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The endomicrobiome and weed invasiveness in Mediterranean ecosystems worldwide

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Mediterranean ecosystems, one of the most significant global hotspots of biodiversity, are threatened by invasive weeds. Although endomicrobiomes – the vast array of microbes colonising living plant tissues – are known to affect plant fitness, their contribution to weed invasiveness remains virtually unknown. Here, we experimentally assess the role of the endomicrobiome in the invasiveness of *Taraxacum officinale* (common dandelion), a widespread weed in Mediterranean ecosystems worldwide. In a culling experiment across five generations, we compare the fitness of *T. officinale* from these ecosystems on five continents grown with intact or reduced native seed-borne endomicrobiomes. Additionally, we report a competition experiment with F_1 and F_5 individuals assessing their impacts on native local Asteraceae species. We found that *T. officinale* individuals harboring intact endomicrobiomes show faster and more favorable trait development compared with individuals with reduced endomicrobiomes. Enhanced competitiveness of endomicrobiome-colonised *T. officinale* plants with local Asteraceae species is apparently caused by increased synthesis of allelochemicals in shoots and rhizosphere soil, with gene expression analyses also showing the endomicrobiome to affect the expression by *T. officinale* of stress response and RNA-directed DNA methylation genes. Our findings provide insights into the mechanisms underlying weed invasiveness in Mediterranean ecosystems.

Mediterranean ecosystems cover only 5% of the Earth's land surface and yet support 20% of vascular plant species, and are thus considered to be global biodiversity hotspots[1]. Currently, these ecosystems face multiple and severe threats, including invasion by alien weed species, which presents a significant risk to their rich native biodiversity and the well-being of their ~500 million human inhabitants[2]. Invasive alien plant species cause huge economic losses, with plant invasions incurring costs totalling ~$4 billion per annum worldwide[3], and almost $10 billion over three decades in the Mediterranean Basin alone[4]. Invasive species can disrupt ecosystem services, such as water availability and nutrient cycling, and also increase the frequency and intensity of wildfires, compounding their ecological and economic impacts[5,6]. Hence, understanding the mechanisms underlying the success of alien plant species remains a fundamental goal in invasion

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ecology[7]. This knowledge is key to curtailing the impacts of alien species and to developing effective programs to manage invasive weeds in Mediterranean ecosystems[8,9].

Non-native plant species colonising new habitats often undergo adaptive evolution, explaining – at least in part – the success of the invasion process[10–12]. Following arrival in a new community, a lag phase occurs until a plant species increases in abundance and transitions to becoming invasive[13]. This lag phase is primarily due to initially low population size and genetic variability, which require time to increase and diversify in response to local selection pressures[8]. For instance, invasive plant species demonstrate remarkable climate adaptability in their invading ranges[14], manifested as differentiation among populations in key functional traits enhancing fitness and mechanisms of environmental tolerance[15,16]. However, although research has focused on genetic differentiation or local adaptation as mechanisms underlying the rapid adaptation rates of invasive species[17], the potential role of the endomicrobiome – i.e., the microbes (predominantly fungi and bacteria) colonising mature and healthy plant tissues[18] – has garnered little attention as a factor explaining the invasiveness of weed species (but see refs. 19,20).

The endomicrobiome is known to confer ecological advantages and physiological benefits to plants, including enhanced nutrient uptake, competitive ability, and tolerance to biotic and abiotic stresses[21–23]. However, its role in plant invasiveness in new habitats remains unknown[7,24,25]. In one of the few studies to have empirically measured feedbacks between the host genotype and the endomicrobiome, repeated exposures to a herbicide led to herbicide-resistant populations of the invasive weed *Echinochloa crus-galli*[26], which stemmed from co-adaptation between host plants and their vertically transmitted seed microbiome[27,28]. After five generations, the selected microbiome showed enrichment in a bacterial taxon (*Pantoea deleyi* SH-355) capable of inducing the expression of genes associated with the metabolism of xenobiotics, such as those encoding for cytochrome P450 monooxygenases and glutathione transferase[27]. Similarly, an initially strong genotypic effect of *Solanum lycopersicum* on its endomicrobiome declined over successive generations, resulting in a convergent yet robust microbiome resistant to external invasions[29]. Although these studies suggest a significant role of the microbiome in plant invasiveness, empirical evidence linking endomicrobiomes to plant competitive ability is still absent from the literature.

Accordingly, we conducted a series of laboratory selection (*i.e.*, culling) experiments using *Taraxacum officinale* F.H. Wigg. (Asteraceae, common dandelion), a species originating in Eurasia that has become one of the most successful and widespread invasive weeds worldwide[30]. For this, we collected seeds of *T. officinale* from Mediterranean ecosystems on five continents and conducted experiments to investigate changes in the invasiveness traits of plants grown across five generations with intact or reduced local seed-borne endomicrobiomes. We selected and reproduced genotypes with the highest performance in each generation, measured by an integrated performance index based on plant fitness proxies. By calculating Haldanes[31], we compared the micro-evolutionary rates of the index across generations. Furthermore, we evaluated the competitive ability of *T. officinale* grown with its intact seed-borne endomicrobiome in the first (F_1) and fifth (F_5) generations against a phylogenetically closely-related plant species native to each of the five Mediterranean ecosystems studied. We explored potential mechanisms involved in this competitive interplay by measuring soil and shoot concentrations of allelochemical phenolic compounds[32]. Finally, the expression by *T. officinale* of genes associated with different aspects of invasiveness, including fitness, environmental tolerance and epigenetic variation, was measured in the F_1 and F_5 generations. Whilst our experiments could not differentiate between changes in plant phenotype caused by the seed-borne endomicrobiome and genetic drift or maternal effects and other factors[33] – and thus did not explicitly test for microbiome-associated adaptive evolution—this approach enabled us to determine whether the endomicrobiome influences the development of fitness traits associated with the invasiveness of a globally important weed.

Results and discussion

Our study provides evidence that the vertically transmitted seed-borne endomicrobiome enhances the development across several generations of traits associated with the invasiveness of *T. officinale*. It indicates that endomicrobiome-associated traits, such as the enhanced expression of stress tolerance genes and production of allelochemicals, confer competitive ability on the weed against native plant species. Although our experiments did not track genetic lineage, measure genome-wide variation, artificially select microbial communities or involve reciprocal transplants of host and microbiome[34], they nevertheless detected consistent, multigenerational shifts in fitness-related traits of *T. officinale* colonised by seed-borne endomicrobiomes. Whilst other factors, notably maternal effects[33], could in part explain the plant phenotypic changes reported here, the observations support responses directly mediated by the seed-borne endomicrobiome.

The endomicrobiome drives plant invasion success

After five generations of experimental selection based on a performance index calculated from integrated measurements of maximum photosynthetic rate, flower head and viable seed production (see "Methods"), distinct developmental trajectories were observed between *T. officinale* individuals grown with their intact or reduced seed-borne endomicrobiomes (hereafter referred to as E^+ and E^- plants, respectively). E^- plants, which were generated using a fungicide and a bactericide with no effects on plant growth (see "Methods"), consistently exhibited slower and less positive trait development than E^+ plants, which was evident in the performance index for the *T. officinale* populations from each continent and the global mean (Fig. 1) and the three individual traits from which the index was calculated (Supplementary Figs. 1–3). The highly significant endomicrobiome × time (generation) factor in all linear mixed models (Supplementary Data 1–4), along with the significant differences in fitted slopes between E^- and E^+ plants (Supplementary Data 5), supported these findings. Microevolutionary rate, expressed in Haldanes (the average change in the performance index, in units of standard deviations and corrected for the number of generations) was significantly faster in E^+ plants than in E^- plants, again for populations from each continent and for the global mean (Fig. 1, and Table 1, Supplementary Fig. 4). Similarly, supplementary experiments confirmed that the endomicrobiome enhanced the performance of *T. officinale*, with E^- plants inoculated with seed-borne microbes displaying the same maximum photosynthetic rate, flower production, biomass and survival as E^+ plants (Supplementary Fig. 5).

These findings highlight the central role of the seed-borne endomicrobiome in enhancing the fitness of the invasive weed species *T. officinale*. The enhanced photosynthetic rate, flower head production and viable seed output observed in E^+ plants across generations demonstrate how the endomicrobiome boosts traits linked to competitive capacity, specifically the ability to convert available resources (i.e., photosynthetic rates) into reproductive output (i.e., flowers and viable seeds). Nevertheless, populations from each continent varied in their responses to seed-borne endomicrobiomes, with clear intergenerational reductions in the performance and micro-evolutionary rates of E^- *T. officinale* plants from Europe, South America and Africa, but null and positive effects on those of E^- *T. officinale* from North America and Oceania over five generations, respectively (Fig. 1). This variation was reflected in the global trend, which, despite showing significant differences between E^- and E^+ plants in both the individual traits and the overall performance index, showed far more variability within the two groups relative to those observed in each Mediterranean ecosystem (Fig. 1; and Supplementary Fig. 1–3).

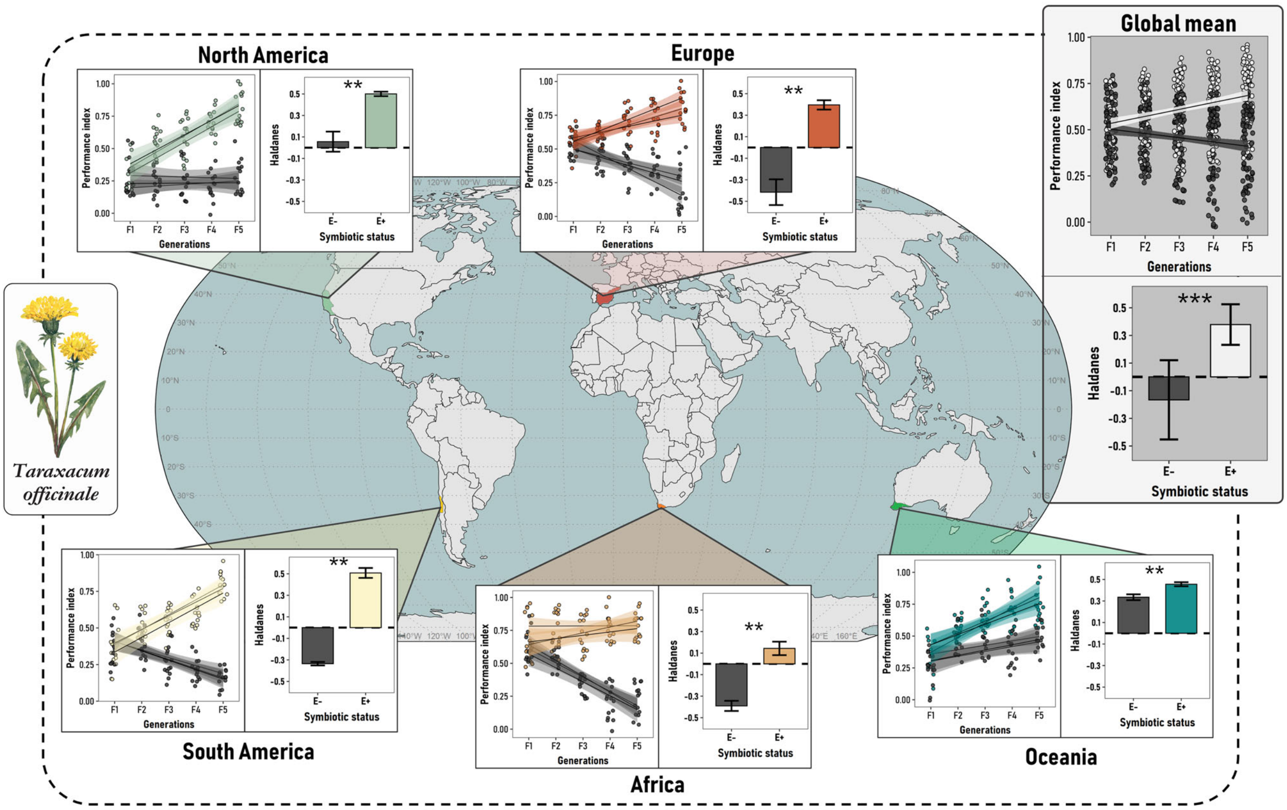

Fig. 1 | Distribution of the sampled populations of *Taraxacum officinale* in Mediterranean ecosystems on five continents. The inset graphs show inter-generational changes in a performance index derived from three fitness-related traits (maximum photosynthetic rate, flower head production and viable seed number; see "Methods"). For each continent, coloured and grey regression lines represent the three sampled populations grown with intact (E$^+$) or reduced (E$^-$) seed endomicrobiomes, respectively, with each point corresponding to one biological replicate ($n = 5$ individuals per population and generation). Accordingly, the global dataset comprises 75 E$^+$ and 75 E$^-$ individuals per generation (15 from each continent). Barplots show the average micro-evolutionary rate (Haldanes) calculated for the three populations within each continent. Comparisons between E$^+$ and E$^-$ rates were performed using two-sample *t*-tests ($n = 3$; two-sided). Values shown in bar graphs are means ± SD, with asterisks denoting differences between means (**; $p < 0.01$ and ***; $p < 0.001$). All p values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$). Detailed results from the LMM analyses and *t*-tests are provided in Supplementary Data 1 and 12, respectively.

The role of the endomicrobiome in interspecific competition

Having established that the endomicrobiome positively influences the fitness of *T. officinale* from Mediterranean ecosystems, we sought to further evaluate the ecological implications of this effect for the invasiveness of the species. To this end, we assessed competition, measured by the relative competition intensity index[35], between E$^+$ *T. officinale* and a local native Asteraceae species from each continent, and compared values of the index between the F_1 and F_5 generations. Although this experimental design did not include a direct comparison between F_5 plants grown with intact or reduced endomicrobiomes, it measured the cumulative impacts of selection over five generations on the competitiveness of *T. officinale* grown with its intact seed-borne endomicrobiome. After five generations, E$^+$ *T. officinale* plants exhibited increased competitiveness, as indicated by the relative biomass gains among F_5 plants compared with F_1 individuals, and the detrimental effect on local native plant species (Fig. 2). Although relative biomass gains among E$^+$ *T. officinale* F_5 plants were not observed in all populations, significant biomass losses were evident across all Mediterranean ecosystems among native Asteraceae species, mainly when grown with E$^+$ *T. officinale* F_5 individuals compared with F_1 plants (relative to monoculture, Fig. 2; Supplementary Data 6). Interestingly, despite the absence of inter-generational changes in relative biomass gain among *T. officinale* plants from California and Chile, these populations nevertheless exerted negative effects on their respective local native species in the F_5 compared with the F_1 generation (Fig. 2).

Although we cannot exclude the possibility of maternal effects influencing the outcome of this experiment[33], these findings suggest that *T. officinale* benefits from seed-borne endomicrobiomes that enhance its competitive advantage over Asteraceae species native to each continent (see "Methods"). They partially support the evolution of increased competitive ability hypothesis[36], and indicate that the endomicrobiome, and not a lack of specialised predators or enemies, could explain the enhanced performance of *T. officinale* in its invaded range. They also suggest that, if microbiomes had been exchanged between *T. officinale* and each Asteraceae species (see "Methods"), then those associated with E$^+$ seeds did not benefit the native plant species. In addition to the increased competitive ability hypothesis, a further mechanism, the novel weapons hypothesis[37,38], has been proposed to explain the role of microbes in improving plant invasiveness[7]. This hypothesis states that the competitive advantage of invasive plants derives from their ability to release allelopathic chemicals that inhibit the growth of native plants lacking protective mechanisms against these compounds. We accordingly measured phenol concentrations in the soil and shoots of *T. officinale* and its local native Asteraceae species when grown in interspecific competition or in monoculture. The experiment revealed that when subjected to competition, E$^+$ *T. officinale* plants increase the production of phenolics in surrounding soil and in shoots, with a more pronounced effect when grown in interspecific competition compared with in monoculture, and with this pattern being consistent across all Mediterranean

Table 1 | Micro-evolutionary rates of *Taraxacum officinale*

Continent	Experimental groups	Photosynthesis (A$_{max}$)	Flower head production (n)	Viable seeds (n)	Performance index
Oceania	E-	0.39 (±0.056) *	0.05 (±0.088) ^{ns}	0.42 (±0.015) *	0.34 (±0.027)*
	E+	0.54 (±0.009) *	0.32 (±0.125) *	0.42 (±0.024) *	0.46 (±0.019)*
North America	E-	−0.04 (±0.112) ^{ns}	−0.24 (±0.028) *	0.35 (±0.093) *	0.06 (±0.094) ^{ns}
	E+	0.46 (±0.036) *	0.31 (±0.029) *	0.55 (±0.016) *	0.5 (±0.021) *
South America	E-	0.11 (±0.083) ^{ns}	−0.3 (±0.042) *	−0.39 (±0.018) *	−0.34 (±0.016) *
	E+	0.5 (±0.007) *	0.08 (±0.134) ^{ns}	0.55 (±0.031) *	0.51 (±0.046) *
Africa	E-	−0.5 (±0.039) *	−0.29 (±0.059) *	−0.35 (±0.033) *	−0.39 (±0.047) *
	E+	0.09 (±0.063) *	0.07 (±0.127) ^{ns}	0.23 (±0.058) *	0.14 (±0.063) ^{ns}
Europe	E-	−0.16 (±0.115) ^{ns}	−0.39 (±0.112) *	−0.43 (±0.119) *	−0.42 (±0.12) *
	E+	0.48 (±0.005) *	0.12 (±0.193) ^{ns}	0.38 (±0.032) *	0.4 (±0.043) *
Global	E-	−0.04 (±0.311) ^{ns}	−0.23 (±0.167) *	−0.08 (±0.399) ^{ns}	−0.17 (±0.287) *
	E+	0.41 (±0.173) *	0.18 (±0.16) *	0.43 (±0.128) *	0.38 (±0.147) *

Rates, expressed in Haldanes, were measured after five generations of artificial selection for best individual performance (see "Methods" for details) in populations of plants grown with intact (E$^+$) or reduced (E$^-$) seed-borne endomicrobiomes ($n = 3$ populations per continent). The sign of each mean rate indicates the direction of change. The standard deviation of each mean value is shown in parentheses. Average rates that were significantly different from zero are marked with an asterisk (* one-sample, two-tailed *t*-tests, $\alpha = 0.05$; Supplementary Data 12). For a given continent and trait, pairs of rates marked with an asterisk differed significantly between experimental groups (E$^-$ vs. E$^+$; two-sample, two sided *t*-test, $\alpha < 0.05$; for details see Supplementary Fig. 4). All *p* values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$). Abbreviations: A$_{max}$, maximum photosynthetic rate; ns, not significant.

ecosystems (Figs. 3–4). In contrast, no changes to phenolic concentrations in soils and shoot tissues were observed between F$_1$ and F$_5$ native Asteraceae plants grown in monoculture (Figs. 3–4).

While the role of host-microbe interactions in shaping the macroevolutionary trajectories of plants is well-recognised[39], our findings suggest that the endomicrobiome significantly influences plant competitiveness over timescales of just a few generations. They build upon previous research demonstrating that microbes can enhance plant fitness by inducing physiological changes such as increased stress tolerance and the production of defence compounds[40–42]. Mechanisms involved include the secretion into the rhizosphere of chemicals mimicking plant hormones, the modulation of plant gene expression to trigger physiological changes enhancing plant stress tolerance, and the synthesis of plant growth-promoting hormones[40]. Collectively, our competition experiments demonstrate that microbial symbionts may significantly enhance the invasive potential of *T. officinale*, primarily through the increased synthesis of phenolic compounds, which have well-established roles in plant defence against herbivory and competitive interactions with other plants[43]. These findings align with recent research showing that inoculation with fungal endophytes from extreme environments augments plant fitness and stress tolerance by promoting the production of allelopathic phenolic compounds in the rhizosphere[44].

Molecular mechanisms drive endomicrobiome-mediated trait development

We compared the relative expression of genes in E$^-$ and E$^+$ *T. officinale* plants in order to explore the role of putative molecular mechanisms in the observed inter-generational changes. Independent *t*-tests showed that, from a global perspective, intact endomicrobiomes typically increased the expression by *T. officinale* of *CHS*, *COR47*, *HSP* and *LEC* genes across generations (Fig. 5). These genes are associated with the synthesis of secondary metabolites such as phenols, tolerance to drought and heat and increased seed production, respectively, supporting the findings described above. In addition, increased expression of CHROMOMETHYLASE3 (*CMT3*), a gene associated with DNA methylation maintenance, was observed in E$^+$ plants (Supplementary Fig. 6), indicating that an increase in DNA methylation activity in E$^+$ plants on specific (although yet to be discovered) genes may enhance their expression levels[45]. Similarly, in the medicinal plant species *Salvia miltiorrizhiza*, increased methylation levels of genes associated with the biosynthesis of phenolic acids and tanshinones is concomitant with both increased gene expression and contents of these compounds[45]. Furthermore, in the plant species *Artemisia annua*, the endophytic symbiont *Pseudonocardia* sp. upregulates genes associated with the synthesis of artemisinin, a potent drug for malaria treatment[46,47], which inhibits the germination and vegetative growth of several other plant species[48]. The only gene that was under-expressed by E$^+$ *T. officinale* plants was *IAA12* (Fig. 5), which is associated with auxin repression, perhaps accounting for the increased flower head production of plants colonised by the endomicrobiome (Supplementary Fig. 2). As for the phenotypic results, gene expression profiles varied to some extent between populations, with no inter-generational effects on the expression of the *CHS* and *HSP* genes in the Spanish population, the *COR47* gene in Australian and American populations and the *LEC* gene in the South African population (Fig. 5). These observations suggest that endomicrobiomes from different geographical locations may differ in their abilities to influence plant gene transcription across generations. However, collectively, our findings suggest that the endomicrobiome affects gene expression in *T. officinale* (including RNA-dependent DNA methylation mechanisms), likely underpinning the invasiveness of the weed in Mediterranean ecosystems.

Summary and outlook

Plant invasions cause huge financial losses each year worldwide[3], notably in densely-populated Mediterranean ecosystems[4]. Advancing our knowledge of plant invasiveness in these ecosystems is hence pivotal to constraining these losses and designing effective weed management programmes. Here, we have shown that the vertically transmitted seed-borne endomicrobiome is a critical factor in the development of invasiveness traits in *T. officinale*, one of the most aggressive invasive weeds worldwide[30]. By suppressing the seed-borne endomicrobiomes of *T. officinale* plants and maintaining this condition over several generations, we were able to slow the trait development of the plant species, with negative effects on fitness-related traits such as photosynthetic rate and fecundity. These findings hold promise for the management of this, and other, invasive plant species in Mediterranean ecosystems through microbiome manipulation[49] rather than through the application of glyphosate, a herbicide with potential adverse effects on human health and the environment[50].

Despite all *T. officinale* plants being grown in the same sterile soil and sand mixture (see "Methods"), variation was observed here in the

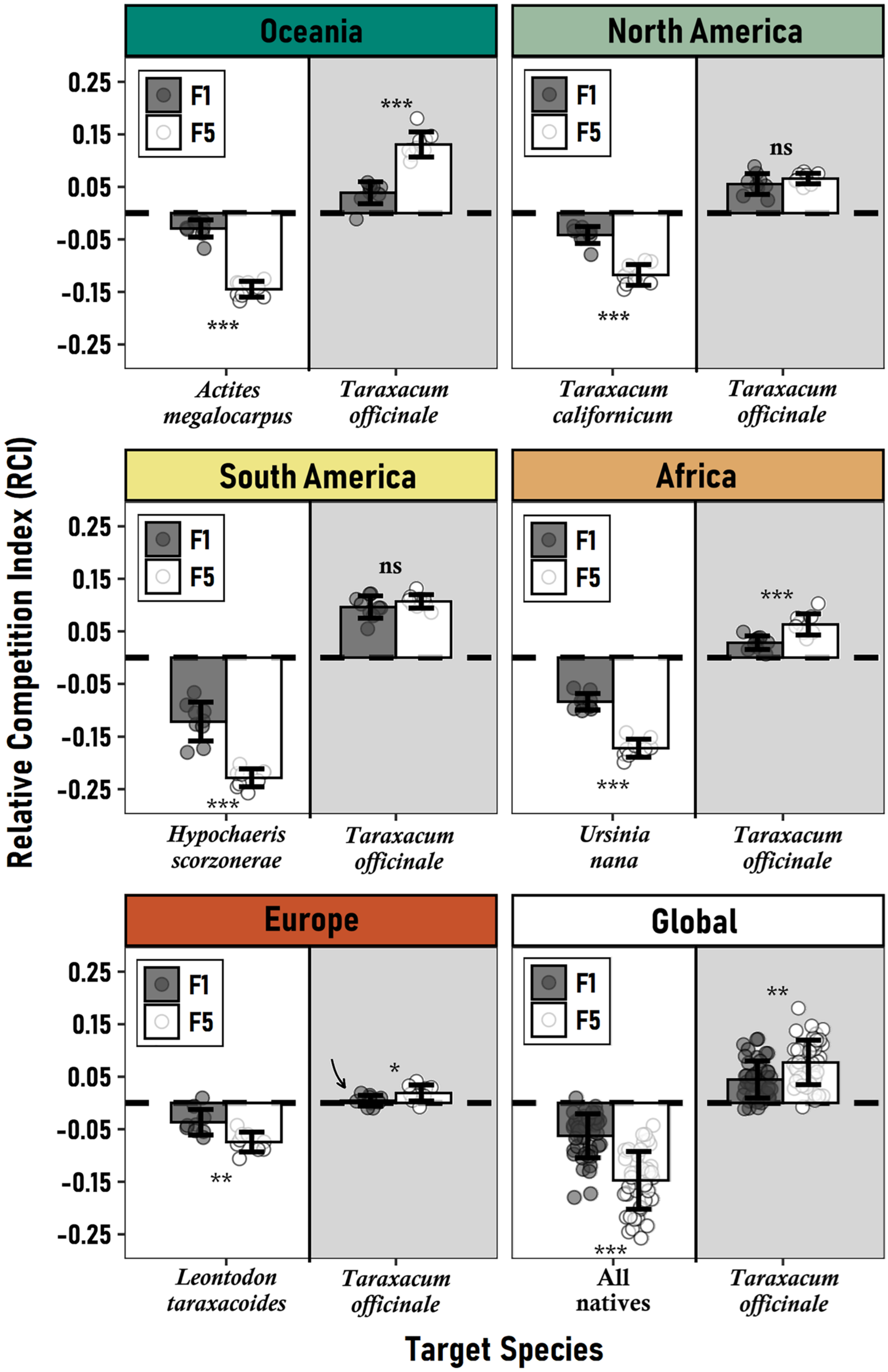

Fig. 2 | Inter-generational (F_1 vs. F_5) changes in the relative competition index (RCI) of native Asteraceae plant species from five continents and the local population of E$^+$ *Taraxacum officinale*. The RCI quantifies the biomass change of plants under competition relative to monoculture (negative = reduced biomass; positive = increased biomass). For each region, the means are the averages of nine biological replicates per generation, each corresponding to an independent plant pair, with bars showing standard deviations. Accordingly, there were 45 replicates per generation in the global analysis. Bars not differing from zero (one-sample, two-sided *t*-tests; Supplementary Data 6) are indicated with a black arrow. Significant inter-generational differences (two-sample, two-sided *t*-tests; $\alpha = 0.05$; Supplementary Data 7) are denoted with asterisks (*; $p < 0.05$, **; $p < 0.01$; ***; $p < 0.001$). Abbreviation: ns, not significant. All p values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$).

phenotypic and genotypic responses of different populations of the species. Whilst all populations of E$^+$ plants showed positive trait development, inter-generational declines in traits were observed in populations of E$^-$ plants from South America, Europe and Africa, with null and positive trends being observed in E$^-$ plants from North America, and Oceania, respectively. These findings, together with the variation observed between populations in gene expression, suggest that different populations of *T. officinale* may be colonised by

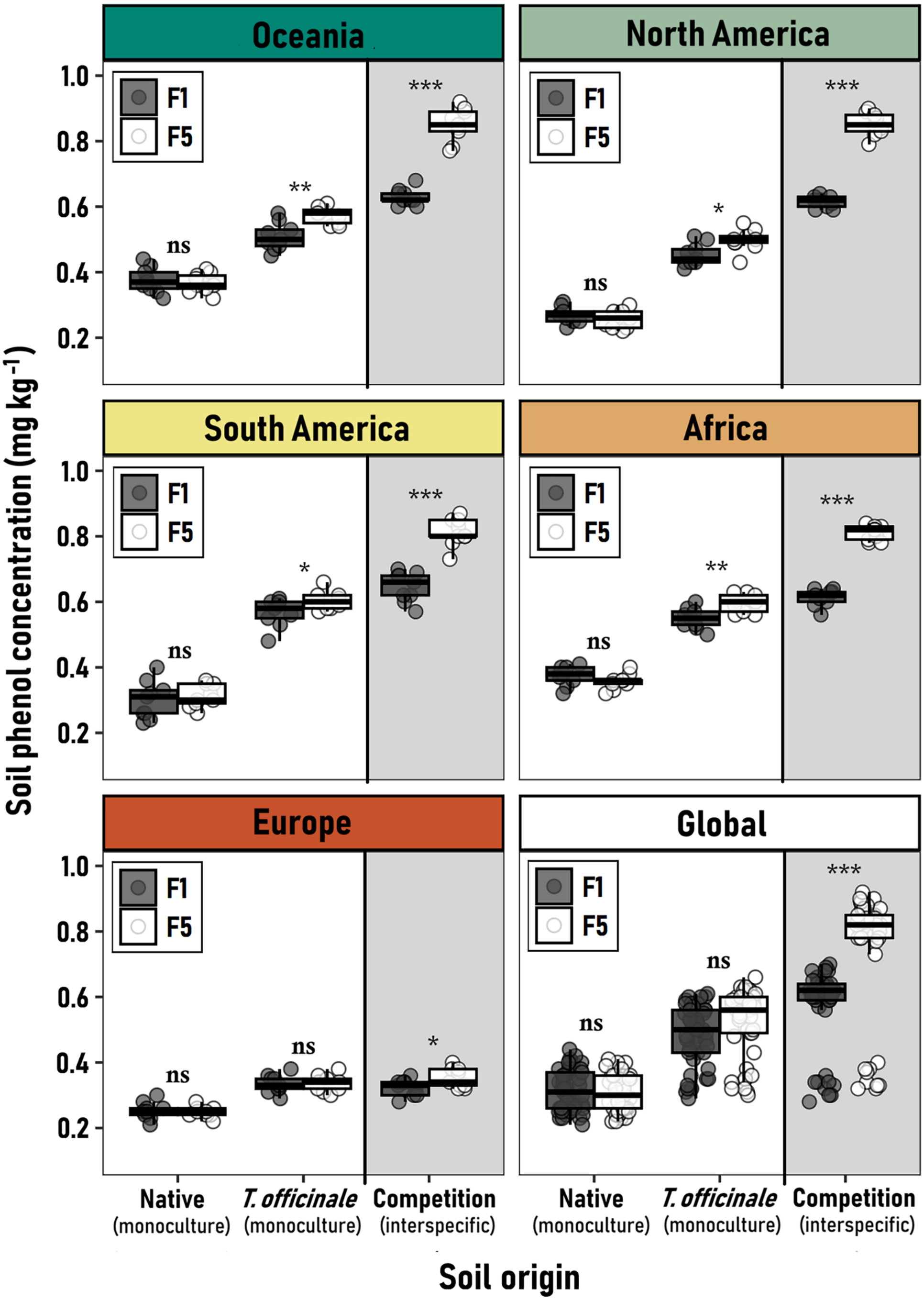

Fig. 3 | Independent comparisons of phenol concentrations in soils of F$_1$ and F$_5$ generations of Asteraceae plant species native to each continent and the corresponding local population of E$^+$ *Taraxacum officinale*. Plants were grown either in monoculture (no shading) or in interspecific competition (grey shading). Boxplots show the interquartile range, and dots represent individual biological replicates (one plant pair). For each region and generation, phenolic measurements were based on nine independent soil samples from an equal number of plant pairs per treatment (Native, *T. officinale*, or Competition). Accordingly, the global dataset consisted of 45 plants per pair type and generation. Significant inter-generational differences (two-sample, two-sided *t*-tests; $\alpha = 0.05$; Supplementary Data 8) are denoted with asterisks (*; $p < 0.05$, **; $p < 0.01$; ***; $p < 0.001$). Abbreviation: ns, not significant. All p values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$).

endomicrobiomes of different taxonomic composition, leading to variation in the development of plant invasiveness traits. Interactions with native soil microbiomes may introduce further variation into the response of *T. officinale* to the seed-borne endomicrobiome[51]. However, the successful establishment of the weed species in all five Mediterranean-type ecosystems studied here, as well as its global success[30], suggests that it benefits from positive effects of the seed-borne endomicrobiome across diverse edaphic conditions.

Genetic mechanisms may also be responsible for the observed variation between *T. officinale* populations in their responses to the endomicrobiome. Since the seeds of *T. officinale* can be of sexual or asexual (apomictic) origin in diploid or polyploid forms[52], choosing those from the fittest plants in each E$^+$ line in the experiments reported here could have selected for either plant genotypes or phenotypes and their associated microbiomes. In the former scenario, we would expect an increase in plant fitness resulting from the co-selection of plant

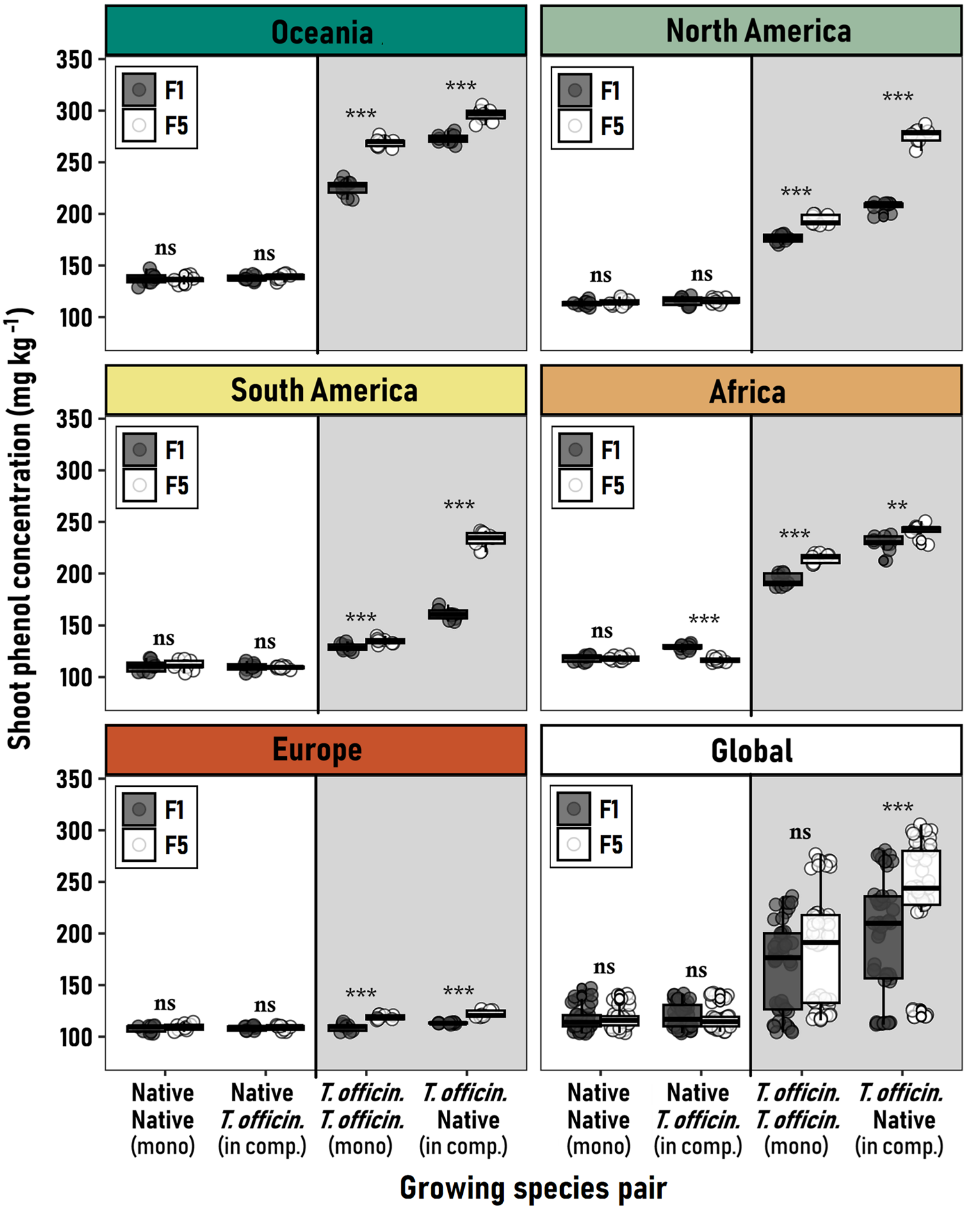

Fig. 4 | Phenol concentrations in shoots of F_1 and F_5 generations of Asteraceae plants native to each continent and the corresponding local population of E^+ *Taraxacum officinale*. The plants were grown either in monoculture (native vs. native or *T. officinale* vs. *T. officinale*) or under interspecific competition (native vs. *T. officinale*, or *T. officinale* vs. native). For each continent, the unshaded panels show the responses of the native Asteraceae species in competition, while the grey-shaded panels show the responses of *T. officinale*. Boxplots represent the interquartile range, and dots represent individual biological replicates ($n = 9$). Significant inter-generational differences (two-sample, two-sided *t*-tests; $\alpha = 0.05$; Supplementary Data 9) are denoted with asterisks (*; $p < 0.05$, **; $p < 0.01$; ***; $p < 0.001$). Abbreviation: ns, not significant). All *p* values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$).

genotypes and their associated microbiomes. In the latter, the majority of phenotypic advancements in E^+ plant lines could be attributed to alterations in the endomicrobiome. The between-continent variability could thus have resulted from interactions with different selected genotypes, potentially influenced by distinct reproductive strategies among the plants. This variability likely led to the differential expression of genes associated with stress tolerance (*COR47* and *HSP*) and growth and seed production (*IAA12* and *LEC*) in E^+ lines compared with E^- lines in the F_1 and F_5 generations. Distinct reproductive strategies among the plants could also explain why some E^+ lines responded and why some E^- lines did not respond to the selective pressure favouring the fittest individuals.

In conclusion, our study shows the enhancement of fitness-related plant traits in the presence of the endomicrobiome across five generations of *T. officinale* from Mediterranean ecosystems on five continents, indicating that the endomicrobiome underpins the invasiveness of this aggressive weed. Contemporary adaptations can amplify the impact of an invading species by increasing its abundance, environmental tolerance and dominance within a community, potentially altering its ecosystem functions[9,53–55]. In an increasingly anthropized world in which native plants are constantly confronted with alien species, studies of invasive plants and their native competitors, as well as the endomicrobiome-mediated interplay between invasive and native species, represent pivotal areas for future research. Our findings are critical for unravelling the role of endomicrobiomes in the development of invasiveness traits in weed species, as well as for ensuring the conservation of hyper-diverse Mediterranean ecosystems in the face of global change.

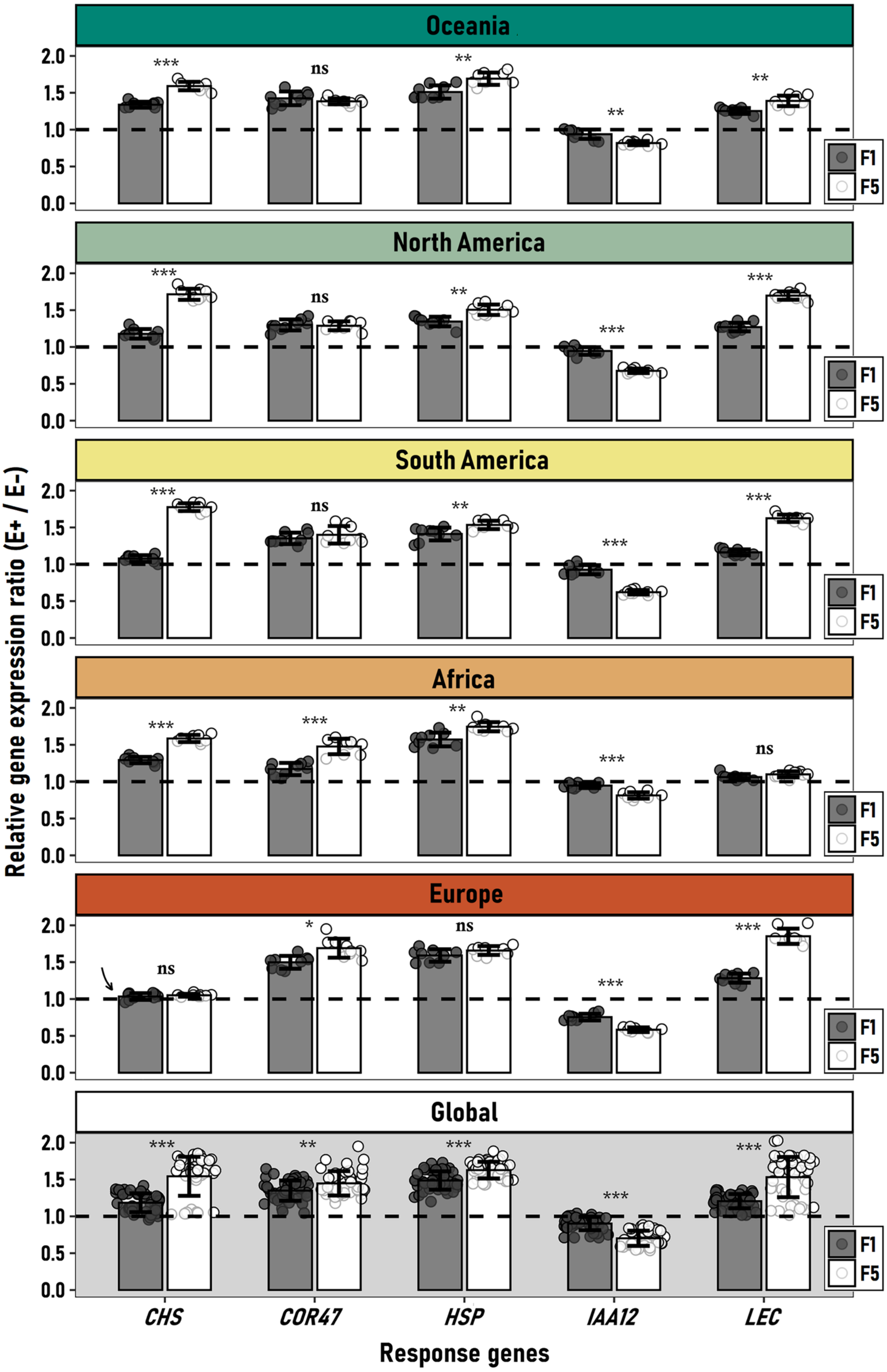

Fig. 5 | Expression of five stress-response genes (*CHS, COR47, HSP, IAA12* and *LEC*) in foliar tissues of *Taraxacum officinale* plants from the F_1 and F_5 generations across five continents. Bars show the mean ratio (+ - SD) between the relative expression levels of plants grown with intact (E^+) or reduced (E^-) seed-borne endomicrobiomes in each generation. Ratios > 1 (dashed line) indicate over-expression in E^+ relative to E^- plants; ratios < 1 indicate under-expression. For each continent and generation, gene-expression ratios were derived from nine biological replicates per treatment (E^+ and E^-), each representing an independent plant. Means not differing statistically from 1 (*i.e.*, no detectable endomicrobiome effect) are indicated with arrows (one-sample, two-sided *t*-test; Supplementary Data 10). Significant between-generation comparisons (F_1 vs. F_5; *t*-tests, Supplementary Data 11) are denoted with asterisks (*; $p < 0.05$, **; $p < 0.01$; ***; $p < 0.001$). Abbreviation: ns, not significant. All *p* values were corrected for multiple comparisons using Benjamini–Hochberg FDR ($q = 0.05$).

Methods

Seed collection and production of plant material

Seeds of *Taraxacum officinale* (Asteraceae) were collected from Mediterranean ecosystems on five continents (Fig. 1). Three populations, geographically distanced by ca. 40–60 km, were selected on each continent (North America: 37°17´N–121°44 W´, 36°55´N–121°31´W and 36°37´N–121°48´W; South America: 34°08´S–70°44´W, 34°37´S–70°52´W and 34°57´N–71°12´W; Europe: 37°44´N–00°54´E, 38°06´N–00°40´E and 37°32´N–01°23´E; Africa: 33°45´S–18°30´E, 34°04´S–18°50´E and 34°20´S–19°12´E; Oceania: 34°43´S–138°39´E, 35°07´S–138°02´E and 35°20´S–139°02´E). In each population, ~five seeds per individual were collected from ca. 50 widely spaced maternal plants in ruderal areas. All seeds were stored in paper bags under dry conditions until their use in the manipulative experiments. Seeds from each of the 15 populations were pooled and germinated under glasshouse conditions (air temperature 29 ± 4 °C and solar radiation 1723 ± 365 µmol m^{-2} s^{-1} PAR during daylight hours). The F_0 generation of *T. officinale* was germinated from this seed pool and was grown in a glasshouse at the University of Talca, Chile. F_0 plants were placed in 750-ml plastic pots filled with autoclaved field soil and sand (2:1), and irrigated every three days with 75 ml of tap water for five months until they produced seeds. These seeds were used to obtain F_1 experimental plants. Plants from the F_1 generation were germinated at 30 ± 2 °C on wet filter paper in plastic boxes, and the seedlings were planted in 1 L capacity plastic pots filled with autoclaved potting soil (field soil and sand, 2:1 v/v).

One week after the appearance of the first true leaf, half of the plants were irrigated with 50 µg mL^{-1} of rifampicin, a potent and broad-spectrum systemic antibiotic, and the commercial broad-spectrum systemic fungicide Benlate, to obtain individuals with a reduced complement of local seed-borne endomicrobiomes (hereafter referred to as E^- plants). The remainder were irrigated with sterile tapwater in order to retain their local endomicrobiomes, *i.e.*, the vertically transmitted seed-borne endomicrobiome acquired from each of the five continents (hereafter E^+ plants). By propagating from the seeds of E^- or E^+ plants over five generations, we were able to maintain plants with reduced or intact endomicrobiomes, respectively (Supplementary Fig. 7). In agreement with previous studies[42,56], treatment with rifampicin or Benlate did not result in any visible symptoms or detectable differences in the growth or development of E^- plants. The presence of the endomicrobiome was confirmed by observing aniline blue-stained fungal hyphae in leaf, stem and root cross-sections in ca. 2% of plants (Supplementary Fig. 7). In addition, surface-sterilised leaf, stem and root fragments from the same *T. officinale* individuals were pressed into potato dextrose agar (PDA, Difco, USA) in 90 mm diameter Petri dishes and incubated for 15 days at 27 ± 2 °C. These analyses confirmed that E^- plants were apparently free of seed-borne endomicrobiomes. Only plants in which fungal hyphae were observed, or from which fungi or bacteria were grown, were considered to be colonised by endomicrobiomes and were used in the experiments described below.

Finally, two seeds from each individual plant from each population were randomly selected to assess for the presence of the seed endomicrobiome. First, one seed was cut in half transversely with a razor blade and was stained with aniline blue prior to observation at 400× magnification (Motic BA310) to record stained fungal hyphae. Second, the remaining seed from each plant was pressed into potato dextrose agar (PDA, Difco) in 90 mm diameter Petri dishes prior to being incubated at 18 °C for 2 weeks. Maternal plants were considered to be endomicrobiome-reduced when no fungal hyphae were visually detected in seeds and no hyphal or bacterial growth was observed in the culture medium. Conversely, plants were considered to have intact endomicrobiomes when stained hyphae were visible in the seeds and when either fungal hyphae or bacteria grew from the seeds onto the medium. Although we did not confirm the absence of bacterial cells from E^- seeds using microscopy, it is unlikely that unculturable bacteria survived in rifampicin-treated seeds, since this antibiotic has a high affinity for bacterial DNA-dependent RNA polymerase[57]. Consequently, irrespective of culturability, it inhibits protein synthesis, halting the growth of, and ultimately killing, bacterial cells.

Culling experiment

To measure the performance of E^- and E^+ *T. officinale* plants, we calculated an integrated index of seed output, flower head production and photosynthetic rate in a five generation laboratory culling experiment[58]. Five E^- and five E^+ plants from each of the 15 populations were grown for five generations at 33 ± 3 °C in the same sterile soil and sand mixture as described above. The use of a single sterilised substrate allowed the effect of the vertically transmitted seed-borne endomicrobiome on *T. officinale* to be isolated, eliminating variability between populations caused by the influence of local soil microbiota on seed-borne endomicrobiomes[51]. The mixture had a water potential of ca. −36 ± 8 kPa, mimicking frequent summer conditions in Mediterranean ecosystems. Capitula from E^- and E^+ individuals from each of the 15 populations were enclosed in nylon mesh bags and were allowed to self-pollinate. Although *T. officinale* is capable of cross-pollination in sexually reproducing diploid individuals, apomixis is common in polyploids, leading to offspring genetically identical to the mother plants[59]. Therefore, any potential variation in the mating and or reproductive traits reflects the characteristics of the experimental populations. From each population in each generation, the three individuals with the highest seed output (or, as tiebreakers, flower head production or photosynthetic rate) were selected to produce the next generation. Seeds from these selected individuals were used to generate five new plants for the next generation, always maintaining 15 individuals per condition (E^- and E^+) and generation in each of the three populations from each continent.

Cumulative flower head production (i.e., the number of floral heads) was recorded every three days on each *T. officinale* individual. Each flower head was labelled in order to avoid duplicate counts. Once a flower head was closed, indicating the start of seed development, it was carefully enclosed in a nylon mesh bag to protect it against seed dispersal. These bagged flower heads were then collected, and the viable seed output was determined by calculating the proportion of filled seeds to the total number of florets per flower head, accounting for both filled, aborted and predated seeds. Finally, maximum photosynthetic rate (A_{max}) was recorded on healthy leaves with an Infra-Red Gas Analyzer (CIRAS-2, PP-Systems Haverhill, Amesbury, MA, USA). During the measurements, the leaf chamber was set at a CO_2 concentration of 400 ppm, temperature of 30 °C and irradiance of 1500 µmol $m^{-2}s^{-1}$ PAR.

Effects of the endomicrobiome on plant competitive ability

The influence of the endomicrobiome on the ability of *T. officinale* to compete with Asteraceae species native to each continent was tested by calculating the relative competition intensity index (RCI;[35]), using final biomass as the response variable. For each of the five Mediterranean ecosystems, 36 pots (1-L capacity) containing the same mixture of sterile soil and sand as described above were prepared, for a total of 180 pots. Nine pots were each planted with two *T. officinale* individuals grown from E^+ seeds, and another nine pots were each planted with two individuals of native Asteraceae species occupying similar ecological niches (*Leontodon taraxacoides* from Europe, *Taraxacum californicum* from North America, *Hypochaeris scorzonerae* from South America, *Ursinia nana* from Africa and *Actites megalocarpus* from Oceania). All native individuals used in the manipulative experiments were obtained from seeds germinated under the same conditions as those described above. The remaining 18 pots were each planted with two individuals of *T. officinale* (nine pots) and two individuals of the native Asteraceae species (nine pots). This assay was conducted with 360 *T. officinale* individuals from F_1 and F_5 (nine individuals × four treatments × two generations × five ecosystems = 360 plants). The 72 pots containing plants from each continent were divided equally between four automated growth chambers set to the same environmental conditions as those described above. The pots were randomised and rotated among chambers to avoid chamber effects. Note that microbiomes may have been exchanged between *T. officinale* and each of the native Asteraceae species (and vice versa) in these experiments. After 75–90 days, the plants were harvested and the relative competitive impact of *T. officinale* ($_{invasive}$) on its native counterpart ($_{native}$) was calculated as RCI *native* = ([biomass $_{native:native}$ − biomass $_{native:invasive}$]/biomass $_{native:native}$), and the resistance of the native counterpart to invasion by *T. officinale* was calculated as RCI *invasive* = ([biomass $_{invasive:invasive}$ − biomass $_{native:invasive}$]/biomass $_{invasive:invasive}$), where *invasive* and *native* represent the biomasses of *T. officinale* and its native counterpart, respectively[42].

To assess the potential effect of plant-to-plant competition mediated through the exudation of allelochemicals, we measured the total content of phenolic compounds in fresh biomass and in the soil in which the plant had been grown using the Folin-Ciocalteu assay (with gallic acid as the standard[60];). Briefly, the phenols in each sample were extracted with methanol/H_2O (4:1, v/v) and homogenised by sonication. The extracts were then stirred for 1.5 h at room temperature and centrifuged at 4,200 *g* before the supernatant was recovered. Supernatant (100 µl) was oxidised with 200 µl 10% (v/v) Folin-Ciocalteu reagent, neutralised with 800 µl sodium carbonate, and incubated for 2 h at room temperature. The absorbance of the resulting solution was measured at 765 nm, using an Epoch microplate spectrophotometer (BioTek Instruments, Winooski, VT, USA). Finally, phenol concentration was calculated using a standard curve of gallic acid[60].

Effects of the endomicrobiome on *T. officinale* gene expression levels

To assess whether the seed-borne endomicrobiome exerts a positive effect on the ecophysiological performance of *T. officinale* through genetic control, we recorded the differential expression of five genes linked to traits related to invasiveness. The gene expression included in our assessment corresponded to those associated with floral development [*IAA12*], drought stress tolerance [*COR47*], synthesis of phenolic compounds [*CHS* – chalcone isomerase], heat tolerance [*HSP*] seed production [*LEC*], and DNA Methylation [*CMT3*]. Gene expression was assessed in E^- and E^+ *T. officinale* plants in generations F_1 and F_5.

To select these genes, a reference transcriptome assembly of *T. officinale* was obtained from publicly available raw Illumina reads (NCBI accession PRJNA316842; SRA libraries SRR5342876, SRR5342878, SRR5342880, SRR5342882, SRR5342884, SRR5342886). These reads were assembled de novo locally using Trinity version 2.15.1 into 102,882 contigs. The transcriptional abundance was then estimated by aligning raw reads to this transcriptome using BOWTIE, and by counting mapped reads with RSEM[61]. This transcriptome was also annotated with Mercator4 V5.0 and the Diamond BlastX alignment tool using the NCBI NR protein database as a reference. From this annotated set, five protein-encoding contigs, involved in different plant molecular mechanisms and showing in silico transcriptional evidence (number of mapped reads > 0), were selected for downstream expression analysis using qPCR. Selected contigs encode for: Chalcone-Flavanone Isomerase type III (*CHS*, “Chalcone”), Dehydrin-COR47 (*COR47*), Heat Shock Protein 70 (*HSP70*), Indole-3-acetic acid inducible 12 (*IAA12*), LEAFY COTYLEDON 1-LIKE (*LEC1-LIKE*) and CHROMOMETHYLASE3 (*CMT3*). Using the contigs’ sequences as templates, specific qPCR primers were designed using NCBI Primer Blast. The primers used are listed in Supplementary Data 14.

Statistical analyses

Linear mixed models (LMMs) were employed to examine inter-generational (temporal) variations in A_{max}, flower head and viable seed production, and the integrated performance index. These analyses were done separately for E^- and E^+ *T. officinale* plants. The continent of origin was integrated into the error structure of the LMMs as a random factor, and its significance was assessed using marginal and conditional R^2 coefficients. In the context of mixed models, these coefficients quantify the variance explained solely by the fixed factors or the overall model (i.e., fixed and random factors), respectively[62]. Hence, within each LMM, the difference between the coefficients equals the role of the random factor in the model’s performance, i.e., to the local inter-population variability present in each region. In addition, to explore the overall trend, a global analysis was also conducted including data from all 15 populations (three from each continent) in the same model.

For each trait, as well as for the integrated performance index, deviations of fitted slopes from zero were tested with LMMs. Moreover, the impacts of symbiotic status on these trends were determined by the statistical significance of the endomicrobiome × generation interaction in LMMs, indicating differences in regression slopes between plants with different endomicrobiome statuses. In addition, we calculated the micro-evolutionary rate for each trait and the integrated performance index in Haldanes[31]. The Haldane unit scales the change in a trait across generations (i.e., the model slope) by the magnitude of trait variation. Specifically, we computed Haldanes as the difference between the mean trait values in the F_1 and F_5 generations standardised by five times the pooled standard deviation of the population[63].

For the competition experiments, we examined differences in the relative competition index (RCI) for soil and shoot phenol concentrations for E^+ F_1 and F_5 *T. officinale* plants, and their corresponding local native Asteraceae species, after being grown together (native – *T. officinale*) or in monoculture (native – native or *T. officinale* – *T. officinale*). Since these variables were derived from competition experiments, the results represent both the effect of invasive *T. officinale* on the performance of the local native Asteraceae species (the “native” experimental group) and the effect on *T. officinale* of competing against the local native species (the “invasive” experimental group). One-sample *t*-tests were used to determine whether RCI averaged for each experimental group was statistically different from zero (where 0 = no effect of competition) and independent two-sample *t*-tests were used to compare the RCI averaged between generations (F_1 *vs.* F_5) within each experimental origin, with significant differences indicating changes to the invasion potential of *T. officinale*.

Finally, we also used one and two-sample, two-tailed *t*-tests, to evaluate whether the endomicrobiome influences the relative gene expression of the five stress response genes evaluated in *T. officinale* across generations. We first obtained a relative ratio between the expression levels of genes in E^- and E^+ *T. officinale* plants averaged among individuals from the F_1 and F_5 generations. We then estimated the significance of the endomicrobiome in determining the relative expression levels of each gene in each generation by determining how different these ratio values were from 1 using one-sample, two-tailed *t*-test (where 1 = no effect of the endomicrobiome). To determine the occurrence of a given inter-generational change, we searched for significant differences in the expression ratios between F_1 and F_5 plants using two-sample, two-tailed *t*-tests, with values > 1 indicating positive effects of the endomicrobiome on gene expression and those <1 indicating significant genetic repression. Consequently, inter-generational changes (F_1 vs. F_5) in relative gene expression levels were obtained for *T. officinale* plants from each Mediterranean ecosystem. To control for multiple comparisons across all pairwise *t*-tests (both one-sample and two-sample), we applied Benjamini–Hochberg false discovery rate correction[64] at $q = 0.05$ within appropriate test families, ensuring conservative and statistically robust data interpretation. All data recorded were incorporated into the analyses. All datasets were tested for normality using the Shapiro-Wilks test, analyses were performed in the *R* language and statistical environment v.4.2.2[65] using the “nlme” package (v. 3.1-163) for fitting LMMs[66], the “emmeans” package (v. 1.11.1) for slopes estimation and paired comparisons[67] and the “ggplot2” package (v. 4.0.0) for data visualisation[68].

All figures and graphical elements were generated by the authors. The world map shown in Fig. 1 was created in R using openly available cartographic data from Natural Earth[69], rendered and customised for visualisation purposes. Additional graphical elements (including the dandelion illustration shown in Fig. 1 and the leaf, flower, and seed images shown in Supplementary Fig. 4) were created using Canva (Canva Pty Ltd.) under an active user license, with individual graphical elements credited to Anna Kuzmina, Hus, DAPA Images, and Graphixmania, respectively.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data tables used for the generation of the plots shown in Figs. 1–5, have been deposited in a publicly available Figshare repository (https://doi.org/10.6084/m9.figshare.28127108). The transcriptome assembly generated in this study, as well as the annotated sequences used as templates for qPCR primer design are available at https://doi.org/10.6084/m9.figshare.30707714. Supplementary Data 1-14 are also provided with this paper, in the Supplementary Information File.

References

1. Myers, N. et al. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
2. Cardinale, B. et al. Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
3. Diagne, C. et al. High and rising economic costs of biological invasions worldwide. *Nature* **592**, 571–576 (2021).
4. Kourantidou, M. et al. Economic costs of invasive alien species in the Mediterranean basin. *Neobiota* **67**, 427–458. 17 (2021).
5. Kumar-Rai, P. & Singh, J. S. Invasive alien plant species: their impact on environment, ecosystem services and human health. *Ecol. Indic.* **111**, 106020 (2020).
6. Moreira, F. et al. Wildfire management in Mediterranean-type regions: paradigm change needed. *Environ. Res. Lett.* **15**, 011001 (2020).
7. Dawson, W. & Schrama, M. Identifying the role of soil microbes in plant invasions. *J. Ecol.* **104**, 1211–1218 (2016).
8. Whitney, K. D. & Gabler, C. A. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity Distrib.* **14**, 569–580 (2008).
9. Pyšek, P. & Richardson, D. M. Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.* **35**, 25–55 (2010).
10. Colautti, R. I. & Lau, J. A. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* **24**, 1999–2017 (2015).
11. Molina-Montenegro, M. A. et al. Is the success of plant invasions the result of rapid adaptive evolution in seed traits? Evidence from a latitudinal rainfall gradient. *Front. Plant Sci.* **9**, 208 (2018).
12. Gioria, M. et al. Why are invasive plants successful?. *Annu. Rev. Plant Biol.* **74**, 635–670 (2023).
13. Robeck, P. et al. Invading plants remain undetected in a lag phase while they explore suitable climates. *Nat. Ecol. Evol.* **8**, 477–488 (2024).
14. Atwater, D. Z. et al. Climate niche shifts are common in introduced plants. *Nat. Ecol. Evol.* **2**, 34–43 (2018).
15. Molina-Montenegro, M. A. et al. Ecophysiological plasticity and local differentiation help explain the invasion success of *Taraxacum officinale* (dandelion) in South America. *Ecography* **36**, 718–730 (2013).
16. Liu, W. et al. Contrasting plant adaptation strategies to latitude in the native and invasive range of *Spartina alterniflora*. *N. Phytol.* **226**, 623–634 (2020).
17. Bossdorf, O. et al. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* **144**, 1–11 (2005).
18. Vandenkoornhuyse, P. et al. The importance of the microbiome of the plant holobiont. *N. Phytol.* **206**, 1196–1206 (2015).
19. Traveset A. & Richardson D. M. *Plant Invasions: The Role Of Biotic Interactions - An Overview*. CABI, Oxfordshire, 455 (2020).
20. Shang, M. et al. Acquisition and evolution of enhanced mutualism—an underappreciated mechanism for invasive success?. *ISME J.* **16**, 2467–2478 (2022).
21. Newsham, K. K. A meta-analysis of plant responses to dark septate root endophytes. *N. Phytol.* **190**, 783–793 (2011).
22. Acuña-Rodríguez, I. S. et al. Functional roles of microbial symbionts in plant cold tolerance. *Ecol. Lett.* **23**, 1034–1048 (2020).
23. Zhang, Z. et al. Soil-microorganism-mediated invasional meltdown in plants. *Nat. Ecol. Evol.* **4**, 1612–1621 (2020).
24. Reinhart, K. O. & Callaway, R. M. Soil biota and invasive plants. *N. Phytol.* **170**, 445–457 (2006).
25. Bard N. W., et al. Fungal endophytes can modulate plant invasion. *Biol. Rev. Camb. Philos. Soc.* **99**, 13085 (2024).
26. Cusaro, C. M. et al. Incidence of resistance to ALS and ACCase inhibitors in *Echinochloa* species and soil microbial composition in Northern Italy. *Sci. Rep.* **14**, 10544 (2024).
27. Hu, T. et al. Seed microbiome-mediated herbicide resistance evolution in weeds. *N. Phytol.* **242**, 333–343 (2024).
28. Zhang, F. et al. Microbiome-conferred herbicides resistance. *N. Phytol.* **242**, 327–330 (2024).
29. Morella, N. M. et al. Successive passaging of a plant-associated microbiome reveals robust habitat and host genotype-dependent selection. *Proc. Natl. Acad. Sci. USA* **117**, 1148–1159 (2020).
30. Global Invasive Species Database (2024). http://www.iucngisd.org/gisd/search.php (2024).
31. Gingerich, P. D. Quantification and comparison of evolutionary rates. *Am. J. Sci.* **293**, 453–478 (1993).
32. John, J. & Sarada, S. Role of phenolics in allelopathic interactions. *Allelopath. J.* **29**, 215–230 (2012).
33. Van Allen, N. et al. Maternal effects and the outcome of interspecific competition. *Ecol. Evol.* **11**, 7544–7556 (2021).
34. Jiang, G. et al. Exploring rhizo-microbiome transplants as a tool for protective plant-microbiome manipulation. *ISME Commun.* **2**, 10 (2022).
35. Grace, J. B. On the measurement of plant competition intensity. *Ecology* **76**, 305–308 (1995).
36. Blossey, B. & Notzold, R. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J. Ecol.* **83**, 887–889 (1995).
37. Callaway, R. M. & Aschehoug, E. T. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* **290**, 521–523 (2000).
38. Hierro, J. L. & Callaway, R. M. Allelopathy and exotic plant invasion. *Plant Soil* **256**, 25–39 (2003).
39. Hassani, M. A. et al. Interactions and coadaptation in plant metaorganisms. *Annu. Rev. Phytopathol.* **57**, 22.1–22.21 (2019).
40. Angulo, V. et al. Plant–microbe eco-evolutionary dynamics in a changing world. *New Phytol.* **234**, 1919–1928 (2022).
41. Petipas, R. H. et al. Microbe-mediated adaptation in plants. *Ecol. Lett.* **24**, 1302–1317 (2021).
42. Molina-Montenegro, M. A. et al. The "Trojan horse" strategy: Seed fungal endophyte symbiosis helps to explain the invasion success of the grass, *Poa annua*, in Maritime Antarctica. *Diversity Distrib.* **29**, 1432–1444 (2023).
43. Mithöfer, A. & Boland, M. Plant defense against herbivores: chemical aspects. *Annu. Rev. Plant Biol.* **63**, 431–450 (2012).
44. Ballesteros, G. I. et al. Extreme environments as sources of fungal endophytes mitigating climate change impacts on crops in

Mediterranean-type ecosystems. *Plants, People, Planet* **6**, 148–161 (2024).
45. He, X. et al. DNA methylation regulates biosynthesis of tanshinones and phenolic acids during growth of *Salvia miltiorrhiza*. *Plant Physiol.* **194**, 2086–2100 (2024).
46. Li, J. et al. An endophytic *Pseudonocardia* species induces the production of artemisinin in *Artemisia annua*. *PLoS ONE* **7**, e51410 (2012).
47. Brader, G. et al. Metabolic potential of endophytic bacteria. *Curr. Opin. Biotechnol.* **27**, 30–37 (2014).
48. Li, Q. et al. Allelopathic effects of artemisinin on ectomycorrhizal fungal isolates in vitro. *Pedobiologia* **57**, 271–276 (2014).
49. Busby, P. E. et al. Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.* **15**, e2001793 (2017).
50. Finger, R. et al. Glyphosate ban will have economic impacts on European agriculture but effects are heterogenous and uncertain. *Commun. Earth Environ.* **4**, 286 (2023).
51. Walsh, C. M. et al. Variable influences of soil and seed-associated bacterial communities on the assembly of seedling microbiomes. *ISME J.* **15**, 2748–2762 (2021).
52. Verduijn, M. H. et al. Distribution, phenology and demography of sympatric sexual and asexual dandelions (*Taraxacum officinale* s.l.): geographic parthenogenesis on a small scale. *Biol. J. Linn. Soc.* **82**, 205–218 (2003).
53. Gianoli, E. & Molina-Montenegro, M. A. Evolution of physiological performance in invasive plants under climate change. *Evolution* **75**, 3181–3190 (2021).
54. Mueller, U. G. et al. Artificial selection on microbiomes to breed microbiomes that confer salt tolerance to plants. *mSystems* **6**, e01125-21 (2021).
55. Strauss, S. Y. et al. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities?. *Ecol. Lett.* **9**, 357–374 (2006).
56. Hereme, R. et al. Fungal endophytes exert positive effects on *Colobanthus quitensis* under water stress but neutral under projected climate change scenario in Antarctica. *Front. Microbiol.* **11**, 264 (2020).
57. Campbell, E. A. et al. Structural mechanism for rifampicin inhibition of bacterial RNA polymerase. *Cell* **104**, 901–912 (2001).
58. Garland T. & Rose M. *R. Experimental Evolution. Concepts, Methods and Applications of Selection Experiments*. University of California Press, (2009).
59. Tas, I. C. & Van Dijk, P. J. Crosses between sexual and apomictic dandelions (*Taraxacum*). I. The inheritance of apomixis. *Heredity* **83**, 707–714 (1999).
60. Ainsworth, E. A. & Gillespie, K. M. Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. *Nat. Protoc.* **2**, 875–877 (2007).
61. Li, B. & Dewey, C. N. RSEM: accurate transcript quantification from RNA-Seq data with or without a reference genome. *BMC Bioinforma.* **12**, 323 (2011).
62. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evolution* **2**, 134–142 (2013).
63. Hendry, A. P. & Kinnison, M. T. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653 (1999).
64. Benjamini, Y. & Hochberg, Y. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B (Methodol).* **57**, 289–300 (1995).
65. R-Core Team *R: A Language And Environment For Statistical Computing. R Foundation for Statistical Computing* (2023).
66. Pinheiro J. & Bates D. *Mixed-Effects Models in S and S-PLUS*. Springer (2000).
67. Lenth R. et al. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.5. (2023).
68. Wickham, H. et al. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag (2016).
69. Natural Earth. Free vector and raster map data. https://www.naturalearthdata.com/ (2025).

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Author contributions

M.A.M-M., I.S.A-R., C.T-D., and C.A. developed the original idea presented in the manuscript. The experiments were designed, and glasshouse data were collected, by M.A.M-M., F.C-U., V.M.E., R.H., F.F-P., P.E.G., A.U., and A.V. Lab analyses were done by G.B., E.C-N., S.G-L., and R.H. Bioinformatic analyses were done by G.B. and R.H. Statistical analyses were done by I.S.A-R. and V.M.E. The first manuscript was written by M.A.M-M. and K.K.N with inputs from co-authors. V.M.E, MD-B., L.Y.G., P.E.G., R.O-H., S.G-L., D.M.R., L.R.P. and A.E.Z. contributed to the writing of subsequent drafts. All co-authors contributed to the final draft.

Competing interests

The authors declare no competing interests.

Additional information

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