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LETTERS

Successful range-expanding plants experience less above-ground and below-ground enemy impact

Tim Engelkes[1], Elly Morriën[1], Koen J. F. Verhoeven[1], T. Martijn Bezemer[1,2], Arjen Biere[1], Jeffrey A. Harvey[1], Lauren M. McIntyre[3], Wil L. M. Tamis[4] & Wim H. van der Putten[1,2]

Many species are currently moving to higher latitudes and altitudes[1–3]. However, little is known about the factors that influence the future performance of range-expanding species in their new habitats. Here we show that range-expanding plant species from a riverine area were better defended against shoot and root enemies than were related native plant species growing in the same area. We grew fifteen plant species with and without non-coevolved polyphagous locusts and cosmopolitan, polyphagous aphids. Contrary to our expectations, the locusts performed more poorly on the range-expanding plant species than on the congeneric native plant species, whereas the aphids showed no difference. The shoot herbivores reduced the biomass of the native plants more than they did that of the congeneric range expanders. Also, the range-expanding plants developed fewer pathogenic effects[4,5] in their root-zone soil than did the related native species. Current predictions forecast biodiversity loss due to limitations in the ability of species to adjust to climate warming conditions in their range[6–8]. Our results strongly suggest that the plants that shift ranges towards higher latitudes and altitudes may include potential invaders, as the successful range expanders may experience less control by above-ground or below-ground enemies than the natives.

Range expansion is a key adaptive feature of species in response to changes in climate, habitat availability and other limiting factors[1,2,6–10]. Currently, a number of species are showing rapid range expansion from warmer into previously colder biomes[11]. As not all species have the same range shift capacity, ecological interactions may become disrupted as the community species pool changes[9]. Rapid range expansion and the loss of control by natural enemies are key features of invasive species[12,13]. However, very few studies have actually investigated range expansion in relation to enemy exposure[5,14]. The aim of our study was to examine how rapidly range-expanding plant species are defended against above-ground and below-ground natural enemies in comparison with related plant species that are native to the expansion zone.

Plants are usually attacked by a wide variety of above-ground and below-ground natural enemies[15]. It is well established that invasive exotic plants are less exposed to above-ground and below-ground control by natural enemies than are related natives in the new range[4,16–20]. However, phylogenetically controlled empirical evidence of exotic plant control by natural enemies is scarce[5,21]. Here we compare range-expanding invasive plants of intercontinental origin and intracontinental range-expanding species with congeneric native plant species, all co-occurring in a riverine area. Above ground, we exposed range-expanding exotic plants of inter- and intracontinental origin and congeneric native species to non-coevolved naive polyphagous herbivores, as well as to cosmopolitan polyphagous herbivores. In the same experiment, we exposed all plants to a general soil community from the invaded range and compared their plant–soil feedback responses[22]. We tested the hypothesis that the plants would not differ in their response to the polyphagous shoot herbivores, as all plants had equal familiarity with them, but that both the inter- and intracontinental range-expanding species would develop soil feedback that is less negative than that of the related natives.

Contrary to our hypothesis, above-ground herbivory influenced plant biomass of range-expanding species differently than it did the native species (plant origin × herbivory interaction: $F_{1,108} = 4.58$, $P = 0.035$; Fig. 1a). Herbivores caused significant biomass loss to native plants (the species mean proportional biomass reduction was −38.7% and differed from zero: $t = -2.98$, d.f. = 8, $P = 0.017$), whereas the effect of herbivory on the range-expanding species was much smaller and not significantly different from zero (effect size was −17.3%: $t = -1.69$, d.f. = 5, $P = 0.151$; Fig. 2a).

Although the range-expanding species overall had more shoot biomass than the native species ($P = 0.001$), locust survival was significantly lower on the range-expanding species than on the native species ($F_{2,52} = 9.57$, $P = 0.0003$; Fig. 3a). Aphid numbers, on the other hand, were not significantly affected by host plant origin ($\chi^2 = 4.09$, d.f. = 2, $P = 0.129$; Fig. 3b). The negative effect of the range-expanding plants on the locusts could not be explained by two general indicators of food quality, namely the carbon/nitrogen ratio (origin effect: $F_{1,99} = 0.19$, $P = 0.662$; origin × herbivory interaction: $F_{1,99} = 1.69$, $P = 0.197$) and the nitrogen content of the foliage (origin effect: $F_{1,101} = 2.65$, $P = 0.107$; origin × herbivory interaction: $F_{1,101} = 0.28$, $P = 0.597$). We note that the levels of phenolic compounds in the foliage were higher in range-expanding plants with herbivory than in range-expanding plants without herbivory and in the native plants with and without herbivory (interaction effect: $F_{1,103} = 13.07$, $P = 0.0005$; Supplementary Fig. 1). This indicates that range-expanding plants were better than natives in inducing general defences against non-coevolved shoot herbivores. The intercontinental range expanders were slightly less negatively affected by herbivory than were the intracontinental range expanders (range expander origin × herbivory interaction: $F_{1,44} = 4.25$, $P = 0.045$; Supplementary Fig. 2a). Nevertheless, the three intracontinental range expanders suffered significantly less from shoot herbivory than did their congeneric natives (origin × herbivory interaction: $F_{1,52} = 6.45$, $P = 0.014$). *Bidens* was the only genus to show contrasting effects between native species within a genus (Supplementary Fig. 3a).

Native plant species also suffered more from below-ground biotic interactions in own soil, in comparison with control soil, than did range-expanding plants (plant origin × soil interaction: $F_{1,112} = 4.16$, $P = 0.043$; Fig. 1b). The native species experienced significantly

[1]Department of Multitrophic Interactions, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, The Netherlands. [2]Laboratory of Nematology, Wageningen University and Research Centre, PO Box 8123, 6700 ES Wageningen, The Netherlands. [3]Departments of Molecular Genetics and Microbiology and Statistics, University of Florida, Gainesville, Florida 32610-1399, USA. [4]Nationaal Herbarium Nederland, Leiden University Branch, PO Box 9514, 2300 RA Leiden, The Netherlands.

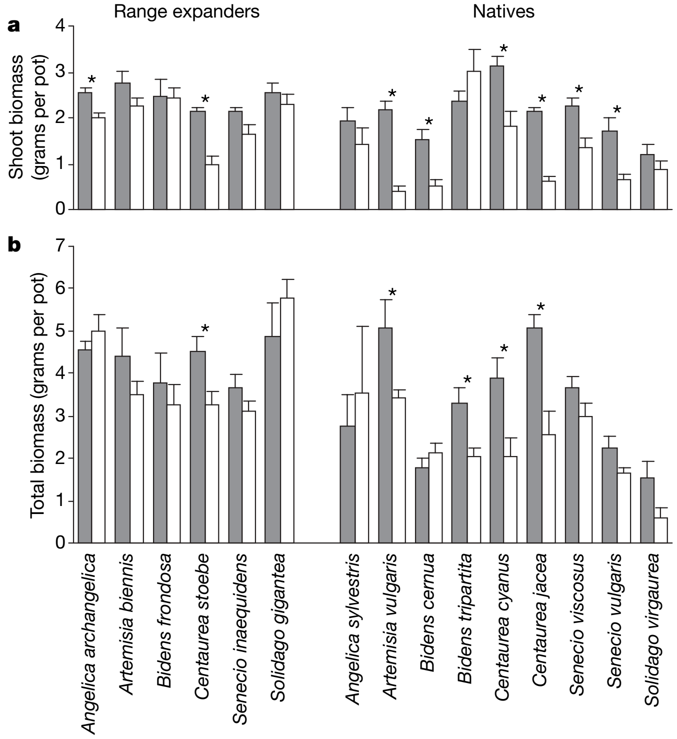

Figure 1 | Effects of shoot herbivores and soil feedback on plant biomass. **a**, Shoot biomass (mean dry weight ± s.e.m.) of range-expanding exotic and congeneric native plants without herbivory (grey bars) and plants exposed to above-ground herbivory by the African desert locust, *Schistocerca gregaria*, and the green peach aphid, *Myzus persicae* (white bars), show that most plants experienced a significant biomass loss during three weeks of exposure, but that biomass loss due to herbivory was severest on native plants. **b**, Total biomass (mean dry mass ± s.e.m.) in 'control' soil (grey bars) and 'own' soil (white bars) (see Methods) shows that natives are reduced more than range-expanding exotic species in own soil in comparison with control soil. Bars show back-transformed means of log-transformed data. In both panels, an asterisk above a pair of bars indicates statistically significant effects of treatment within plant species (*t*-test, $P < 0.05$).

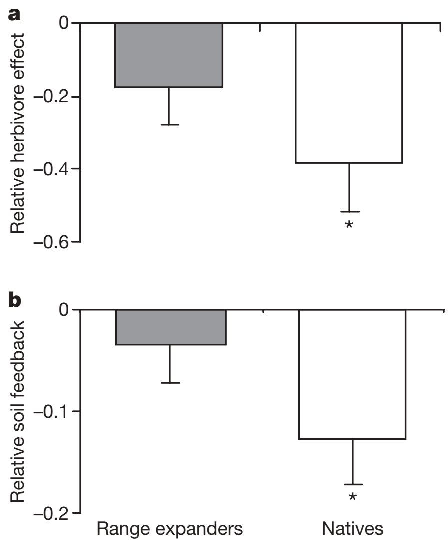

Figure 2 | Relative change in plant biomass due to shoot herbivores and soil feedback. **a**, Relative shoot biomass effects of above-ground herbivory by the locust *S. gregaria* and the aphid *M. persicae*, calculated as (shoot biomass with herbivores – shoot biomass without herbivores)/(shoot biomass without herbivores) ± s.e.m., on range-expanding exotic plants (grey bars; $n = 6$ species averages) and related native plants (white bars; $n = 9$ species averages) using plant species as replicates. **b**, The feedback effect of the soil community, calculated as (total biomass own soil – total biomass control soil)/(total biomass control soil) ± s.e.m., based on back-transformed means of log-transformed data using species as replicates. Bar codes are the same as in **a** (see above). Native species on average experienced significant shoot biomass reduction by shoot herbivory and significant negative soil feedback (*$P < 0.05$), whereas exotic range expanding plants did not differ from a neutral response in either case ($P > 0.05$).

negative soil feedback (−12.8%; difference from zero: $t = -2.52$, d.f. = 8, $P = 0.036$), whereas that of the range expanders was much smaller and not different from a neutral effect (−3.7%; difference from zero: $t = -0.96$, d.f. = 5, $P = 0.381$; Fig. 2b). The performance in own soil versus control soil did not differ between the intra- and intercontinental range expanders (range expander origin, soil and origin × soil interaction: respectively $F_{1,46} = 0.41$, $P = 0.526$; $F_{1,46} = 2.39$, $P = 0.129$; $F_{1,46} = 0.84$, $P = 0.363$; Supplementary Fig. 2b). As observed for above-ground herbivores, a contrasting effect between native species within genus was observed for *Bidens* only (Supplementary Fig. 3b).

Across the herbivory and soil feedback treatments, in 14 out of 18 within-genus comparisons the biomass reduction of the natives was stronger than that of the range expanders (non-parametric sign test: $M = -5$, $P = 0.031$; see Supplementary Information). However, above- and below-ground biotic interactions did not vary in concert with each other; the Spearman's rank-order correlations of the shoot herbivore and soil feedback effects on species within sets of native and range-expanding plant species were not significant ($P = 0.865$ and $P = 0.329$, respectively; see Supplementary Information). We conclude that range-expanding plants were less sensitive to shoot herbivory and negative soil feedback than were natives; however, the rank order in which plants were affected by shoot herbivory differed from the rank order in which they were affected by negative soil feedback.

Our results provide new evidence that plants which are successful in range expansion towards higher latitudes interact differently with shoot herbivores than do congeneric plant species that are native to the invaded range. Although all plant species were equally new to the desert locust, the locusts experienced reduced survival on the successful range expanders, but not on the related native plants. On the other hand, the cosmopolitan aphid was not influenced differentially by plant origin. Our hypothesis predicted no differences; however, the shoot herbivores reduced the biomass of the range-expanding plants less than they did that of the related native plant species. In comparison with the range expanders, the negative soil feedback of the native plants was more in line with our hypothesis. Thus far, studies of enemy exposure to exotic invasive weeds have usually focused either on enemies from the invaded range or on invasive enemies[23]. Our results suggest that the plant species successfully expanding their range towards higher latitudinal riparian areas possess superior defence traits in comparison with related native species. In this respect, these successful range expanders have similarities with invasive exotic plants[21], which also are superior in short-term resource acquisition[24], although there was no correlation between the strengths of above- and below-ground enemy effects.

Thus far, most attention has focused on the uncoupling of food-chain interactions due to regional climate warming[14,25,26]. Here we show that some successful range-expanding riparian plant species[11] experience less above-ground and below-ground enemy impacts, even when exposed to non-coevolved and cosmopolitan polyphagous above-ground herbivores. Thus, the successful range expanders differed in defence trait characteristics from the congeneric natives. We focused our sampling strategy on plants successfully expanding their range into northern riparian habitats. Future studies should also explore other habitats, as well as less successful range expanders, to test whether, for example, trees and dry land plant species show similar responses. Poor range shift capacity has been predicted to result in a loss of diversity[6,7]. However, the prediction of consequences of climate warming and other changes that result in range expansion require inputs from different fields in ecology[27]. Our

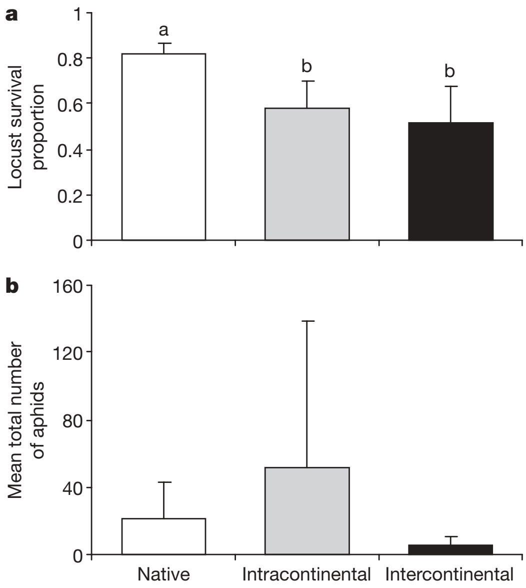

Figure 3 | Performance of herbivores on native and non-native plants. **a**, The survival proportion of the naive generalist herbivore *S. gregaria*, which did not have any previous experience with any of the plant species used, on native plants (white bars; $n = 9$ plant species), intracontinental range expanders (grey bars; $n = 3$) and intercontinental range expanders (black bars; $n = 3$). The survival proportion was calculated as back-transformed means $\pm$ s.e.m. from arcsine data on numbers recaptured divided by numbers added. The locust survival proportion was on average lower on range expanders from both origins than it was on native host plant species. Different letters above the bars indicate significant differences between bars ($P < 0.05$). **b**, Mean total numbers (per pot) $\pm$ s.d. of the generalist aphid *M. persicae* after a three-week feeding assay demonstrate that the average population increase did not significantly differ between plant origins ($P > 0.05$) (bar colours as in **a**).

results suggest that successful range-expanding plant species may include species with invasive properties, which is crucial information for the future conservation of biodiversity in temperate and northern latitudes.

METHODS SUMMARY

We analysed floristic data to identify exotic plant species in riparian areas in the Netherlands, which all have become well established in the twentieth century. We surveyed plants with a strong increase in abundance over the past few decades and congeneric relatives in the same habitat. We obtained seedlings of three intracontinental range expanders, three species that originated from other continents and became naturalized in southern Europe before their northward range expansion, and nine natives (Supplementary Table 1). Three extra native plant species were included to test the sensitivity of our phylogenetic comparison for species-specific effects.

Soil samples were collected from Millingerwaard (an area along the Waal River in the Netherlands), inoculated into sterilized sandy loam soil, placed in four-litre pots and planted with four individuals of one species per pot. After eight weeks in a greenhouse, the plants were harvested and the soils were used for a second growth experiment in order to measure plant–soil feedback effects[22,28]. In this second stage, each plant species was grown in own soil (previously containing individuals of the same species) and control soil (a mixture of soil from all other plant species, excluding species from the same genus). After seven weeks, we placed all pots individually in cages and added above-ground herbivores to half the control-soil pots that had been assigned to the herbivory treatment at the start of the experiment ($n = 5$). We used five-day-old, first-instar locust nymphs of the African desert locust, *Schistocerca gregaria*, which is highly polyphagous throughout all stages of its development and is non-coevolved with any of the tested plant species. We also used the green peach aphid, *Myzus persicae* (Hemiptera: Aphididae), a highly polyphagous herbivore that has a cosmopolitan distribution. Three weeks after adding the herbivores, all plants were harvested, dried, weighed and analysed.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Information Reprints and permissions information is available at www.nature.com/reprints. Correspondence and requests for materials should be addressed to W.H.v.d.P. (w.vanderputten@nioo.knaw.nl).