plant species was affected by the experimental treatments after both the drought period and rewetting. We included origin of the conditioning plant community

(range expander or native plant legacy), soil inoculum origin (north or south), species origin (range expanders or natives), species genera (*Centaurea*, *Geranium*, *Tragopogon*, and *Rorippa*), and drought (control or drought) as the fixed factors and mesocosm nested within block (mesocosm [block]) and species nested within genera as the random factors.

We then used a general linear mixed-effect model (PROC mixed in SAS) to test how plant aboveground biomass of range expanders and congeneric native plant species was affected by the experimental treatments after both the drought period and after rewetting phases. We added up all values of the four range expanders and of the four natives in each mesocosm as two subgroups. We included origin of the conditioning plant community (range expander or native plant legacy), soil inoculum origin (north or south), species origin (range expander or native), and drought (control or drought) as fixed factors and mesocosm nested within block (mesocosm [block]) as a random factor.

We used general linear mixed-effect models to test how the drought resilience of range expanders and congeneric native plant species was affected by the experimental treatments during summer drought and rewetting. We included origin of the conditioning plant community (range expander or native legacy), soil inoculum origin (north or south), and species origin (range expander or native) as fixed factors and block as a random factor.

We then used general linear mixed-effect models to test how litter decomposition (green tea and rooibos tea leaves), soil N availability (nitrate and ammonium content in each resin bag), soil nematode abundance and community indices, and soil microbial biomass in each mesocosm were affected by the experimental treatments during summer drought and rewetting. We included the origin of the plant community that had conditioned the soils in the years prior to the present study (range expander or native legacy), soil inoculum origin (north or south), and drought (control or drought) as fixed factors and block as a random factor.

Prior to all tests, we checked that data were meeting the assumptions for ANOVA (PROC univariate in SAS). We used the Bonferroni correction methods to adjust the p values in each individual analysis. All statistical tests were performed using SAS version 9.4 (SAS Institute, Cary, NC, USA).

RESULTS

Performance of range expanders and congeneric native plants after drought

In the mixed community, range expanders generally had more shoot biomass than congeneric natives in the mixed plant community (significant species origin effect, Figure 3; Appendix S1: Table S3). However, this effect was particularly driven by *Centaurea* spp. (significant species origin × genus effect, Figure 3; Appendix S1: Table S3). Generally, our results showed that plant shoot biomass was greater in soils that had been conditioned by natives in the preceding years (significant soil conditioning effect, Figure 3; Appendix S1: Table S3). Again, this result was particularly caused by *Centaurea* spp. (significant soil conditioning × genus effect, Figure 3; Appendix S1: Table S3). In the mixed plant community, *Centaurea* spp. had the most shoot biomass, and *Tragopogon* had the least shoot biomass (significant genus effect, Figure 3; Appendix S1: Table S3). The species responses varied between soil origins; *Centaurea* spp. had more shoot biomass in the north soil but *Rorippa* spp. had greater shoot biomass in the south soil (significant soil origin × genus effect, Figure 3; Appendix S1: Table S3). *Centaurea* plants (*Centaurea jacea* and *Centaurea stoebe*) had more shoot biomass in soils conditioned by native plant community when growing in north soils but only in soils conditioned by native plant community when growing in south soils for *Centaurea* native plant (*Centaurea jacea*) (significant "Soil origin × soil conditioning × species origin × genus" effect, Figure 3; Appendix S1: Table S3).

When we added the four range expanders and four natives together as two subgroups in the same community, we found that the range expanders produced significantly ($p < 0.05$) more shoot biomass than congeneric natives in the mixed community (Figure 6a; Appendix S1: Table S4). Plant biomass was also determined by the origin of the plants that had conditioned the soils in the preceding years (Figure 6a; Appendix S1: Table S4), whereas native plants produced less shoot biomass on soils conditioned by range expanders, while there was no such plant legacy effect for range expanders (Figure 6a; Appendix S1: Table S4). Drought decreased the plant shoot biomass of range expanders, but not of natives (Figure 6a; Appendix S1: Table S4). Plant legacy effects did not change the response of natives or range expanders to summer drought since there was no significant interaction between these factors with respect to shoot biomass, and soil origin did not affect shoot biomass and biomass allocation to leaves (no significant soil conditioning × drought × species origin effect; Appendix S1: Table S4).

Performance of range expanders and congeneric native plants after rewetting

During rewetting, *Centaurea* spp. generally had highest survival rate, then *Tragopogon* spp., then *Rorippa* spp., whereas *Geranium* spp. had the lowest survival rate (significant genus effect, Figure 4; Appendix S1: Table S5). Range expanders generally had higher survival rate than congeneric natives (significant species origin effect, Figure 4; Appendix S1: Table S5), particularly *Geranium* and *Rorippa*

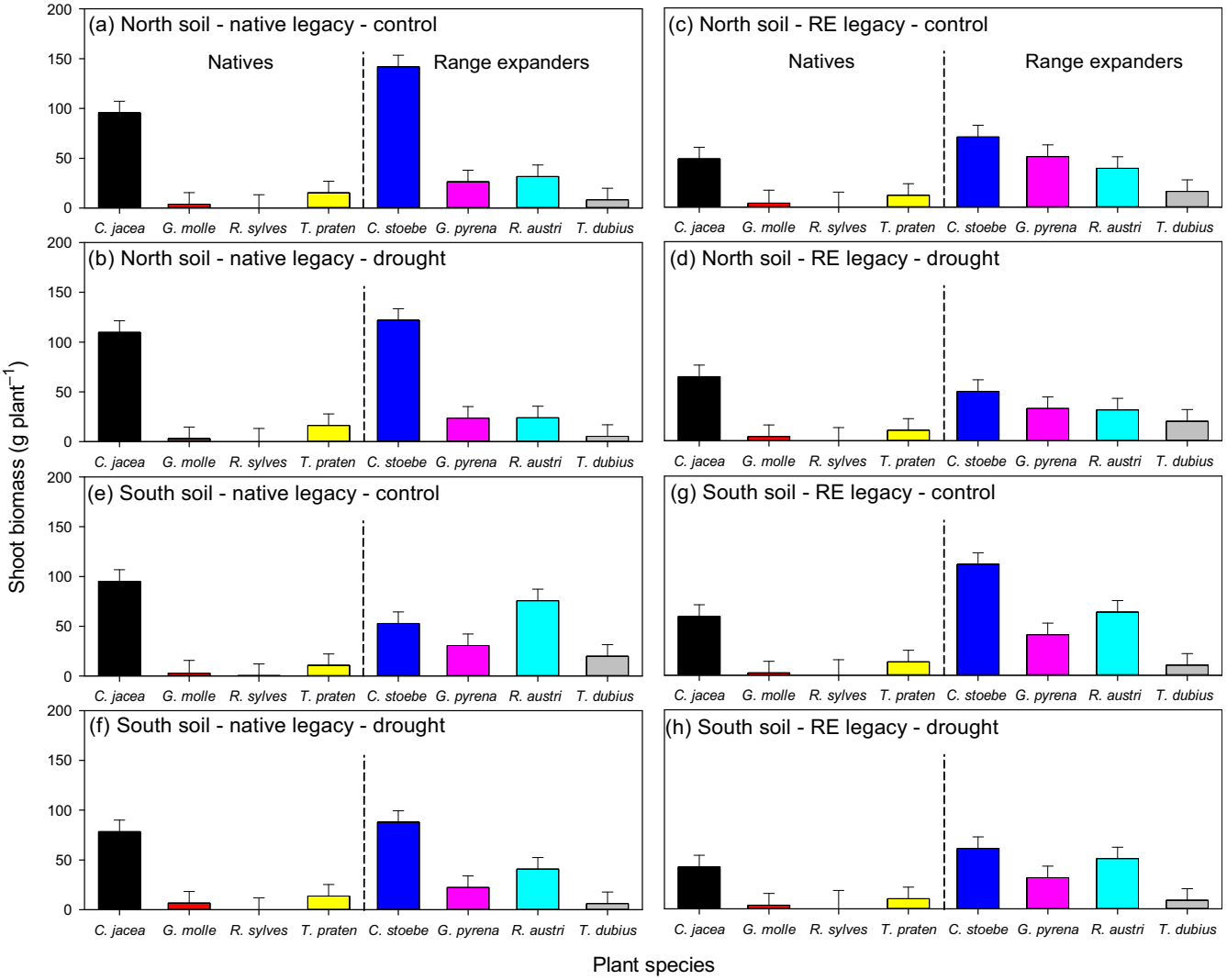

FIGURE 3 Shoot biomass of range expanders and congeneric natives in soil conditioned by natives (native legacy: a, b, e, f) and range expanders (RE legacy: c, d, g, h) without and with summer drought (control: a, c, e, g; and drought: b, d, f, h) after summer drought. Soils were from the Netherlands (north: a, b, c, d) and Hungary (south: e, f, g, h) representing novel and original range sites, respectively. Means ± 1 standard error. Black: *Centaurea jacea* L. (*C_jacea*); Red: *Geranium molle* L. (*G_molle*); Green: *Rorippa sylvestris* (L.) Besser (*R_sylves*); Yellow: *Tragopogon pratensis* L. (*T_praten*); Blue: *Centaurea stoebe* L. (*C_stoebe*); Pink: *Geranium pyrenaicum* (Burm. F.) (*G_pyrena*); Cyan: *Rorippa austriaca* (Crantz) Besser (*R_austri*); Grey: *Tragopogon dubius* (Scop.) (*T_dubius*).

spp. but *Tragopogon* spp.had the opposite pattern (significant species origin × genus effect, Figure 4; Appendix S1: Table S5). Range expanders had higher survival rates except for plants growing in north soils conditioned by range expanders (significant soil origin × soil conditioning × species origin effect, Figure 4; Appendix S1: Table S5). Moreover, range expanders had higher survival rates depending on plant conditioning and summer drought, except in mesocosms conditioned by natives without summer drought (significant soil conditioning × drought × species origin effect, Figure 4; Appendix S1: Table S5).

The plant shoot biomass of each species was determined by genus and plant species × genus (Figure 5; Appendix S1: Table S5), where *Centaurea jacea*, a native plant, had more shoot biomass, while for the other species there was no difference between drought treatments, soil origin, and origin of the conditioning community (Figure 5; Appendix S1: Table S5).

When we added the four range expanders and four natives together as two subgroups in the same community, we found that more plant shoot biomass was produced in mesocosms with a history of summer drought (significant drought effect, Figure 6b; Appendix S1: Table S6), and native plant species had more shoot biomass than range expanders (significant species origin effect, Figure 6b; Appendix S1: Table S6). There was no legacy of soil origin or soil conditioning on shoot biomass during rewetting (Appendix S1: Table S6).

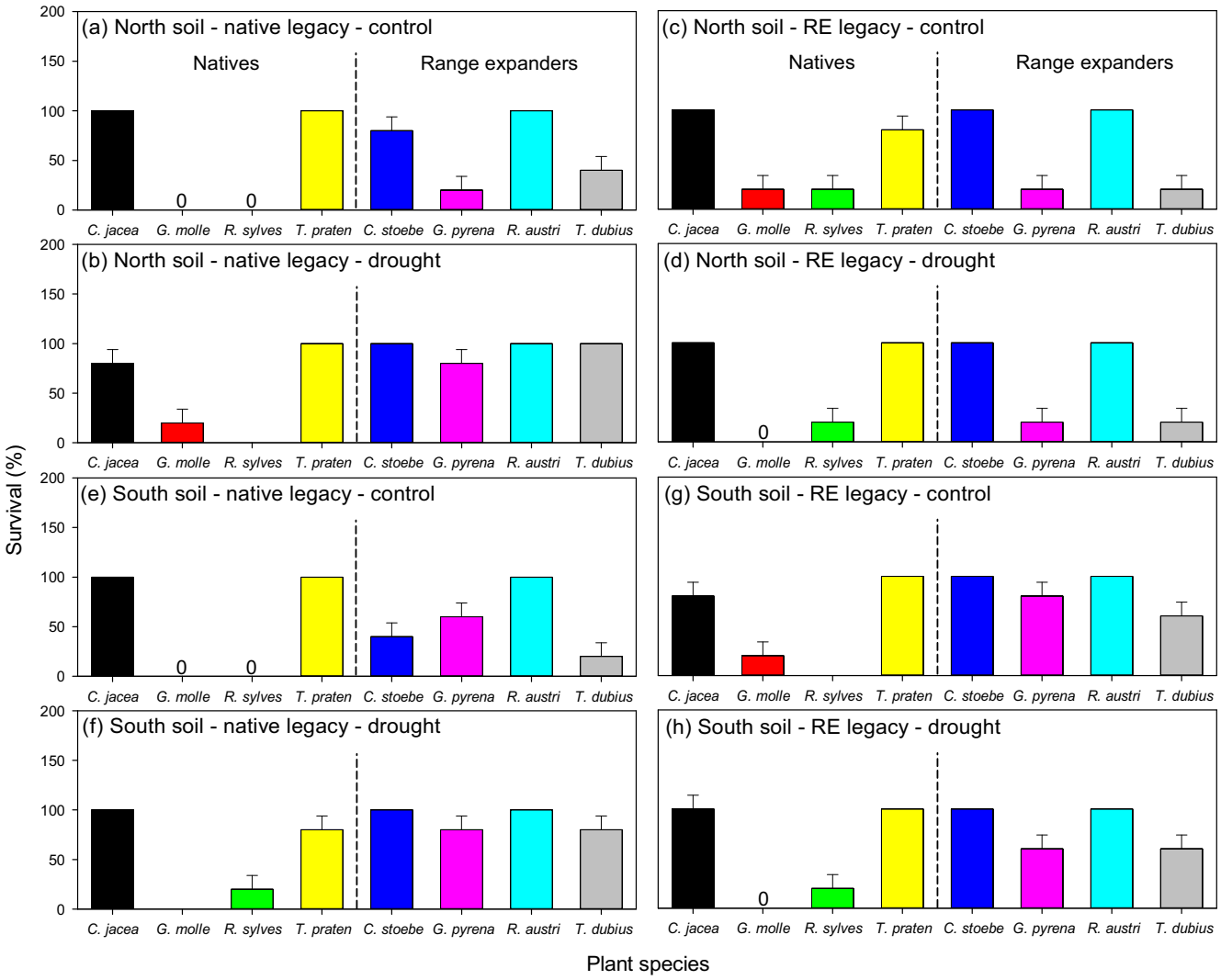

FIGURE 4 Plant survival of range expanders and congeneric natives in soil conditioned by natives (native legacy: a, b, e, f) and range expanders (RE legacy: c, d, g, h) without and with summer drought legacy (control: a, c, e, g; and drought: b, d, f, h) after rewetting. Soils were from the Netherlands (north: a, b, c, d) and Hungary (south: e, f, g, h) representing novel and original range sites, respectively. Means ± 1 standard error. Black: *Centaurea jacea* L. (*C_jacea*); Red: *Geranium molle* L. (*G_molle*); Green: *Rorippa sylvestris* (L.) Besser (*R_sylves*); Yellow: *Tragopogon pratensis* L. (*T_praten*); Blue: *Centaurea stoebe* L. (*C_stoebe*); Pink: *Geranium pyrenaicum* (Burm. F.) (*G_pyrena*); Cyan: *Rorippa austriaca* (Crantz) Besser (*R_austri*); Grey: *Tragopogon dubius* (Scop.) (*T_dubius*).

Drought resilience of range expanders and congeneric native plants

During rewetting, range expanders turned out to be more resilient in their survival than natives (Figure 7), albeit only in soils previously conditioned by natives (significant species origin × soil conditioning effect in Appendix S1: Table S7; Figure 7).

Ecosystem functioning

Soil nitrate and ammonium contents in the resin bags were not affected by drought, soil origin, or legacy of plant conditioning during drought (Appendix S1: Figure S1 and Appendix S1: Table S8). During rewetting, nitrate content was higher in mesocosms with a history of summer drought (significant drought effect; Appendix S1: Figure S1 and Appendix S1: Table S8). There was no such pattern for ammonium content in the rewetting phase (Appendix S1: Figure S1 and Appendix S1: Table S8).

Summer drought significantly decreased rooibos tea decomposition rate, but the effects were influenced by both soil conditioning and soil origin. In the control mesocosms, range-expander-conditioned soil had a higher litter decomposition rate in northern soil but a lower litter decomposition rate than congeneric native-conditioned southern soil; however, these patterns disappeared in the drought mesocosms (significant soil origin × soil conditioning × drought effect; Appendix S1:

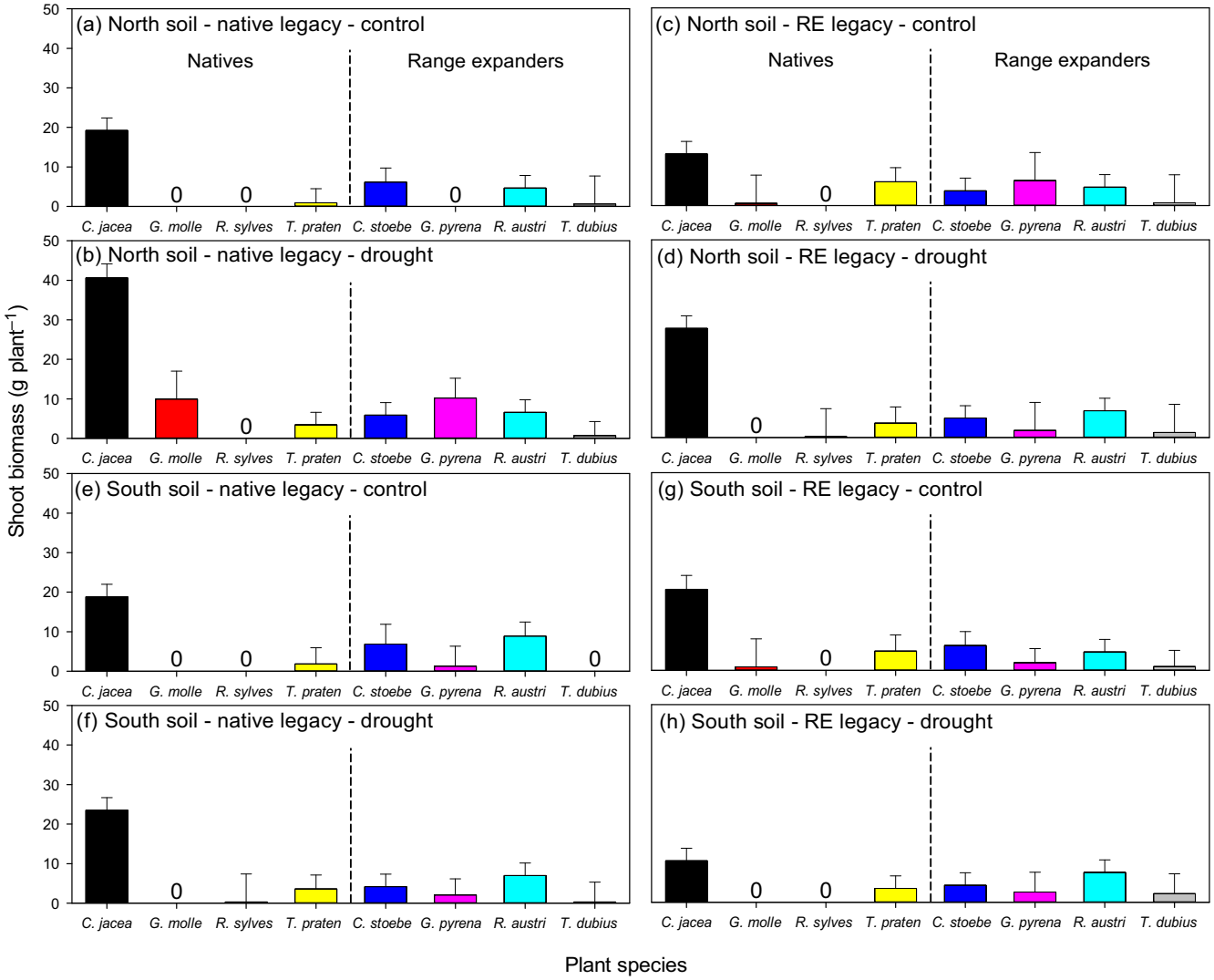

FIGURE 5 Shoot biomass of range expanders and congeneric natives in soil conditioned by natives (native legacy: a, b, e, f) and range expanders (RE legacy: c, d, g, h) without and with summer drought (control: a, c, e, g; and drought: b, d, f, h) after rewetting. Soils were from the Netherlands (north: a, b, c, d) and Hungary (south: e, f, g, h) representing novel and original range sites, respectively. Means ± 1 standard error. Black: *Centaurea jacea* L. (*C_jacea*); Red: *Geranium molle* L. (*G_molle*); Green: *Rorippa sylvestris* (L.) Besser (*R_sylves*); Yellow: *Tragopogon pratensis* L. (*T_praten*); Blue: *Centaurea stoebe* L. (*C_stoebe*); Pink: *Geranium pyrenaicum* (Burm. F.) (*G_pyrena*); Cyan: *Rorippa austriaca* (Crantz) Besser (*R_austri*); Grey: *Tragopogon dubius* (Scop.) (*T_dubius*).

Figure S2 and Appendix S1: Table S9). The decomposition rate of green tea was not affected by any experimental treatment (Appendix S1: Figure S2 and Appendix S1: Table S9). During rewetting, there were no significant differences in tea decomposition among any treatment (Appendix S1: Figure S2 and Appendix S1: Table S9).

Soil nematode community

Total soil nematode abundance was reduced by summer drought ($F_{1,26} = 33.20$, $p < 0.0001$) (Figure 8; Appendix S1: Figure S3). After 7 weeks of rewetting, the total abundance of soil nematodes was still lower in mesocosms that had experienced summer drought earlier in the season ($F_{1,26} = 5.11$, $p = 0.0323$) (Figure 8; Appendix S1: Figure S3), but this effect was only apparent in soil conditioned by natives, as indicated by interactions between soil conditioning × drought ($F_{1,26} = 5.29$, $p = 0.0298$) (Figure 8; Appendix S1: Figure S3).

The relative abundance of bacterivorous nematodes was reduced by summer drought, but only in soils conditioned by native plant species (Appendix S1: Figure S4a and Appendix S1: Table S10). During rewetting, differences in relative abundance of bacterivorous nematodes disappeared (Appendix S1: Figure S4b and Appendix S1: Table S10). Summer drought reduced the relative abundance of fungivorous nematodes (Appendix S1:

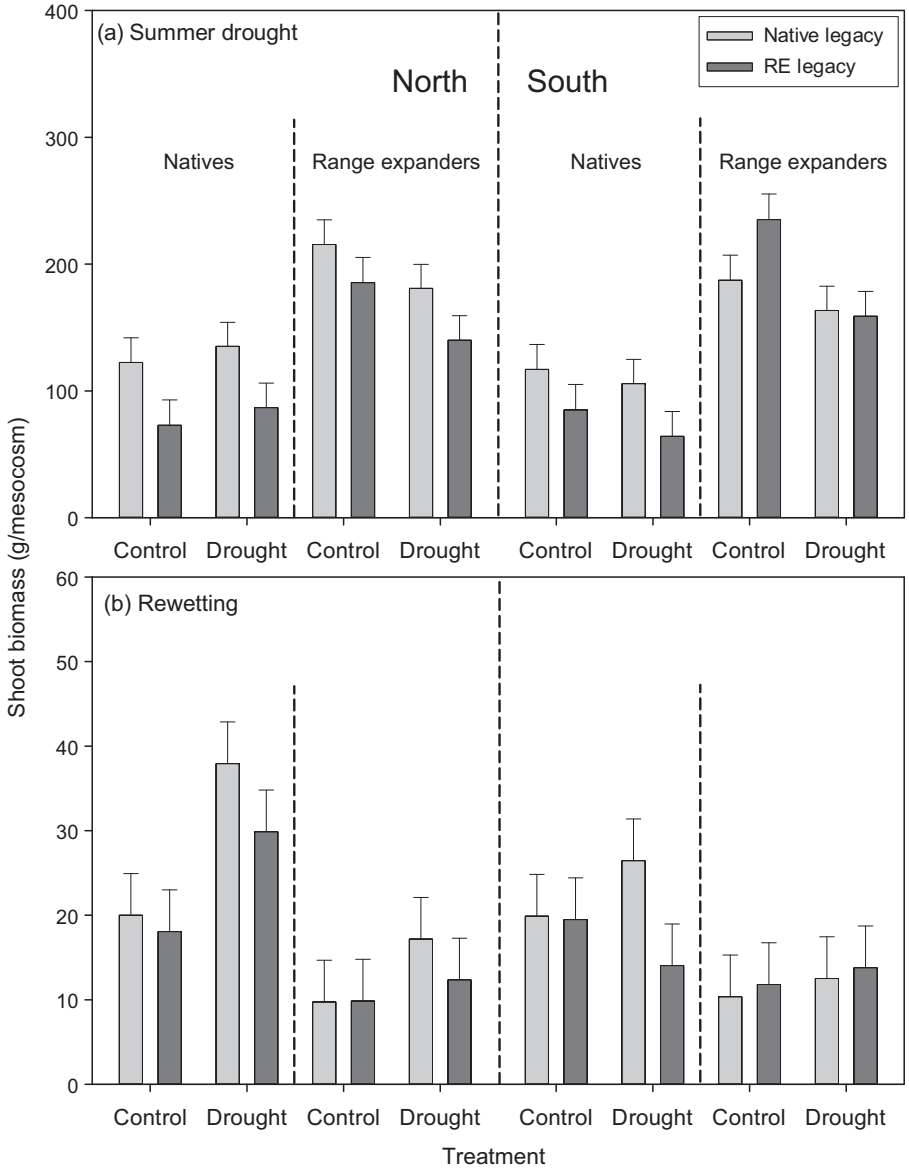

FIGURE 6 Shoot biomass of mixed plant communities (a) under summer drought events; (b) regrowth after clipping during rewetting under legacy effects from previous year of soil conditioning by natives (native legacy) and range expanders (RE legacy) in northern European soils inoculated with live soils from northern Europe (north, Netherlands) or southern Europe (south, Hungary). Means ± 1 standard error (SE).

Figure S5a and Appendix S1: Table S10). In addition, in soils conditioned by range expanders, the relative abundance of fungivorous nematodes was lower than soil conditioned by congeneric native plants during rewetting (Appendix S1: Figure S5 and Appendix S1: Table S10). For root-feeding nematodes, relative abundances were not affected by soil conditioning or soil origin during summer drought (Appendix S1: Figure S6a and Appendix S1: Table S10). After rewetting, soils with a history of summer drought had the highest relative abundances of root-feeding nematodes (Appendix S1: Figure S6b and Appendix S1: Table S10). Summer drought reduced the relative abundance of omnivorous nematodes, but this effect disappeared during rewetting (Appendix S1: Figure S7 and Appendix S1: Table S10). Drought, plant, and soil legacies did not affect the relative abundance of predator nematodes (Appendix S1: Table S10).

Among the several indices calculated for nematode communities, generally the CI values of nematodes was higher during summer drought than during rewetting. During summer drought, we found significant three-way interaction among soil origin, soil conditioning, and summer drought affecting the CI values of nematodes. Generally summer drought increased CI values, not only in soils previously conditioned by range expanders in

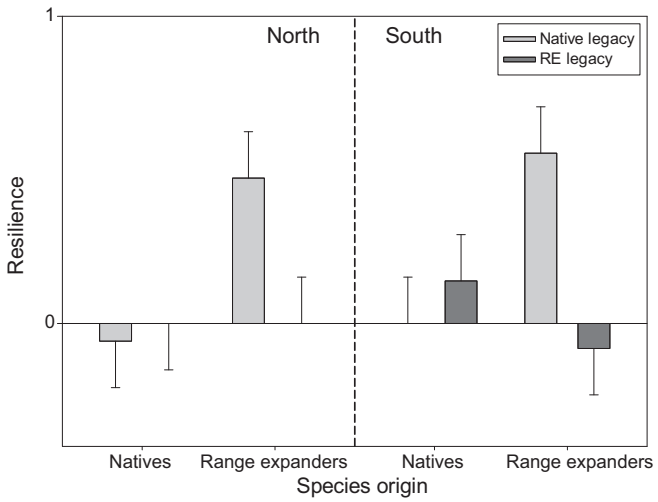

FIGURE 7 Plant drought resilience (survival) of mixed plant communities of four range expanders and four congeneric native plant species under legacy effects from previous year of soil conditioning by natives (native legacy) and range expanders (RE legacy) grown in northern European soils inoculated with live soils from northern Europe (north, Netherlands) or southern Europe (south, Hungary). Means ± 1 standard error.

northern soils, but also in soils previously conditioned by natives in southern soils. However, during rewetting, the CI of nematodes was unaffected by any of the experimental treatments (Appendix S1: Table S11 and Appendix S1: Figure S8a,b). Generally, the Structure Index (SI) of nematodes was lower during summer drought than during rewetting. During summer drought, the SI of nematodes was unaffected by any of the experimental treatments. However, the SI of nematodes was higher in soils conditioned by natives than in soils conditioned by range expanders during rewetting (Appendix S1: Table S11 and Appendix S1: Figure S8c,d).

Soil microbial biomass

Soil microbial biomass measured as PLFA and NLFA was reduced by summer drought (significant drought effect, Figure 9; Appendix S1: Table S12). Total microbial and bacterial biomass was higher in northern soils than in soils with southern soil inocula, particularly when conditioned by native plants (significant soil origin × soil conditioning effect in Appendix S1: Table S12 and Figure 9). Northern soils had more fungal biomass than southern soils (significant soil origin effect, Figure 9; Appendix S1: Table S12). The biomass of actinomycetes was higher in northern than southern soils and in soils conditioned by native plants (significant soil origin or soil conditioning effects, Figure 9; Appendix S1: Table S12). Protozoa biomass and AMF biomass were not affected by any of the treatments (Figure 9; Appendix S1: Table S12).

DISCUSSION

We studied how legacy effects of soil origin and soil conditioning by range expanders and congeneric natives affected their shoot biomass in mixed plant communities. We also analyzed the associated soil communities and soil processes, especially decomposition and soil N availability, after 7 weeks of summer drought and after 7 weeks of rewetting. Our results showed that range expanders on average produced more shoot biomass and were more resilient to drought than congeneric natives. Moreover, soil origin and the legacy effects of the plants that had conditioned the soils during the preceding years affected plant responses to drought. Plants generally recovered fastest in soils that had been conditioned by a native community or in soils with an inoculum from northern Europe. Together our results make it clear that in mixed plant communities, the performance of range-expanding versus congeneric native plant species and their respective resilience to extreme summer drought events depend on both plant and soil origin, as well as on the recent history of soil conditioning by range-expanding or native plant species.

As we grew range-expanding plant species and related natives in mixed plant communities, the responses of both plant origin groups may depend not only on their own responses but also on the responses of the other group. Therefore, we focused on range-expanding and native plant responses in ecological communities rather than on the responses of range expanders and natives individually (Engelkes et al., 2008; Koorem et al., 2018). However, not all range expanders showed the same pattern. Within plant communities, the general pattern was determined by *Centaurea* spp. that determined most of the biomass production. In other plant pairs, the range expanders did not necessarily show the same pattern as in the *Centaurea* pair. Although this community experiment did not allow for testing the individual responses of range expanders versus congeneric native species, as was done in previous studies (e.g., Engelkes et al., 2008; Van Grunsven et al., 2014), it provides valuable insights into how plants of different origins may perform in novel plant communities (Dostálek et al., 2016; Koorem et al., 2020; Meisner et al., 2013; Tomiolo & Ward, 2018). In the present case, it showed that not all range expanders were similar in their responses compared to congeneric natives from the same habitat.

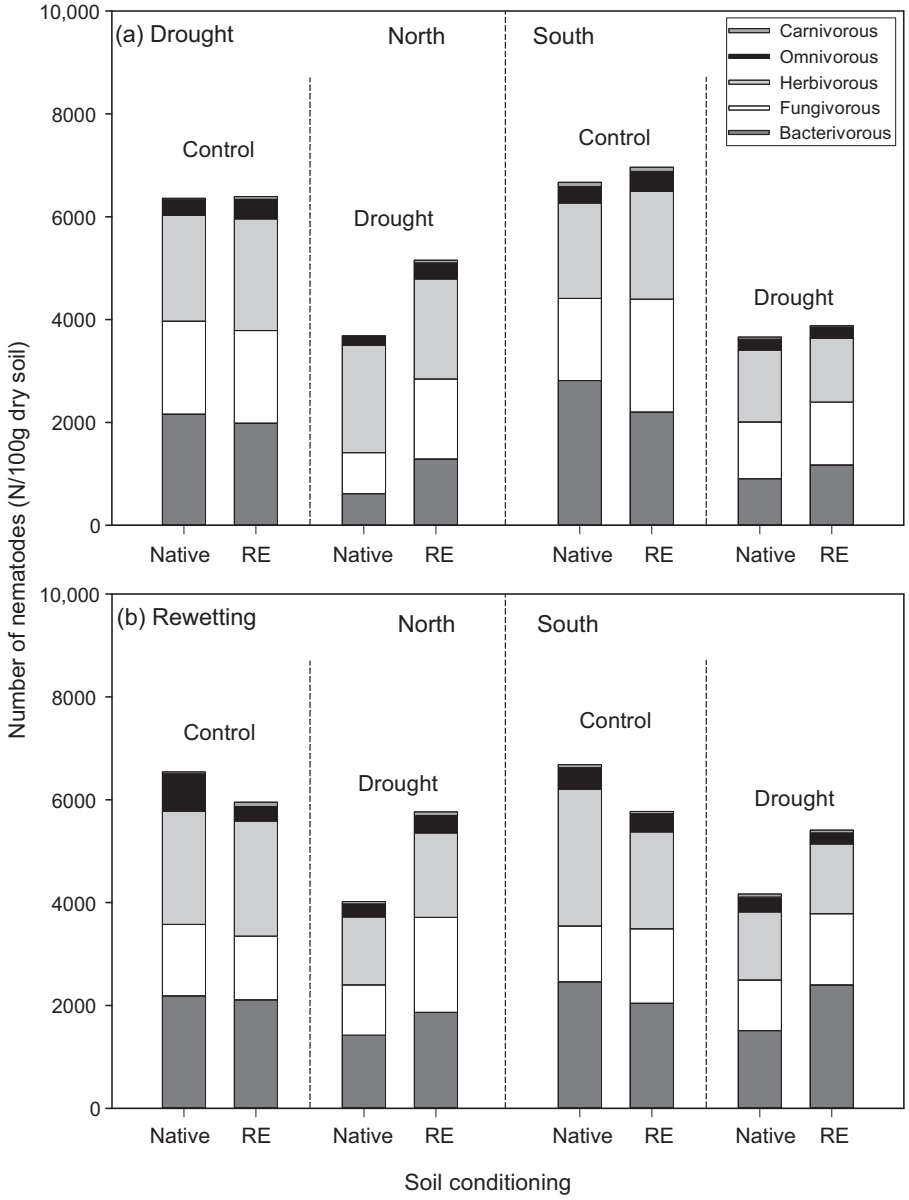

FIGURE 8 Soil conditioning (native: native conditioning; RE: range-expander conditioning) and summer drought effects (control and drought) on soil nematode abundance (numbers 100 g^{-1} dry soils) (a) during summer drought phase and (b) during rewetting phase grown in northern European soils inoculated with live soils from northern Europe (north, Netherlands) or southern Europe (south, Hungary).

Responses of range expanders and congeneric native plants to drought and rewetting

Our results showed that the total shoot biomass of range expanders were, on average, more responsive to extreme summer drought than the total shoot biomass of congeneric natives despite the fact that range expanders performed better in mixed communities. This suggests that plant species that expand their range from continental or Mediterranean climate regions to Atlantic climate regions in northwestern Europe are less resistant to extreme drought events and less preadapted to the increasing droughts in their novel range than we expected in our hypothesis. Aside from the fact that those effects were dominated by the responses of *Centaurea* spp. and that the results were influenced by growing natives and range expanders in mixed communities, the results nevertheless are in line with previous work in the same mesocosms when range expanders and natives were still growing in separate communities (Manrubia et al., 2019).

During rewetting, range expanders were more resilient in their survival than congeneric natives despite the fact that congeneric natives had more shoot biomass. While this is contrary to our hypothesis, it indicates that range expanders and congeneric natives on average

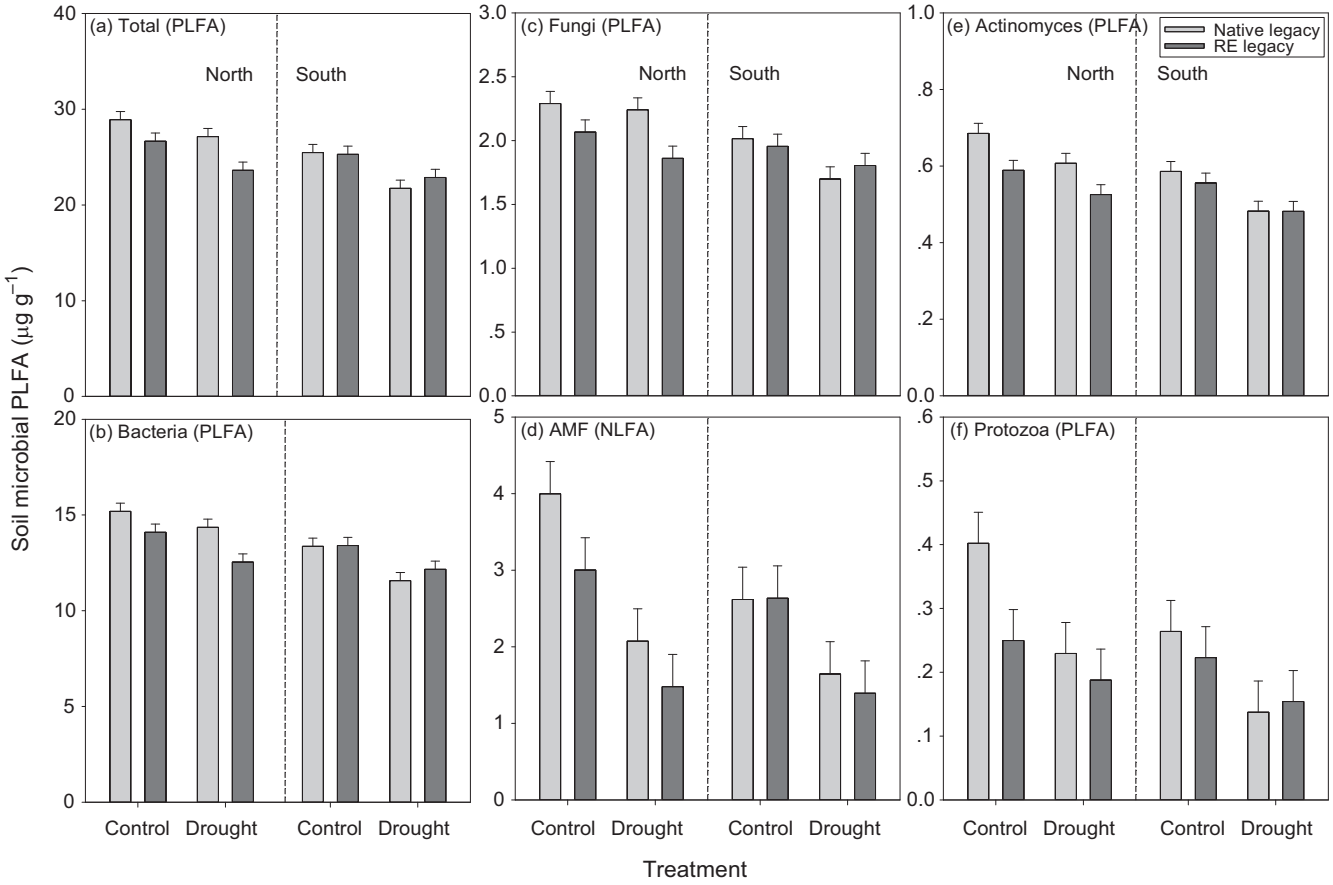

FIGURE 9 Soil conditioning (native legacy: native conditioning; RE legacy: range-expander conditioning) and summer drought effects (control and drought) on soil microbial community after rewetting phase grown in northern European soils inoculated with live soils from northern Europe (North, Netherlands) or southern Europe (South, Hungary). Means ± 1 standard error (SE).

showed different strategies under conditions of extreme summer drought and rewetting; species from the south had a different strategy for surviving unfavorable conditions, and, though congeneric natives respond quickly to rewetting, range expanders were more conservative in their responses to rewetting. The same responses have been demonstrated for soil-biota-related ecosystem processes (Manrubia et al., 2019).

Performance of range expanders and congeneric native plants in connection with soil origins

Our results showed that the plant shoot biomass of each species was determined by soil origins, as well as by the origin of the plants that had conditioned the soils in preceding years. In particular, *Centaurea* spp. had more shoot biomass in northern soil, whereas *Rorippa* spp. had more shoot biomass in soil from the south. Therefore, though the co-introduction of soil biota from the native range did not benefit range expanders in general, it had a differential effect on range-expanding species within the plant communities. *Centaurea stoebe* performed especially better in novel soil communities, which would suggest that it may benefit from enemy release (Engelkes et al., 2008). We do not know the source of the benefit to *Rorippa* in soil from the north, but because these species are nonmycorrhizal, like most crucifers, it is unlikely that arbuscular mycorrhizal fungi from the native range was responsible for the benefit.

Our results also showed that the co-introduction of soil biota from the native range did not benefit range expanders when they encountered extreme drought events in the new range. Therefore, our results do not support our hypothesis regarding a possible benefit of the co-introduction of plants and their soil microbes. Because we used only four pairs of range expanders and congeneric natives, more studies need to be carried out before more general conclusions may be drawn. For example, several studies found enhanced performance of individual range-expanding plant species in response to soil communities from a new range compared to those from the original range (De Frenne et al., 2014; Van Grunsven

et al., 2010; Van Nuland et al., 2017). However, we did not find the same pattern when range expanders and congeneric natives were grown in the same communities, under either drought or control conditions. In mixed plant communities, other processes, such as competition (Callaway et al., 2013) and facilitation (Brooker et al., 2006), may have influenced the capacity of single plant species to respond to soil conditioning.

In this study, we compared range expanders and congeneric natives in live soil from a region in the new range with and without live soil from a region in the original range. Two aspects of soil inoculation need to be considered. The first is that it may take time for soil biota to become established. Nevertheless, other researchers showed that the current incubation time of 5–6 years might have resulted in a significant soil biota effect (Wubs et al., 2019). Second, the soil collection in our study was limited to two regions, one in the south and one in the north. While there were replicates within each of the regions, future studies may require collecting soils from a wider set of regions in order to cover the original and new ranges more broadly.

Performance of range expanders and congeneric native plants under soil conditioning

In this study, we observed that soil conditioning by range expanders had legacy effects that decreased plant community shoot biomass in the mixed communities, whereas we had expected that range-expanding plant species would perform better in soils conditioned by range expanders. A previous study with plants grown as singles found that range-expanding plant species on average had more neutral plant–soil feedback, whereas congeneric natives on average had significant negative plant–soil feedback when they were grown individually in soil from the northern areas (Engelkes et al., 2008). In a previous community study, however, plant–soil interactions of range expanders were found to be similar to those of their closely related native plant species in the range-expanding soils (Koorem et al., 2020). Also, soils conditioned by mixtures of plant species may show more moderate plant–soil feedback effects than is the case in feedback experiments using single plant species (Callaway et al., 2013; Hendriks et al., 2015). Therefore, our results suggests that understanding the consequences of the role of plant–soil feedback in plant community productivity requires a plant community approach when examining the effects of plant–soil feedback. We propose that this represents just one of the challenges among others that may lead to the further incorporation of plant–soil feedback into community ecology (Gundale & Kardol, 2021).

We found no significant difference between drought responses of range expanders and congeneric natives in soils conditioned by range expanders versus congeneric natives, which was contrary to our hypothesis. Still, there were legacy effects of soil conditioning that might have influenced plant community responses to extreme weather events, for example, during rewetting, soil conditioning by natives had positive legacy effects on the drought resilience of range expanders. This suggests that native plants might indirectly benefit range expanders in coping with unfavorable conditions via soil legacy effects. Such effects of soil conditioning on the way in which plants deal with drought have been demonstrated in other cases (Fry et al., 2018; Kaisermann et al., 2017), but not for plant range expansions. Under the proposed mechanism, plants select specific microbial populations to cope with drought by regulating carbon allocation (Hasibeder et al., 2015; Preece & Penuelas, 2016). Our results suggest that such effects may show up in random situations, such as occur with range expanders in new habitats, and that they are not necessarily the result of long-term co-evolution.

Soil functions

It is well known that soil functions such as decomposition generally are hampered by extreme drought events. Interestingly, in this study, soil conditioning by range expanders accelerated litter decomposition in northern soils but decreased decomposition in southern soils compared to soil conditioning by congeneric natives. Analysis of the CI of soil nematodes (Ferris et al., 2001) suggested that the effects of an expanded role of fungi in litter decomposition during summer drought (Hawkes et al., 2011) trickled up in the soil food web. As expected (Birch, 1958), soil functions related to decomposition and mineralization accelerated under subsequent rewetting.

In contrast to our hypothesis, we found that northern and southern soils generally responded to drought in the same way. However, soils with an inoculum from northern Europe (the Netherlands) recovered more robustly from drought in terms of nitrogen mineralization rate, which was contrary to our hypothesis. Soils of range-expanding plant species appeared to be more resistant to recover function when soil was rewetted after drought. These results suggest that range expanders are more susceptible to drought in their original-range soil or that they may have different ecological strategies in warm areas (e.g., growing outside the drought period) (Manrubia et al., 2019). A possible escape

from soil-borne enemies (Van Grunsven et al., 2010) did not increase their drought resistance and resilience in soil from the novel range. Our results did not support studies showing that soil microbial communities originating from dry regions were more resistant to drought than those from wetter regions (Averill et al., 2016; Hawkes et al., 2017; Hawkes & Keitt, 2015; Manzoni et al., 2012), which might be explained by our approach of inoculating live southern soil into live northern soil. This is a scenario for climate-warming-induced range expansion of all soil biota, but it may mimic less well the differences between soils from dry and wet regions.

Soil nematode community and soil microbial community

We found that summer drought decreased total nematode abundance, and this long-lasting effect persisted during rewetting when soils had been conditioned by congeneric native plants (as indicated by interactions between drought and soil conditioning during rewetting). This suggests that soils conditioned by range expanders have a greater ability to recover under extreme weather conditions in terms of total nematode abundance. Drought suppressed predatory nematode relative abundance and suppressed root herbivorous nematode relative abundance during rewetting, independent of soil origin. This finding is contrary to that of a previous study showing that drought suppresses soil predators and promotes root herbivores in mesic but not xeric grasslands (Franco et al., 2019). Soil conditioning by range expanders decreased fungivorous nematodes under a extreme drought/rewetting cycle. Soil conditioning by natives decreased the relative abundance of bacterivore nematode relative abundance during summer drought, but this pattern disappeared during rewetting. Thus, we conclude that soil conditioning by range expanders and congeneric natives exerts different legacy effects on soil nematode community composition (Mörrien et al., 2012; Wilschut et al., 2016, 2017). Further understanding these effects may help to understand the mechanisms underlying soil legacy effects.

The nematode abundances presented in our study represent the net effects of bottom-up and top-down control by both the plants and the microorganisms present in the soils (Wilschut et al., 2016). Our results show that soil conditioning by range-expander communities had a negative legacy effect on the biomass of soil fungi and bacteria. Previous studies found the same pattern that individual range expanders decreased soil fungal biomass compared to congeneric natives (Mörrien & van der Putten, 2013). This suggests that not only for individual plant species but also for plant communities, range-expanding plant species have less fungal hyphal biomass around their roots than congeneric natives. This might have been caused by relatively fewer pathogens in and around the roots of range expanders. However, there were no interaction effects among extreme drought, soil origin, and soil conditioning on soil microbial biomass in this study. Because soil conditioning by range expanders did not increase soil AMF biomass, our results do not support the *enhanced mutualist associations* hypothesis (Lekberg et al., 2013). Moreover, according to our study, extreme drought and rewetting cycles could decrease soil microorganism abundance. Together, these results suggest that plant range expansions could change the structure of soil food webs by altering both soil microbes and soil nematodes, but we cannot exclude the possibility that these effects were due to single plant species and not a general aspect of range expansions of plant species (Wilschut et al., 2016).

CONCLUSIONS

Understanding the temporal dynamics of performance of range expanders and congeneric native plants facing extreme drought events is critical for the successful establishment of range expanders in northern areas. Our results showed that the total biomass of range expanders and congeneric native plant species exhibited different patterns when encountering an extreme drought event and subsequent rewetting. Range expanders on average produced shoot biomass and were more resilient to drought than congeneric natives. Our results also demonstrated that congeneric natives responded quickly to rewetting, whereas range expanders were more conservative in their responses to rewetting. The co-introduction of soil biota neither benefited nor hampered range-expanding plant species when encountering extreme drought events. However, soil conditioning by range expanders was disadvantageous for congeneric natives. Soil functions were constrained by extreme drought but accelerated during rewetting. Range-expanding plant species reduced soil fungal biomass and numbers of soil fungivorous nematodes, suggesting that the effects of range-expanding plant species could trickle up in the soil food web. Though we treated range-expanding plant species as a group, our detailed analyses of individual plant species in their communities showed that the responses of range expanders were dominated by the species that produced the most biomass. In the mixed communities, not all range expanders showed the exact same responses.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Yang et al., 2022) are available from Dryad at https://doi.org/10.5061/dryad.pnvx0k6pf.

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REFERENCES

Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. "Enemy Release? An Experiment with Congeneric Plant Pairs and Diverse above- and Belowground Enemies." *Ecology* 86: 2979–89.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. "Novel Competitors Shape species' Responses to Climate Change." *Nature* 525: 515–8.

Ashton, L. A., H. M. Griffiths, C. L. Parr, T. A. Evans, R. K. Didham, F. Hasan, Y. A. Teh, H. S. Tin, C. S. Vairappan, and P. Eggleton. 2019. "Termites Mitigate the Effects of Drought in Tropical Rainforest." *Science* 363: 174–7.

Averill, C., B. G. Waring, and C. V. Hawkes. 2016. "Historical Precipitation Predictably Alters the Shape and Magnitude of Microbial Functional Response to Soil Moisture." *Global Change Biology* 22: 1957–64.

Barnard, R. L., C. A. Osborne, and M. K. Firestone. 2013. "Responses of Soil Bacterial and Fungal Communities to Extreme Desiccation and Rewetting." *The ISME Journal* 7: 2229–41.

Berg, M. P., E. T. Kiers, G. Driessen, M. van der Heijden, B. W. Kooi, F. Kuenen, M. Liefting, H. A. Verhoef, and J. Ellers. 2010. "Adapt or Disperse: Understanding Species Persistence in a Changing World." *Global Change Biology* 16: 587–98.

Binkley, D., and P. Matson. 1983. "Ion-Exchange Resin Bag Method for Assessing Forest Soil-Nitrogen Availability." *Soil Science Society of America Journal* 47: 1050–2.

Binkley, D., R. Bell, and P. Sollins. 1992. "Comparison of Methods for Estimating Soil-Nitrogen Transformations in Adjacent Conifer and Alder-Conifer Forests." *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 22: 858–63.

Birch, H. F. 1958. "The Effect of Soil Drying on Humus Decomposition and Nitrogen." *Plant and Soil* 10: 9–30.

Bongers, T. 1990. "The Maturity Index - an Ecological Measure of Environmental Disturbance Based on Nematode Species Composition." *Oecologia* 83: 14–9.

Bongers, T., and G. W. Yeates. 1988. "Report on Workshop - Nematodes in Natural Systems - the Use of Nematodes in Environmental-Studies." *Pedobiologia* 32: 88–8.

Brooker, R. W., D. Scott, S. C. F. Palmer, and E. Swaine. 2006. "Transient Facilitative Effects of Heather on Scots Pine along a Grazing Disturbance Gradient in Scottish Moorland." *Journal of Ecology* 94: 637–45.

Callaway, R. M., D. Montesinos, K. Williams, and J. L. Maron. 2013. "Native Congeners Provide Biotic Resistance to Invasive *Potentilla* through Soil Biota." *Ecology* 94: 1223–9.

Chen, I. C., J. K. Hill, R. Ohlemuller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333: 1024–6.

Dai, A. G. 2011. "Drought under Global Warming: A Review." *Wiley Interdisciplinary Reviews-Climate Change* 2: 45–65.

De Frenne, P., D. A. Coomes, A. De Schrijver, J. Staelens, J. M. Alexander, M. Bernhardt-Romermann, J. Brunet, et al. 2014. "Plant Movements and Climate Warming: Intraspecific Variation in Growth Responses to Nonlocal Soils." *New Phytologist* 202: 431–41.

De Vries, F. T., R. I. Griffiths, M. Bailey, H. Craig, M. Girlanda, H. S. Gweon, S. Hallin, et al. 2018. "Soil Bacterial Networks Are less Stable under Drought than Fungal Networks." *Nature Communications* 9, 3033.

De Vries, F. T., R. I. Griffiths, C. G. Knight, O. Nicolitch, and A. Williams. 2020. "Harnessing Rhizosphere Microbiomes for Drought-Resilient Crop Production." *Science* 368: 270–4.

De Vries, F. T., M. E. Liiri, L. Bjornlund, M. A. Bowker, S. Christensen, H. M. Setala, and R. D. Bardgett. 2012. "Land Use Alters the Resistance and Resilience of Soil Food Webs to Drought." *Nature Climate Change* 2: 276–80.

Dostálek, T., Z. Munzbergova, A. Kladivova, and M. Macel. 2016. "Plant–Soil Feedback in Native Vs. Invasive Populations of a Range Expanding Plant." *Plant and Soil* 399: 209–20.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. "Climate Extremes: Observations, Modeling, and Impacts." *Science* 289: 2068–74.

EEA. 2016. *Meteorological and Hydrological Droughts* 19. Copenhagen: European Environment Agency.

Engelkes, T., E. Morrien, K. J. F. Verhoeven, T. M. Bezemer, A. Biere, J. A. Harvey, L. M. McIntyre, W. L. M. Tamis, and W. H. van der Putten. 2008. "Successful Range-Expanding Plants Experience Less above-Ground and below-Ground Enemy Impact." *Nature* 456: 946–8.

Ferris, H., T. Bongers, and R. G. M. de Goede. 2001. "A Framework for Soil Food Web Diagnostics: Extension of the Nematode Faunal Analysis Concept." *Applied Soil Ecology* 18: 13–29.

Franco, A. L. C., L. A. Gherardi, C. M. de Tomasel, W. S. Andriuzzi, K. E. Ankrom, E. A. Shaw, E. M. Bach, O. E. Sala, and D. H. Wall. 2019. "Drought Suppresses Soil Predators and Promotes Root Herbivores in Mesic, but Not in Xeric Grasslands." *Proceedings of the National Academy of Sciences of the United States of America* 116: 12883–8.

Frostegård, A., and E. Bååth. 1996. "The Use of Phospholipid Fatty Acid Analysis to Estimate Bacterial and Fungal Biomass in Soil." *Biology and Fertility of Soils* 22: 59–65.

Fry, E. L., J. Savage, A. L. Hall, S. Oakley, W. J. Pritchard, N. J. Ostle, R. F. Pywell, J. M. Bullock, and R. D. Bardgett. 2018.

"Soil Multifunctionality and Drought Resistance Are Determined by Plant Structural Traits in Restoring Grassland." *Ecology* 99: 2260–71.

Fuchslueger, L., B. Wild, M. Mooshammer, M. Takriti, S. Kienzl, A. Knoltsch, F. Hofhansl, M. Bahn, and A. Richter. 2019. "Microbial Carbon and Nitrogen Cycling Responses to Drought and Temperature in Differently Managed Mountain Grasslands." *Soil Biology & Biochemistry* 135: 144–53.

Funk, J. L., and P. M. Vitousek. 2007. "Resource-Use Efficiency and Plant Invasion in Low-Resource Systems." *Nature* 446: 1079–81.

Gundale, M. J., and P. Kardol. 2021. "Multi-Dimensionality as a Path Forward in Plant–Soil Feedback Research." *Journal of Ecology* 109: 3446–65.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. "Climate Effects on Mountain Plants." *Nature* 369: 448–8.

Hacket-Pain, A. J., J. G. A. Lageard, and P. A. Thomas. 2017. "Drought and Reproductive Effort Interact to Control Growth of a Temperate Broadleaved Tree Species (*Fagus Sylvatica*)." *Tree Physiology* 37: 744–54.

Hasibeder, R., L. Fuchslueger, A. Richter, and M. Bahn. 2015. "Summer Drought Alters Carbon Allocation to Roots and Root Respiration in Mountain Grassland." *New Phytologist* 205: 1117–27.

Hawkes, C. V., and T. H. Keitt. 2015. "Resilience vs. Historical Contingency in Microbial Responses to Environmental Change." *Ecology Letters* 18: 612–25.

Hawkes, C. V., S. N. Kivlin, J. D. Rocca, V. Huguet, M. A. Thomsen, and K. B. Suttle. 2011. "Fungal Community Responses to Precipitation." *Global Change Biology* 17: 1637–45.

Hawkes, C. V., B. G. Waring, J. D. Rocca, and S. N. Kivlin. 2017. "Historical climate controls soil respiration responses to current soil moisture." *Proceedings of the National Academy of Sciences of the United States of America* 114: 6322–7.

Heinen, R., S. E. Hannula, J. R. De Long, M. Huberty, R. Jongen, A. Kielak, K. Steinauer, F. Zhu, and T. M. Bezemer. 2020. "Plant Community Composition Steers Grassland Vegetation Via Soil Legacy Effects." *Ecology Letters* 23: 973–82.

Hendriks, M., J. M. Ravenek, A. E. Smit-Tiekstra, J. W. van der Paauw, H. de Caluwe, W. H. van der Putten, H. de Kroon, and L. Mommer. 2015. "Spatial Heterogeneity of Plant–Soil Feedback Affects Root Interactions and Interspecific Competition." *New Phytologist* 207: 830–40.

Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. "Resistance and Resilience of a Grassland Ecosystem to Climate Extremes." *Ecology* 95: 2646–56.

IPCC. 2014. "Climate Change 2014: Synthesis Report." In *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by R.K.P.a.L.A.M.e. Core Writing Team, 151. Geneva, Switzerland: IPCC.

Kaisermann, A., F. T. de Vries, R. I. Griffiths, and R. D. Bardgett. 2017. "Legacy Effects of Drought on Plant–Soil Feedbacks and Plant–Plant Interactions." *New Phytologist* 215: 1413–24.

Keuskamp, J. A., B. J. J. Dingemans, T. Lehtinen, J. M. Sarneel, and M. M. Hefting. 2013. "Tea Bag Index: A Novel Approach to Collect Uniform Decomposition Data across Ecosystems." *Methods in Ecology and Evolution* 4: 1070–5.

KNMI. 2015. KNMI'14-klimaatscenario's voor Nederland; Leidraad voor professionals in klimaatadaptatie. pp. 34. De Bilt.

Koorem, K., O. Kostenko, L. B. Snoek, C. Weser, K. S. Ramirez, R. A. Wilschut, and W. H. van der Putten. 2018. "Relatedness with Plant Species in Native Community Influences Ecological Consequences of Range Expansions." *Oikos* 127: 981–90.

Koorem, K., B. L. Snoek, J. Bloem, S. Geisen, O. Kostenko, M. Manrubia, K. S. Ramirez, C. Weser, R. A. Wilschut, and W. H. van der Putten. 2020. "Community-Level Interactions between Plants and Soil Biota during Range Expansion." *Journal of Ecology* 108: 1860–73.

Lekberg, Y., S. M. Gibbons, S. Rosendahl, and P. W. Ramsey. 2013. "Severe Plant Invasions Can Increase Mycorrhizal Fungal Abundance and Diversity." *ISME Journal* 7: 1424–33.

Liang, M. X., X. B. Liu, I. M. Parker, D. Johnson, Y. Zheng, S. Luo, G. S. Gilbert, and S. X. Yu. 2019. "Soil Microbes Drive Phylogenetic Diversity-Productivity Relationships in a Subtropical Forest. Science." *Advances* 5: 5.

Manrubia, M., W. H. van der Putten, C. Weser, F. C. ten Hooven, H. Martens, E. P. Brinkman, S. Geisen, K. S. Ramirez, and G. F. Veen. 2019. "Soil Functional Responses to Drought under Range-Expanding and Native Plant Communities." *Functional Ecology* 33: 2402–16.

Manzoni, S., J. P. Schimel, and A. Porporato. 2012. "Responses of Soil Microbial Communities to Water Stress: Results from a Meta-Analysis." *Ecology* 93: 930–8.

Meisner, A., G. B. De Deyn, W. de Boer, and W. H. van der Putten. 2013. "Soil Biotic Legacy Effects of Extreme Weather Events Influence Plant Invasiveness." *Proceedings of the National Academy of Sciences of the United States of America* 110: 9835–8.

Meisner, A., S. Jacquiod, B. L. Snoek, F. C. ten Hooven, and W. H. van der Putten. 2018. "Drought Legacy Effects on the Composition of Soil Fungal and Prokaryote Communities." *Frontiers in Microbiology* 9: 294.

Meisner, A., B. L. Snoek, J. Nesme, E. Dent, S. Jacquiod, A. T. Classen, and A. Priemé. 2021. "Soil Microbial Legacies Differ Following Drying-Rewetting and Freezing–Thawing Cycles." *The ISME Journal* 15: 1207–21.

Mörrien, E., H. Duyts, and W. H. Van der Putten. 2012. "Effects of Native and Exotic Range-Expanding Plant Species on Taxonomic and Functional Composition of Nematodes in the Soil Food Web." *Oikos* 121: 181–90.

Mörrien, E., and W. H. van der Putten. 2013. "Soil Microbial Community Structure of Range-Expanding Plant Species Differs from Co-Occurring Natives." *Journal of Ecology* 101: 1093–102.

Olsson, P. A., E. Baath, I. Jakobsen, and B. Soderstrom. 1995. "The Use of Phospholipid and Neutral Lipid Fatty-Acids to Estimate Biomass of Arbuscular Mycorrhizal Fungi in Soil." *Mycological Research* 99: 623–9.

Oostenbrink, I. C. 1960. "Estimating Nematode Populations by some Selected Methods." In *Nematology*, edited by J. N. Sasser and W. R. Jenkins, 439–42. Chapel Hill, Raleigh: University of North Carolina Press.

Parmesan, C. 2006. "Ecological and Evolutionary Responses to Recent Climate Change." *Annual Review of Ecology Evolution and Systematics* 37: 637–69.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421: 37–42.

Pecl, G. T., M. B. Araujo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I. C. Chen, T. D. Clark, et al. 2017. "Biodiversity Redistribution under Climate Change: Impacts on Ecosystems and Human Well-Being." *Science* 355: eaai9214.

Pfisterer, A. B., and B. Schmid. 2002. "Diversity-Dependent Production Can Decrease the Stability of Ecosystem Functioning." *Nature* 416: 84–6.

Pimm, S. L. 1984. "The Complexity and Stability of Ecosystems." *Nature* 307: 321–6.

Preece, C., and J. Penuelas. 2016. "Rhizodeposition under Drought and Consequences for Soil Communities and Ecosystem Resilience." *Plant and Soil* 409: 1–17.

Putnam, A. E., and W. S. Broecker. 2017. "Human-Induced Changes in the Distribution of Rainfall." *Science Advances* 3: e1600871.

Ramirez, K. S., L. B. Snoek, K. Koorem, S. Geisen, L. J. Bloem, F. ten Hooven, O. Kostenko, et al. 2019. "Range-Expansion Effects on the Belowground Plant Microbiome." *Nature Ecology & Evolution* 3: 604–11.

Schroeder, J. W., J. T. Martin, D. F. Angulo, I. Arias-Del Razo, J. M. Barbosa, R. Perea, E. Sebastian-Gonzalez, and R. Dirzo. 2019. "Host Plant Phylogeny and Abundance Predict Root-Associated Fungal Community Composition and Diversity of Mutualists and Pathogens." *Journal of Ecology* 107: 1557–66.

Sheik, C. S., W. H. Beasley, M. S. Elshahed, X. H. Zhou, Y. Q. Luo, and L. R. Krumholz. 2011. "Effect of Warming and Drought on Grassland Microbial Communities." *The ISME Journal* 5: 1692–700.

Sletvold, N., and J. Agren. 2015. "Climate-Dependent Costs of Reproduction: Survival and Fecundity Costs Decline with Length of the Growing Season and Summer Temperature." *Ecology Letters* 18: 357–64.

Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. "A Framework for Assessing Ecosystem Dynamics in Response to Chronic Resource Alterations Induced by Global Change." *Ecology* 90: 3279–89.

Smith, R. S., T. Z. Osborne, I. C. Feller, and J. E. Byers. 2019. "Detrital Traits Affect Substitutability of a Range-Expanding Foundation Species across Latitude." *Oikos* 128: 1367–80.

Tilman, D. 1996. "The Benefits of Natural Disasters." *Science* 273: 1518–8.

Tomiolo, S., and D. Ward. 2018. "Soil Properties and Climate Mediate the Effects of Biotic Interactions on the Performance of a Woody Range Expander." *Ecosphere* 9: e02186.

Van der Putten, W. H. 2012. "Climate Change, Aboveground-Belowground Interactions, and species' Range Shifts." *Annual Review of Ecology, Evolution, and Systematics* 43: 365–83.

Van der Putten, W. H., R. D. Bardgett, J. D. Bever, T. M. Bezemer, B. B. Casper, T. Fukami, P. Kardol, et al. 2013. "Plant–Soil Feedbacks: The Past, the Present and Future Challenges." *Journal of Ecology* 101: 265–76.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. "Predicting Species Distribution and Abundance Responses to Climate Change: Why it Is Essential to Include Biotic Interactions across Trophic Levels." *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 2025–34.

Van Grunsven, R. H. A., W. H. van der Putten, T. M. Bezemer, F. Berendse, and E. M. Veenendaal. 2010. "Plant–Soil Interactions in the Expansion and Native Range of a Poleward Shifting Plant Species." *Global Change Biology* 16: 380–5.

Van Grunsven, R. H. A., T. W. Yuwati, G. A. Kowalchuk, W. H. van der Putten, and E. M. Veenendaal. 2014. "The Northward Shifting Neophyte *Tragopogon dubius* Is Just as Effective in Forming Mycorrhizal Associations as the Native *T. pratensis*." *Plant Ecology & Diversity* 7: 533–9.

Van Nuland, M. E., J. K. Bailey, and J. A. Schweitzer. 2017. "Divergent Plant–Soil Feedbacks Could Alter Future Elevation Ranges and Ecosystem Dynamics." *Nature Ecology & Evolution* 1: 0150.

Van Ruijven, J., and F. Berendse. 2010. "Diversity Enhances Community Recovery, but Not Resistance, after Drought." *Journal of Ecology* 98: 81–6.

Walther, G. R. 2010. "Community and Ecosystem Responses to Recent Climate Change." *Philosophical Transactions of the Royal Society B-Biological Sciences* 365: 2019–24.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. "Ecological Responses to Recent Climate Change." *Nature* 416: 389–95.

Wilschut, R. A., S. Geisen, H. Martens, O. Kostenko, M. de Hollander, F. C. ten Hooven, C. Weser, et al. 2019. "Latitudinal Variation in Soil Nematode Communities under Climate Warming-Related Range-Expanding and Native Plants." *Global Change Biology* 25: 2714–26.

Wilschut, R. A., S. Geisen, F. C. ten Hooven, and W. H. van der Putten. 2016. "Interspecific Differences in Nematode Control between Range-Expanding Plant Species and their Congeneric Natives." *Soil Biology & Biochemistry* 100: 233–41.

Wilschut, R. A., J. C. P. Silva, P. Garbeva, and W. H. van der Putten. 2017. "Belowground Plant-Herbivore Interactions Vary among Climate-Driven Range-Expanding Plant Species with Different Degrees of Novel Chemistry." *Frontiers in Plant Science* 8: 1861.

Wubs, E. R. J., W. H. van der Putten, S. R. Mortimer, G. W. Korthals, H. Duyts, R. Wagenaar, and T. M. Bezemer. 2019. "Single Introductions of Soil Biota and Plants Generate Long-Term Legacies in Soil and Plant Community Assembly." *Ecology Letters* 22: 1145–51.

Yang, Q., C. Veen, R. Wagenaar, M. Manrubia, F. ten Hooven, and W. van der Putten. 2022. "Temporal Dynamics of Range-Expander and Congeneric Native Plant Responses during and after Extreme Drought Events." Dryad, Dataset. https://doi.org/10.5061/dryad.pnvx0k6pf.

Yeates, G. W., T. Bongers, R. G. M. Degoede, D. W. Freckman, and S. S. Georgieva. 1993. "Feeding-Habits in Soil Nematode

Families and Genera - an Outline for Soil Ecologists." *Journal of Nematology* 25: 315–31.

Yeates, G. W., D. A. Wardle, and R. N. Watson. 1993. "Relationships between Nematodes, Soil Microbial Biomass and Weed-Management Strategies in Maize and Asparagus Cropping Systems." *Soil Biology & Biochemistry* 25: 869–87.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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