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Plant–soil interactions during the native and exotic range expansion of an annual plant

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Abstract

Range expansions, whether they are biological invasions or climate change-mediated range shifts, may have profound ecological and evolutionary consequences for plant–soil interactions. Range-expanding plants encounter soil biota with which they have a limited coevolutionary history, especially when introduced to a new continent. Past studies have found mixed results on whether plants experience positive or negative soil feedback interactions in their novel range, and these effects often change over time. One important theoretical explanation is that plants locally adapt to the soil pathogens and mutualists in their novel range. We tested this hypothesis in *Dittrichia graveolens*, an annual plant that is both expanding its European native range, initially coinciding with climate warming, and rapidly invading California after human introduction. In parallel greenhouse experiments on both continents, we used plant genotypes and soils from 5 locations at the core and edge of each range to compare plant growth in soil inhabited by *D. graveolens* and nearby control microsites as a measure of plant–soil feedback. Plant–soil interactions were highly idiosyncratic across each range. On average, plant–soil feedbacks were more positive in the native range than in the exotic range. In line with the strongly heterogeneous pattern of soil responses along our biogeographic gradients, we found no evidence for evolutionary differentiation between plant genotypes from the core to the edge of either range. Our results suggest that the evolution of plant–soil interactions during range expansion may be more strongly driven by local evolutionary dynamics varying across the range than by large-scale biogeographic shifts.

Keywords: *Dittrichia graveolens*, range shift, invasion, range expansion, plant–soil feedback, local adaptation, Asteraceae, evolution, global change

Introduction

Range expansions, such as those enabled by current climate warming and biological invasions caused by human introductions, are widespread and shape changing patterns of biodiversity (Lenoir et al., 2020; Parmesan & Yohe, 2003; Pimentel et al., 2000). In plants, a key biological process disrupted in the new range are plant–soil feedbacks (van der Putten et al., 2016), which are fundamental to plant performance and species coexistence (Bever, 2003). Plant–soil interactions in the novel environment can constrain or promote range expansions in a plant species' native range (Van Nuland et al., 2017) and alter the trajectory of intercontinental plant invasions via both positive (Lee et al., 2012) and negative (Nijjer et al., 2007) feedbacks. Plant–soil interactions are driven by a range of ecological and evolutionary processes operating at different spatial and temporal scales, which may explain why a wide variety of plant responses to novel soil environments has been found across studies (Chung, 2023). Understanding the drivers of plant–soil interactions and their impacts on plant populations on a biogeographic scale is essential to make general predictions of how plant–soil feedbacks will respond to global change (Gundale & Kardol, 2021; van der Putten et al., 2016).

Much work has been dedicated to the possible positive and negative effects the soil microbial community in the new range might have on plant growth, and the resulting changes in plant–soil feedbacks compared to the historic range (Van der Putten, 2012). Range expansion has a beneficial effect on plant growth when plants encounter fewer pathogens (enemy release hypothesis; Elton, 1958) or increased numbers of highly beneficial mutualists relative to pathogens (enhanced mutualism hypothesis; Reinhart & Callaway, 2004, 2006) in the novel range. For example, plant species that have expanded their native range have been found to accumulate fewer pathogenic soil microbes than similar, locally native species (Engelkes et al., 2008; Grunsven et al., 2007; Morriën & van der Putten, 2013), increasing plant performance (Grunsven et al., 2009). A negative response to range expansion will occur when a plant relies on specialist mutualists not present in the novel range (missed mutualism hypothesis; Catford et al., 2009). For example, Nuske et al. (2021) found that seedlings of *Pinus contorta* had reduced growth in soil collected at the invasion front away from plantations, where beneficial ectomycorrhizal species are less abundant.

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In addition to these ecological changes experienced by range-expanding plants, the new environment may also cause evolutionary changes in plant–soil interactions, analogous to other rapid evolutionary shifts in plant traits observed during invasions, such as phenology or climate tolerance (reviewed by Colautti & Lau, 2015). Evolutionary processes driving plant–soil feedbacks in general are gathering increased attention (discussed by Bailey & Schweitzer, 2016; terHorst & Zee, 2016; Van Nuland et al., 2016). Soil microbes can alter selection on plant growth and phenology (Lau & Lennon, 2011; Wagner et al., 2014) and contribute to local adaptation in tree seedlings (*Populus* spp, Pregitzer et al., 2010; Douglas fir, Pickles et al., 2015). Lower intraspecific population densities at the invasion front of the herb *Alliaria petiolata* selected for an increased production of allelochemicals that harmed mycorrhizal fungi, promoting plant competition with heterospecifics (Evans et al., 2016). Despite these compelling examples, little is known about plant genetic variation driving plant–soil feedbacks that selection could act upon because most work has been at the species level. A recent study compared inter- and intraspecific variation in plant–soil feedbacks in three grass species but found no evidence for the latter (Rallo et al., 2023).

Many evolutionary studies in an invasion context have focussed on the evolution of increased competitive ability (EICA) hypothesis (Blossey & Notzold, 1995), which predicts that invasive populations evolve to be more competitive after enemy release by reallocating resources that are no longer needed for defence against (above- or below-ground) natural enemies. However, ongoing coevolution between plants and microbes in the novel range could cause plant–soil feedbacks to become increasingly negative with time since introduction, as has been observed in some studies (Diez et al., 2010; Dostál et al., 2013; but see McGinn et al., 2018). Especially if plant–soil feedbacks are driven by generalist natural enemies, EICA effects could be transient as plants reallocate resources to defences against generalist microbial antagonists (rather than their native specialist enemies) in the new range (shifting defence hypothesis, Joshi & Vrieling, 2005). It is therefore essential to consider how eco-evolutionary feedbacks between plants and soil biota change over the course of range expansion, but limited empirical studies incorporating evolution have been conducted to date (as discussed by Schweitzer et al., 2018; terHorst & Zee, 2016; Van Nuland et al., 2016).

Range-expanding plants invading a new continent (referred to here as "exotic range expansion") and tracking climate change ("native range expansion") have in common that they both encounter a novel soil microbial community that they share a limited coevolutionary history with, shifting plant–soil feedbacks (Engelkes et al., 2008; Morriën et al., 2010). However, these two scenarios differ in three key ways that may influence eco-evolutionary processes (Bardgett & van der Putten, 2014; Urban, 2020). First, enemy release and missing mutualism effects may be stronger and less transient in the exotic range than in a native range expansion. Although soil microbes, on average, spread more slowly than plants, leading to the expectation that they will lag behind as plants spread to higher latitudes and altitudes (Álvarez-Garrido et al., 2019; Berg et al., 2010), these interactions may hypothetically re-establish during a native range expansion as microbes "catch up" (Bardgett & van der Putten, 2014). Re-association with mutualists can promote plant growth (Keymer & Lankau, 2017), and the arrival of native natural enemies catching up could select for increased specialist defenses.

Second, genetic diversity and ongoing gene flow from the historic range should be higher in native than in exotic range expansions (Moran & Alexander, 2014). Limited genetic diversity may constrain plant evolutionary potential in the invaded range, although in reality, genetic bottlenecks in invasions (especially for quantitative traits) may be modest and/or overcome by admixture of multiple introductions (Dlugosch & Parker, 2008; Dlugosch et al., 2015). In the native range with ongoing gene flow, theory shows that plant adaptation to the novel soil environment at the leading edge will depend on the balance between selection, drift, and the steepness of the environmental gradient. Range expansion should occur if selection is strong relative to drift and the environmental gradient is shallow (Polechová & Barton, 2015). Therefore, we may expect greater evolutionary changes in the native than in the exotic range.

Third, the abiotic environmental gradient is expected to be much shallower in an expanding native range compared to the abrupt change in the environment resulting from the introduction to a new continent (Urban, 2020). Variation in abiotic conditions along biogeographic gradients may affect the local balance between pathogens and mutualists, and plant responses to microbes highly depend on the environmental context (Chung, 2023; Gundale & Kardol, 2021). During native range expansions triggered by climate change, plants will gradually spread along latitudinal or altitudinal clines in abiotic soil conditions. In contrast, plant populations introduced to a new continent are abruptly exposed to the soil environment of the exotic range, which may or may not be abiotically similar to their historic native range. Thus, changes in plant–soil feedbacks may be relatively more predictable in the native range, while in the exotic range, the response to the abiotic environment and association with local microbes could develop in a more idiosyncratic and unpredictable way (Figure 1).

How these differences between native and exotic range expansions affect plant–soil interactions has mostly been explored conceptually (Bardgett & van der Putten, 2014). Comparing both scenarios empirically provides an opportunity to test these hypotheses on a biogeographic scale. In this study, we evaluate changes in plant–soil interactions for a plant species that is currently engaged in both native and exotic range expansion. *Dittrichia graveolens* (L.) Greuter is an annual plant from the Asteraceae family with a ruderal life history. Originally distributed around the Mediterranean basin (Brullo & De Marco, 2000), the species has greatly expanded its native range poleward since the mid-20th century (Lustenhouwer & Parker, 2022; McEvoy et al., 2023), now occurring as far north as Poland (Kocián, 2015). Populations at the northern range edge in the Netherlands evolved earlier flowering time (Lustenhouwer et al., 2018), suggesting that evolutionary change in other plant traits may be found on this timescale. The native range expansion was associated with an expansion of *D. graveolens*' climate niche to more temperate climates (Lustenhouwer & Parker, 2022). Regarding the soil community, previous work found a decrease in the ratio of microbial pathogens to mutualists in the rhizosphere of *D. graveolens* along a range expansion gradient in Europe (Ramirez et al., 2019), indicating potential for enemy release effects. However, the community

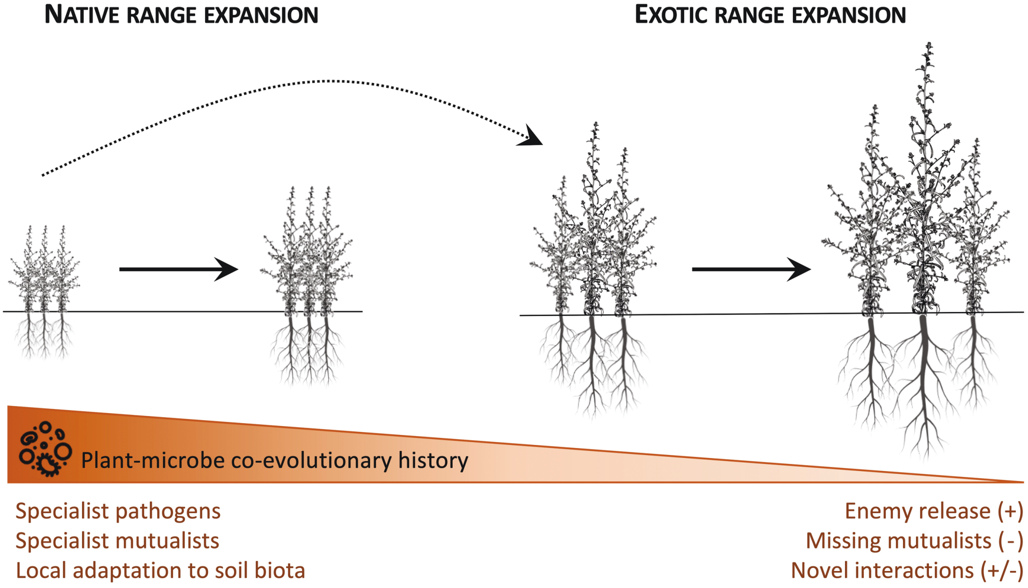

Figure 1. Hypotheses of how plant–soil interactions change during the expansion of a native range (e.g., tracking climate change) or exotic range (after introduction to a new continent). Plant size represents the overall effect of plant–soil interactions on plant growth, with more positive plant–soil feedbacks indicated by larger plants.

composition of root-feeding nematodes did not change from the historic to the expanded range (Wilschut et al., 2018). Globally, *D. graveolens* has been introduced to most other regions with a Mediterranean climate, including Australia, South Africa (GBIF.org, 2020), California (Brownsey et al., 2013b) and Chile (Santilli et al., 2021). We studied the exotic range expansion of *D. graveolens* in California, where it is considered a noxious weed and has rapidly spread across the state since the first record in 1984 (Brownsey et al., 2013b; Preston, 1997).

Using parallel greenhouse experiments in the Netherlands (expanded zone of the native range) and California (exotic range), we examined changes in plant–soil interactions over the course of both range expansions. We compared the core region (historic native range/site of first introduction) and edge region (recently colonized native range/invasion front) of the native and exotic range and studied plant responses to local soil biota, as well as evolutionary changes in plant populations between core and edge. We ask the following questions: (1) Does the impact of the soil microbial community on plant growth differ between core and edge in each range (ecological change)? (2) Do we see differentiation between plant populations from the core and edge of each range in their response to these soils (evolutionary change)? (3) Does the direction, magnitude and variability of shifts in plant–soil interactions differ between native and exotic range expansions? Lacking previous studies of plant–soil feedbacks of *D. graveolens* in its historic native range, we did not have a priori expectations of whether plant–soil feedbacks would be predominantly negative or positive. Our study system thus provides a "negative control" as compared to species already known to be strongly controlled by negative plant–soil interactions, where some degree of enemy release is likely to be found.

We hypothesized that the soil microbial community would have a less negative net effect on plant growth at the range edge compared to the range core (question 1). From an evolutionary perspective (question 2), we hypothesized that plant populations would be adapted to their local soil microbial community, resulting in more positive plant–soil feedbacks in local plant genotypes than in genotypes originating from elsewhere in the range. We expected such local adaptation to be less likely at the range edge than in the range core due to the shorter residence time in the edge region. Finally, comparing the native and exotic range expansion (question 3), we hypothesized that ecological shifts in plant–soil interactions would occur in the same direction but be more consistent across sampling sites in the native range than in the exotic range. We also expected that net plant–soil feedbacks would be more positive overall in the exotic range compared to the native range (Figure 1).

Materials and methods

Species life history and habitat

Dittrichia graveolens has a ruderal life history and grows in a variety of disturbed habitats, including roadsides, agricultural land, riverbanks, and urban areas. Soil types in the native range in France have basic to slightly acidic pH, are often nitrogen-rich, and can have a wide range of moisture levels (Rameau, 2008). Plants flower in late summer or autumn and are insect pollinated or self-fertilized (Brownsey, 2012; Lustenhouwer et al., 2018; Rameau, 2008). Individuals can produce several thousands of wind-dispersed seeds (Brownsey et al., 2013a; Brullo & De Marco, 2000).

Seed and soil collection

We collected seeds and soil from five study sites at the core and edge of each range (Figure 2; Supplementary Table S1). Sites within a region were located an average of 79 km (native range) or 50 km (exotic range) apart, with distances ranging from 6 to 182 km. In the native range in Europe, the core region was located at the historic (pre-expansion) northern range limit (central France; Lustenhouwer & Parker, 2022; Lustenhouwer et al., 2018). The edge region was located in the Netherlands, where populations have been spreading since the early 2000s (Stouthamer, 2007). In the exotic range in California, the core region was located in Santa Clara County, including the site where the species was first recorded in 1984 (Preston, 1997), and the edge region was located at the current invasion front in the foothills of the Sierra Nevada Mountains (Figure 2). In autumn 2018, we collected seeds from 10 haphazardly selected plants growing at each field site, comprising 10 maternal families. Seeds from each family were used to grow plants in a greenhouse common garden experiment at UC Santa Cruz in 2019, using neutral potting soil. Individuals were bagged prior to flowering to produce self-fertilized seeds. We used seeds from five families per site in this study. Using this selfing generation ensures that all seeds used in the experiment were produced in a common environment, reducing the impact of maternal or environmental effects on our results.

In autumn 2019, we returned to all 20 sites in California, central France, and the Netherlands to collect soil for this experiment. To evaluate plant–soil feedbacks of *D. graveolens* in the field, we used a field-conditioned soil approach where we collected soil from two microsites per site: the rhizosphere of *D. graveolens* plants (*Dittrichia* soil) and a nearby grassland of at least 100 m away where *D. graveolens* was absent (control soil). All tools were thoroughly cleaned with alcohol between sampling sites to avoid cross-contamination. After collection, soils were sieved with a 4 mm mesh sieve and stored in sealed bags in the fridge. If soils were too wet to sieve, they were air-dried prior to sieving.

Greenhouse experiments

Due to the logistical and ethical challenges of transporting soil with live pathogens between continents, we conducted two parallel greenhouse experiments (Figure 2); native range seeds and soil were used at the Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands (N 51.98689, E 5.67257) and exotic range seeds and soil were used at the University of California, Santa Cruz coastal campus greenhouses (N 36.95308, W −122.06639). Both experiments followed the same design. To evaluate changes in plant–soil interactions over the course of range expansion, core and edge sites were paired randomly into five combinations. Plants originating from each site (using seeds produced by the selfing generation) were grown in soil from both microsites of their own site and from both microsites of their paired site on the other end of the range expansion (core vs. edge; Figure 2). We replicated each combination of seed and soil origins in five randomized blocks, using a different maternal family in each block. Thus, each combination of soil type and seed origin within a pair of core and edge sites was replicated 5 times (Figure 2).

Both experiments started in mid-February 2020. We germinated seeds on filter paper in a growth chamber set to 28 °C and a 16 hr/8 hr day/night cycle. Seeds started germinating between 3 and 8 days after sowing and were planted within 1–3 days of germination. We grew plants in plastic pots with a volume of 0.65 L (exotic range experiment) or 0.55 L

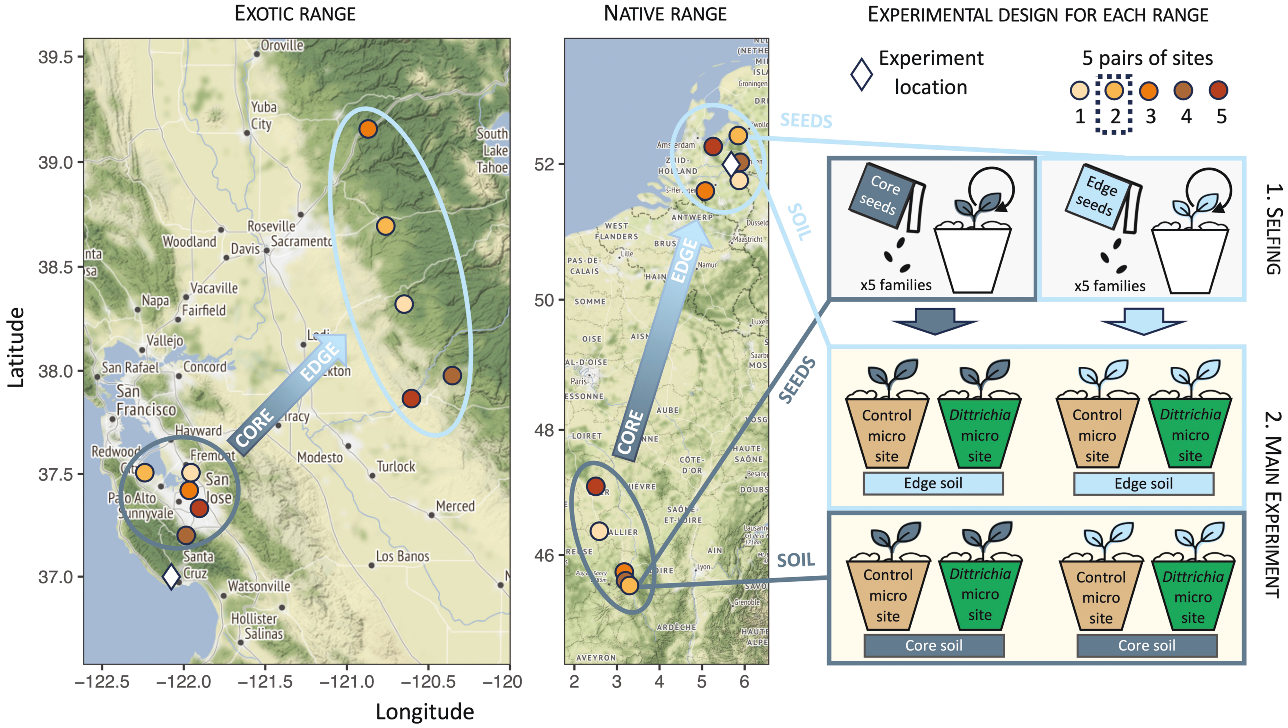

Figure 2. Experimental design with sampling locations in the native range (comparing the core region in central France and the edge region in the Netherlands) and exotic range (comparing the invasion core and invasion edge in California). Circles indicate study sites in each range, which were divided randomly into five pairs of core (dark ellipse) and edge (light ellipse) sites. At each site, we sampled soil from two microsites: the rhizosphere of *D. graveolens* and a nearby grassland control microsite. Seeds from five plants (maternal families) per site were first grown in the greenhouse in neutral soil for one generation of selfing (1). For the main experiment (2), seeds produced by the selfing generation were then planted reciprocally in soil from both microsites of their own site of origin and from the paired site at the other side of the range. Leaf colours indicate seed origin (dark shading for core, light shading for edge). The figure illustrates the design for one pair of sites in the native range, which was replicated across the five maternal families per site, the five pairs of sites, and the two ranges. To avoid moving live soil between continents, separate greenhouse experiments were conducted in each range (diamonds). Map data © 2023 Google.

(native range experiment). Two seedlings were planted in each pot to act as a replacement in case of mortality; the smallest seedling was removed after up to three weeks. Seedlings were mist-watered in the first few weeks to increase survival. In the exotic range experiment, the soil from one site (Alviso, a salt marsh) had to be replaced after the first 10 days of the experiment because all seedlings planted died within 24 hr. The soil had very high salinity, and no natural germination of weeds occurred in it either. Therefore, we collected soil from two new microsites in Alviso on a roadside with a lower salinity approximately 500 m away (Table S1).

The watering protocol was designed to keep the moisture content of each soil to 60% of its maximum water-holding capacity (moisture content of water-saturated soil) to maintain constant conditions for the soil biota. We watered all pots 3 times a week using DI water. Once a week, all pots were weighed, and the volume of water to be added was adjusted individually to maintain 60% water holding capacity. Unfortunately, in California, we had to simplify the watering protocol on 16 March due to the start of the COVID-19 pandemic, when the scaling down of research operations forced us to stop measuring the weight of the pots each week and instead aim to water all plants at approximately the right level based on previous experience with the soils. In the Netherlands, the watering schedule could continue as planned.

After 3 weeks of growth, we counted the number of leaves on each plant and measured the length and width of the longest leaf. The native range experiment finished after 55–56 days of growth, and the exotic range experiment lasted 90–97 days because safety protocols did not allow for an earlier harvest. At the end of each experiment, we washed the roots of each plant, dried plants in a drying oven for 3 days and obtained aboveground and belowground biomass.

Data analysis

All analyses were conducted in R version 4.2.1 (R Core Team, 2022). To quantify whether plants responded positively or negatively to *Dittrichia*-conditioned field soil, we calculated a plant–soil feedback metric using the log response ratio of plant growth (g/day based on total biomass) in soil from the *Dittrichia* microsite and the control microsite. Feedbacks were calculated for each family (the five replicates) using siblings planted in the respective microsites. We analyzed the data for the native and exotic range experiments separately. Figures were produced using *ggplot2* (Wickham, 2016).

To test whether plant–soil feedback differed between soil regions and seed regions of origin, we fit a linear mixed effects model with feedback as the response variable, seed region and soil region and their interaction as fixed effects, and seed site and soil site as random effects (*lme4* package; Bates et al., 2015). We initially also included block as a random effect in both models, but dropped this effect in the exotic range model because block explained so little variance that it resulted in a singular fit. We removed three outlier data points from the analysis for which the residuals were 5 or more SD away from the mean—two from the native range and one from the exotic range. The two native range outliers had extremely low growth in soil from the *Dittrichia* microsite (<0.0002 g/day), and the exotic range outlier had very low growth in soil from the control microsite (0.001 g/day). These numbers skewed the feedback values to be exceptionally low or high, respectively.

We interpreted the plant–soil feedback model results as follows. A significant effect of soil region on plant–soil feedback would indicate that soil microbial communities at the edge produced less negative plant–soil feedback than those in the core or vice versa (question 1, ecological change), whereas an effect of seed region or an interaction between seed region and soil region would demonstrate differentiation between core and edge genotypes in plant–soil feedback (question 2, evolutionary change). An effect of seed region alone would indicate that plants originating from one region consistently had more positive/negative feedbacks than plants from the other region (e.g., if edge populations evolved to have more beneficial interactions with soil biota overall), whereas an interaction effect would show that core and edge plant populations diverged, but that the direction depends on the soil origin (like in a local adaptation scenario where core plants have the most positive feedbacks in core soil and edge plants have the most positive feedbacks in edge soil).

Main and interaction effects in our fitted feedback models were evaluated using Type III Wald *F*-tests with Kenward–Rogers degrees of freedom using the *car* package (Fox & Weisberg, 2019). Because the interaction between seed region and soil region was not statistically significant ($\alpha = 0.05$) in either range, and the models without the interaction had lower AIC values (Supplementary Appendix 2; Supplementary Table S2), we removed the interactions from the models before interpreting the main effects of soil region and seed region. Marginal mean feedback by seed and soil region of origin was calculated using the *emmeans* package (Lenth, 2023). We also used *emmeans* to estimate the effect sizes of the soil region and seed region in each range (expressed as the difference in feedback between the edge and core, with positive values indicating more positive feedback at the edge). To better understand the variance of the effects of region (core vs. edge) and site, we extracted variances from the feedback mixed effects models for each range using the *insight* package (Lüdecke et al., 2019). The get_variance function returns the variance of the fixed effects (seed region and soil region together), the random intercept variances for seed site, soil site, and block, and the residual variance.

Results

Plant–soil interactions varied greatly across sites in both ranges, showing a range of positive, neutral, and negative feedbacks (expressed as the log response ratio of plant growth rate in *Dittrichia* and control soil; Figure 3; Table 1). However, we found no effect of soil region on feedback in either range (native: 0.13 ± 0.63 SE, $F_{1,\,7.69} = 0.042$, $p = 0.84$; exotic: −0.005 ± 0.49 SE, $F_{1,\,7.97} = 0.0001$, $p = 0.99$), answering our first question that the impact of the soil microbial community on plant growth did not differ systematically between core and edge. Second, we asked whether plants originating from the core and edge region differed in their response to these soils. We found no significant effect of seed region on feedback in either range (native: −0.17 ± 0.15 SE, $F_{1,\,4} = 1.31$, $p = 0.32$; exotic: 0.03 ± 0.08 SE, $F_{1,\,3.99} = 0.092$, $p = 0.78$), nor a significant interaction between seed region and soil region (native: $F_{1,\,73.68} = 0.17$, $p = 0.68$, exotic: $F_{1,\,79.59} = 3.29$, $p = 0.07$; Supplementary Table S2), indicating there was no evidence of evolution in the plant populations during range expansion from core to edge. Consistent with their small overall effect, the variance of the fixed effects (core

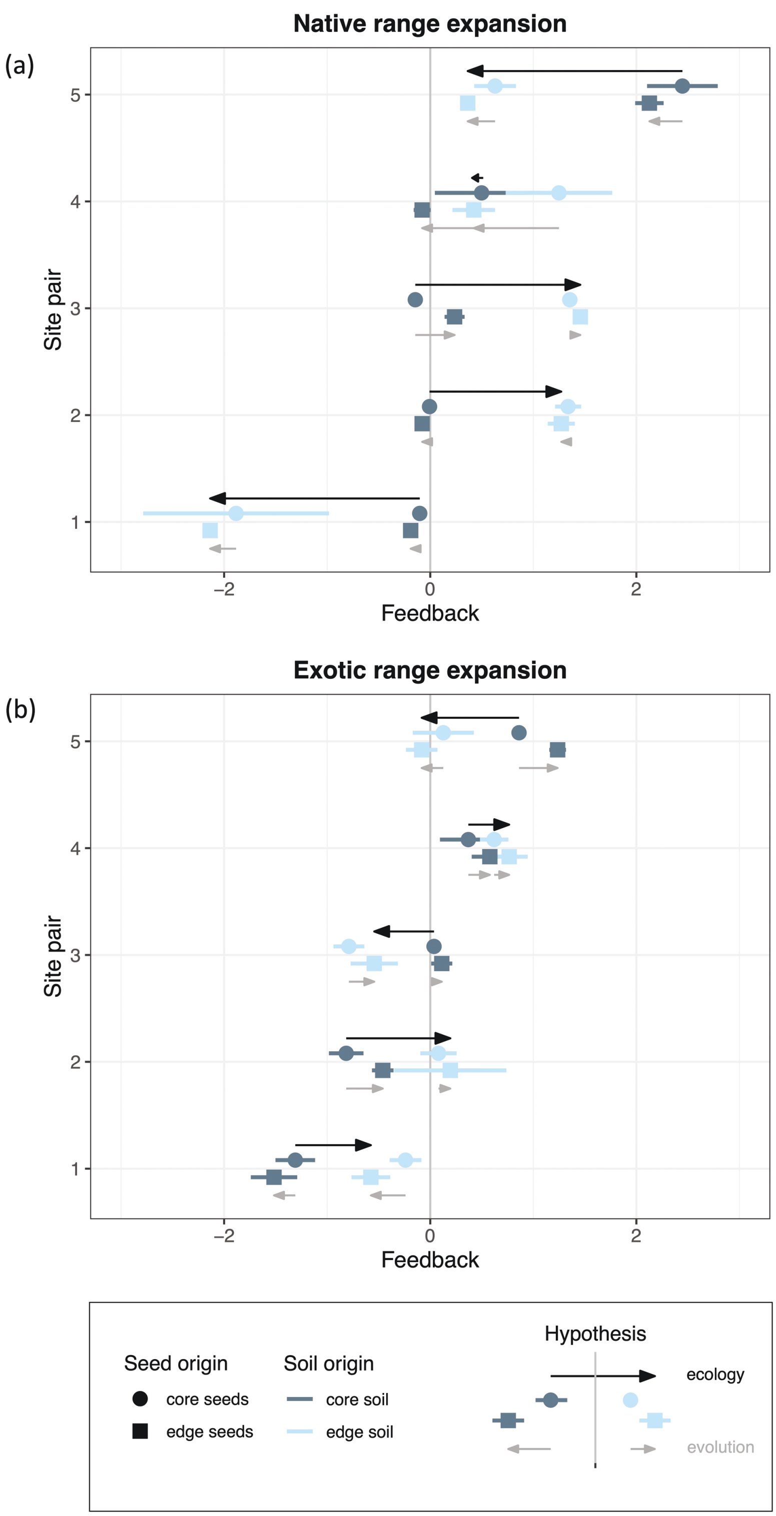

Figure 3. Changes in feedback (log response ratio of growth rate in *Dittrichia*/ control microsite soil) between core and edge in (A) the native range and (B) the exotic range. Mean ± SE for $n = 5$ plants originating from core sites (circles) or edge sites (squares) grown in soil from the core (dark symbols) or edge (light symbols). Black arrows indicate the direction of range expansion from core seeds growing in core soil (dark circle) to edge seeds growing in edge soil (light square), representing the ecological change in soil microbial interactions plants experienced. Grey arrows connect core and edge genotypes grown in the same soils, representing evolutionary differentiation between core and edge genotypes in their response to these soils.

vs. edge) was low (0.012 and 0.005 in the native and exotic range, respectively; Figure 4). Instead, feedback primarily varied among soil sites across both ranges. In line with the lack of differentiation between seed sources, seed sites also had very low variance (Figure 4).

Comparing the native and exotic range expansions, we found that contrary to our expectations, plant–soil interactions were more positive in the native range than in the exotic range (Figure 3; Table 1). In the core of the native range in France, most feedbacks were neutral, except in pair 5, which

Table 1. Estimated marginal mean feedback (log[*Dittrichia*/control]) by soil origin and seed origin in each range.

	Native range	Exotic range
Soil origins		
Core soil	0.47 ± 0.45 SE	−0.09 ± 0.35 SE
Edge soil	0.60 ± 0.45 SE	−0.09 ± 0.35 SE
Seed origins		
Core seeds	0.62 ± 0.33 SE	−0.10 ± 0.25 SE
Edge seeds	0.45 ± 0.33 SE	−0.08 ± 0.25 SE

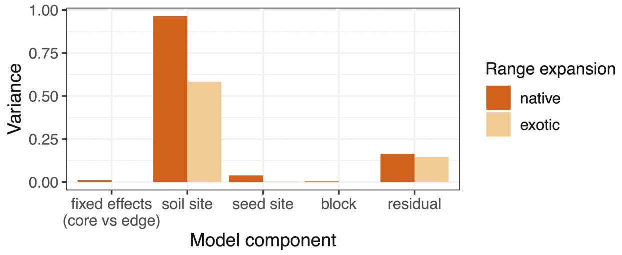

Figure 4. Variance of the fixed effects (seed and soil region, i.e., core vs. edge), the random intercept variance of soil site, seed site, and block, and the residual variance. Values were extracted from the linear mixed-effects models of soil feedback fitted for the native (dark shading) and exotic (light shading) ranges. No bar is displayed for the random intercept variance for the block in the exotic range because it was too small to be estimated, resulting in model singularity.

was strongly positive. At the range edge in the Netherlands, plants grew much better in soil from *Dittrichia* microsites, except in pair 1, which had strong negative feedback. The net result was that when comparing core to edge, plant–soil interactions were more positive at the edge for three pairs and more negative for two pairs (Figure 3). The average feedback in the native range was slightly positive (Table 1). In the exotic range in California, we found a more idiosyncratic pattern in plant–soil interactions, with both positive and negative feedbacks present at core and edge sites, changing in both directions. The marginal mean feedback estimated at both the core and edge fluctuated around zero (Table 1).

Our feedback metric, defined as the log response ratio in plant growth between *Dittrichia* soil and control soil, is most useful to interpret changes in the strength and direction of plant–soil interactions but may obscure absolute differences between soil types or seed origins. In both ranges, plant growth rates strongly differed between soil (micro) sites (Supplementary Appendix 3; Supplementary Figure S1). However, we found no overall effect of soil microsite (*Dittrichia* soil vs. control soil) or soil region of origin (core vs. edge) on plant growth in either range (Supplementary Table S4; Supplementary Figure S1). These results match our findings that feedback greatly differed between soil sites across each range. In the native range, plants originating from the edge had slightly higher growth rates than core plants overall (around 2 mg/day; Supplementary Appendix 3), regardless of soil origin. However, the effect of soil microsite or soil region on plant growth did not depend on seed origin (non-significant interaction effects, Supplementary Table S3), consistent with our results that no differentiation in plant–soil feedback evolved between core and edge plant populations.

Discussion

As plant populations spread to new areas, whether this is an expansion of their native range driven by climate change or the colonization of a new continent after human introduction, they face new interactions with the soil microbial community that can strongly affect plant growth and fitness. Using the annual plant *Dittrichia graveolens* that is currently expanding both its native and exotic range, we asked how plant–soil interactions changed over the course of range expansion and whether plant populations from the core and edge of each range were locally adapted to the soil microbial community. We expected that in an enemy release scenario, plant–soil feedbacks would become less negative during range expansion. Instead, we found no systematic difference in plant–soil feedbacks between the core and edge region in either range, with a patchwork of different plant–soil interactions observed across sites. We also predicted that plant populations from the core of each range would be locally adapted to home soil biota, with less (but potentially some) local adaptation in the edge populations. Adaptive defences against local pathogens and enhanced interactions with local mutualists should result in less negative plant–soil feedbacks in plants grown from local seeds, especially in core soils. However, we found no evidence of evolutionary change in feedback between core and edge populations; the effect of soil type was highly consistent across plant genotypes from core and edge sites (circles and squares in Figure 3).

Our results match previous studies that found no evidence of plant population differentiation despite broad-scale changes in plant–soil interactions during the range expansion of two other Asteraceae species. Andonian and Hierro (2011) compared the native and invaded range of *Centaurea solstitialis* and found more positive plant–soil feedbacks in invaded range soils, regardless of plant origin. Similarly, Wilschut et al. (2020) studied the native range expansion of *Centaurea stoebe* and found that plants originating from both the historic and new range accumulated fewer pathogenic soil nematodes in range-edge soil. Yet, other studies have found variation in plant–soil feedbacks between plant populations in a range expansion context. The perennial herb *Rorippa austriaca* experiences negative soil feedbacks in its native range, but in the expanded native range, feedbacks are neutral, and plants grow faster than in historic populations (Dostálek et al., 2016). The ability to cultivate mutualistic soil microbes may also be lost during range expansion. Van Nuland et al. (2017) found that populations of the tree *Populus angustifolia* were adapted to their local soil biota in the range interior, but not at the altitudinal range edge (comparing tree genotypes from local and lower altitudes); this results in the loss of positive plant–soil feedbacks at the expanding edge. Finally, Felker-Quinn et al. (2011) found that invasive populations of the tree *Ailanthus altissima* had developed both positive and negative site-specific plant–soil feedbacks (quantified by comparing home soil and all away soils in a factorial experiment with seed and soil origins). Our inferences about shifts in plant–soil feedbacks from core to edge were highly variable across the individual pairs of sites in our study (Figure 3), and overall, we found no evidence for consistent evolutionary change in plant–soil feedback from core to edge regions.

One major goal of our study was to compare changes in plant–soil interactions and plant phenotypic differentiation from core to edge between the native and exotic range expansion. Contrary to our expectations under enemy release, plant–soil feedbacks were more negative on average in the exotic range than in the native range (Figure 3; Table 1). This pattern may be a result of missed mutualisms in the exotic range (Nuske et al., 2021), but more data on mutualists associated with *D. graveolens* in California would be needed to confirm this hypothesis. Previous work in the native range demonstrated an increase in the ratio of mutualist to pathogen abundance in the *D. graveolens* rhizosphere at the Dutch range edge compared to the historic native range (Ramirez et al., 2019), which would match the positive plant–soil feedbacks observed at four of five sites in the expanded native range (Figure 3). In the exotic range, we observed a range of positive, neutral and negative feedbacks at both core and edge. The association of plants and novel soil biota may have been more idiosyncratic, or other environmental factors at individual sites were of greater importance in explaining plant growth. This result is in line with our hypothesis that shifts in plant–soil interactions in the exotic range may be highly variable (Figure 1), although we do note that the overall variance between soil sites was higher in the native range than in the exotic range (Figure 4). Considering local adaptation patterns, we expected these to be more pronounced during the native range expansion, because it included the historic native range and a range edge where the species has been resident for 20 years (as compared to the younger range edge in California). Notwithstanding the lack of overall differentiation between core and edge populations, we did find that the absolute growth rate of edge genotypes was higher than core genotypes at some sites in the expanded native range (Supplementary Appendix 3).

Experimental design considerations

Several aspects of our study design may have influenced our results. We used field-collected soil to compare *Dittrichia*-conditioned soil to “away” soil rather than a two-phase conditioning experiment in the greenhouse. While we made great efforts to collect “away” soil from nearby microsites that appeared to differ only in not having a *D. graveolens* plant growing there, inevitably, there may be additional variation in soil characteristics apart from the soil microbial community. Including a soil sterilization treatment would have helped to separate abiotic and biotic differences in these soil microsites, but given our larger pot size and greenhouse constraints, we were not able to incorporate such a treatment. Compared to greenhouse soil, field-conditioned soil contains a microbial community strongly influenced by local soil characteristics and the whole surrounding community both above- and belowground; this environmental context will influence plant–soil feedback results (Beals et al., 2020; Koorem et al., 2020). By comparing microsites with and without *Dittrichia*, we aimed to isolate *Dittrichia*-specific soil conditioning effects (sampling directly from the rhizosphere) while preserving the context of the local soil community, which is highly relevant to our study. On the whole, a recent meta-analysis (Beals et al., 2020) found no difference in plant–soil feedbacks quantified in-home vs. away comparisons using greenhouse-conditioned soil (96 experiments across 25 publications) or field-conditioned soil (90 experiments across 19 publications).

We used whole field soil rather than field soil inoculum applied to a common background soil. Using whole soil preserved other abiotic properties of the microsite soil that may have affected plant growth and could have obscured differences caused by soil biota. On the other hand, comparing two nearby microsites allowed us to expose plants to a greater volume of field-conditioned soil biota than is possible with a soil inoculum. Using a soil inoculum introduces a bias of which microbial taxa are able to colonize the background soil during the short time window of the experiment, changing microbial community composition and relative abundance (Brinkman et al., 2010; Kulmatiski & Kardol, 2008). Whole field soil best represented the microbial community cultivated by our focal species under the natural field conditions experienced across each range.

It is theoretically possible that the control microsites contained *Dittrichia* plants in previous years, which could have left a legacy in the soil biota. However, this is very unlikely to be the case at the range edge, where populations are few and far between and represent the very front of the range expansion. Even in the core of the native and exotic ranges, *Dittrichia* plants tend to be distributed around adult plants from the previous generation—a pattern that is well known and exploited by practitioners managing this species in its invaded range. It is not a species that shows marked local colonization–extinction dynamics. Therefore, we are fairly confident that the control microsites have not been conditioned by *Dittrichia* plants in recent years.

Evaluating evolution during range expansion in the wild is limited by the availability of historical events to study. Species have only one native range to expand, and we only considered a single exotic range expansion. As such, the sites in our edge regions share an evolutionary history originating from the core regions, which was inferred from molecular evidence in the native range (Lustenhouwer et al., 2018) and from the first record of the species in California (Preston, 1997). We accounted for this shared history by modelling the sites as random effects, representing draws from each core or edge region. We explore the power of our experimental design to detect changes in feedback between soil regions and seed regions in Supplementary Appendix 4. To further test the generality of our findings, future studies could include additional independent invasions of *D. graveolens* in Australia or South Africa.

Finally, due to access restrictions caused by the start of the COVID-19 pandemic, the California experiment was harvested ~40 days later than the Wageningen experiment. Fortunately, we were able to measure plant size at 3 weeks of age in both experiments, which produced qualitatively similar results to the final harvest data.

Plant–soil feedback at the local vs. biogeographic scale

Our ability to forecast biogeographic shifts in plant–soil interactions during range expansion will depend on the scale at which they vary across the landscape. Although we did not find an overall effect of microsite (*Dittrichia* vs. control soil), plant growth did differ greatly among soils (Supplementary Appendix 3), indicating that microhabitat suitability plays an important role in this system. We explored whether water-holding capacity or soil organic matter explained these differences but found no conclusive patterns. Soil site explained most variance in plant growth responses across the landscape (Figure 4). The community composition of plant-associated soil biota may be more strongly driven by site environmental variation than by plant genotypes, as observed by De Bellis et al. (2022) for root fungi and mycorrhizae associated with the native range expansion of sugar maple. The re-association of plants, pathogens, and mutualists in a new range can be idiosyncratic and context dependent, limiting general predictions (Gundale & Kardol, 2021). More general patterns may be identified with an increased knowledge of the functional biogeography of the soil microbial community across the landscape (Brunel et al., 2020). For example, populations of the grass *Milium effusum* along a latitudinal gradient in Europe grew better in soils from colder, northern sites, which were expected to harbour more favourable microbial communities based on known latitudinal gradients in nitrogen deposition and soil acidity driving the abundance of mycorrhizae and soil pathogens, respectively (De Frenne et al., 2014).

The nature of specialization in host range is key to understanding how both mutualistic and pathogenic microbes affect plant community ecology (Semchenko et al., 2022), including how plant–soil feedbacks will change with range expansion. The greatest change in the net effect of microbial communities on range-expanding plants will occur when species are constrained by specialist (rather than generalist) natural enemies that they leave behind in the range core (van der Putten et al., 2013), and when pathogens are more specialized than mutualists, resulting in a relative shift to more positive interactions. However, recent work has highlighted that generalist soil biota may play an important role in plant–soil feedbacks (Semchenko et al., 2022; Wilschut et al., 2023). If *D. graveolens* primarily interacts with generalist pathogens, this may help explain why we did not see a clear pattern of shifting plant–soil interactions from core to edge.

Future studies of range expansion chronosequences are needed to better understand and predict plant ecological and evolutionary responses to the soil microbial community in their new range. It would be valuable to consider a variety of species with negative, neutral, and positive feedbacks in their native range to capture scenarios involving both pathogenic and mutualistic interactions. Technical advances in metabarcoding provide an expanding opportunity to understand the contributions of particular soil microbes to plant–soil feedback and how plant–microbe interactions change during range expansion in native and exotic ranges (sensu Brunel et al., 2020; Ramirez et al., 2019).

Conclusions

We found that *Dittrichia graveolens* showed a wide range of responses to soils across its expanding native and exotic ranges. The large heterogeneity in soil responses overwhelmed any general patterns in plant–soil feedbacks from core to edge and even comparisons between the native range expansion and cross-continental invasion. In this context, any signal of local adaptation to resident microbial communities in the core of the range (or rapid adaptation to microbial communities at the range edge) would be hard to detect. Even when selection mediated by the soil biota at an individual site is strong, variable selection across the landscape combined with substantial gene flow during range expansion would limit evolutionary changes in plant–soil feedbacks between core and edge (Schweitzer et al., 2014). In contrast to the rapid evolution of traits responding to latitudinal clines in climate or photoperiod during biological invasions or range shifts (Colautti & Lau, 2015; Lustenhouwer et al., 2018), eco-evolutionary dynamics in plant–soil interactions may be better understood as a geographic mosaic of coevolution (Thompson, 2005) between plant hosts and soil microbes, in which idiosyncratic patterns across the range are expected.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

The data underlying this article are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.3n5t-b2rr0.

Author contributions

Nicky Lustenhouwer (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Funding acquisition [equal], Investigation [lead], Methodology [lead], Project administration [lead], Resources [equal], Software [lead], Supervision [supporting], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Tom Chaubet (Conceptualization [supporting], Data curation [supporting], Formal analysis [supporting], Investigation [supporting], Methodology [supporting], Project administration [supporting], Software [supporting], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), Miranda Melen (Conceptualization [supporting], Data curation [supporting], Investigation [supporting], Methodology [supporting], Project administration [supporting], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), Wim H. van der Putten (Conceptualization [supporting], Formal analysis [supporting], Funding acquisition [supporting], Methodology [supporting], Project administration [supporting], Resources [equal], Supervision [supporting], Validation [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), and Ingrid Parker (Conceptualization [supporting], Formal analysis [supporting], Funding acquisition [equal], Methodology [supporting], Project administration [supporting], Resources [equal], Supervision [lead], Validation [supporting], Writing—original draft [supporting], Writing—review & editing [supporting])

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Conflicts of interest

The authors declare no conflicts of interest.

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