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ARTICLE

Acquisition and evolution of enhanced mutualism—an underappreciated mechanism for invasive success?

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Soil biota can determine plant invasiveness, yet biogeographical comparisons of microbial community composition and function across ranges are rare. We compared interactions between *Conyza canadensis*, a global plant invader, and arbuscular mycorrhizal (AM) fungi in 17 plant populations in each native and non-native range spanning similar climate and soil fertility gradients. We then grew seedlings in the greenhouse inoculated with AM fungi from the native range. In the field, *Conyza* plants were larger, more fecund, and associated with a richer community of more closely related AM fungal taxa in the non-native range. Fungal taxa that were more abundant in the non-native range also correlated positively with plant biomass, whereas taxa that were more abundant in the native range appeared parasitic. These patterns persisted when populations from both ranges were grown together in a greenhouse; non-native populations cultured a richer and more diverse AM fungal community and selected AM fungi that appeared to be more mutualistic. Our results provide experimental support for evolution toward enhanced mutualism in non-native ranges. Such novel relationships and the rapid evolution of mutualisms may contribute to the disproportionate abundance and impact of some non-native plant species.

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INTRODUCTION

Plant invasions cause tremendous ecological and economic damage [1, 2], and dozens of hypotheses have been generated to explain the increased abundance and impact of some non-native plant species [3, 4]. Several hypotheses posit altered biotic interactions—particularly between plants and their associated soil biota—as key determinants of plant invasive success [5]. Invasive plants may escape from pathogens [6], produce defensive and antimicrobial chemicals unknown to the resident native plant and microbial communities [7, 8], benefit more from mutualists than competing native species [9], and form novel interactions with bacteria and fungi resulting in more rapid carbon and nutrient cycling [10, 11]. Many of these predictions assume range-mediated disruptions of coevolved relationships [12, 13], yet most studies on plant-soil biotic interactions have occurred within a single range and have compared non-native to native plants [14]. Further, range comparisons conducted to date have tended to focus on the escape from inhibitory biota [6, 15, 16], and we have limited information related to biogeographical shifts in other plant soil–biota interactions. Here we address the inverse of the enemy release hypothesis and ask if plant invasive success is related to finding novel and stronger soil mutualists in the non-native range, which is the basis for the enhanced mutualism hypothesis (EMH) [9].

As one of the most prevalent and important group of mutualists, arbuscular mycorrhizal (AM) fungi provide an excellent opportunity to explore the ecological and evolutionary processes underlying the EMH. These fungi colonize >70% of terrestrial plants [17], and in exchange for carbon from their plant hosts, they can provide increased access to certain nutrients, drought tolerance, and pathogen protection [18]. Due to their ubiquity and location in the root-soil interface, AM fungi have been referred to as keystone mutualists [19]. Still, interactions can become parasitic when costs of hosting the symbiont exceed benefits, e.g., when nutrient availability is high and light levels are low [20, 21]. Because the symbiosis lacks specificity, AM fungi were initially thought to play a minor role in plant invasions [22], but several invasive species grow larger and become more competitive with AM fungi [23–25]. Function also differs among AM fungal taxa [26, 27]. Yet, whether individual plant species moving across

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ranges encounter novel and potentially more beneficial AM fungal taxa is little known because biogeographical patterns documented for AM fungi derive mostly from database submissions involving different plant species [28] or global sampling from dissimilar ecosystems [29]. Further complicating range comparisons of biotic interactions is that novel interactions with soil biota can drive shifts in abiotic conditions and vice versa [10, 11, 30–33], and both biotic and abiotic variation may select for rapid evolution in the traits of non-native plants [34] as well as native soil biota [35]. For example, if non-native plants experience fewer pathogens due to enemy release, allocation to defense may decline, which in turn may promote productivity [36] and select for increased associations with mutualists that can acquire limiting resources. Thus, both ecological and evolutionary processes may underlie the mechanisms by which plant-AM fungal interactions affect invasions [37].

Conyza canadensis L. (hereafter *Conyza*), commonly known as Canadian horseweed (Asteraceae), is an archetypical weed native to North America and non-native to large parts of the Northern hemisphere [38]. *Conyza* has an annual life cycle, indeterminate flowering, self-compatibility, pronounced environmental plasticity, and a very high output of small and wind-dispersed seeds [39]. This combination of traits may explain why it has become a problematic invader in parts of its non-native range and an agricultural weed in its native range [39]. In addition, *Conyza* can benefit from AM fungal inoculations [40], appears highly colonized by AM fungi in the field [41, 42], and greenhouse experiments with a non-native *Conyza* population showed that it promotes AM fungal abundance and other microbes involved in nutrient cycling, resulting in positive plant-soil feedback [43].

Here we explored if the greater performance and competitive ability of *Conyza* observed in the non-native range [38, 44] coincides with eco-evolutionary shifts in plant-AM fungal associations. We sampled from 17 *Conyza* populations in each of the native and non-native ranges along roadsides spanning similarly wide and representative climate and soil fertility gradients (Table S1, Figs. S1 and S2). We targeted comparable gradients in climate and soil conditions across ranges, because sampling from few or non-representative populations in either range while not accounting for potential within-range adaptation or environmental conditions, can result in false conclusions about range effects [45, 46]. The wide distribution of *Conyza* makes it an excellent model system to study how plant-AM fungal interactions vary across environmental gradients, which remains poorly quantified, and ensures that results are not restricted to narrow spatio-environmental contexts. Within each population, we measured *Conyza* shoot biomass, fecundity, and community productivity, and estimated AM fungal abundance. We also characterized AM fungal community composition in roots and rhizosphere soil. To assess if the biogeographical patterns we found were uniquely associated with *Conyza*, we measured productivity and rhizosphere AM fungal communities in adjacent communities that did not harbor *Conyza*. Finally, to determine if non-native populations differ from native populations in their ability to form associations with AM fungi, we evaluated if patterns observed in the field persist under common garden conditions. To do so, we conducted a greenhouse experiment with native and non-native populations exposed to the same species pool of AM fungi collected in the native range (Table S2). This study provides insight into how eco-evolutionary shifts in plant-AM fungal associations are related to plant performance and invasiveness and depend on environmental context.

METHODS

Field sampling

In both the native and the non-native ranges, we sampled *Conyza* populations in four different biogeographical regions: four Mediterranean populations (California and Jordan), four continental populations (Intermountain Western USA and Central China), four temperate populations (East Canada and Kashmir), and five subtropical populations (Florida and South China). Populations sampled within each region were separated by 2–642 km, and distances between regions ranged from 672 to 13,704 km (Fig. 1). To study comparable habitat conditions across our 34 populations, we sampled disturbed sites along roads or railways that were neither fertilized nor irrigated. A population had to have at least ten *Conyza* individuals and cover at least 10 m in one dimension. Populations varied in size, but our sampling was restricted to a distance of 30 m to reduce the likelihood of substantial spatial variation in edaphic properties and AM fungal communities. Within each population, we recorded data on plant performance. When plants set seeds, we randomly selected five *Conyza* plants per population (>2 m apart). To assess potential differences in community composition among sites, we estimated the cover of grasses, forbs, and bare ground in a 1 m × 1 m area centered on the focal *Conyza* individual. To quantify productivity in the *Conyza* plots, we collected the aboveground biomass in a 0.5 m × 0.5 m area where the upper right corner of the quadrate was placed next to (but excluding) each of the five focal plants. We then harvested the aboveground biomass of the five *Conyza* plants and counted the number of flower heads (capitula). Data for shoot biomass and capitula numbers from eight of the 34 populations have been included in a previous study [38]. The five *Conyza* individuals were dug up and fine roots (<1.5 mm in diameter) were collected, along with rhizosphere soil (0–15 cm depth), which was sieved through a 2 mm sieve. At each site, we also targeted an adjacent community where *Conyza* was absent. We randomly selected five focal non-*Conyza* individuals, surveyed the plant community, and collected the aboveground biomass in a 0.5 m × 0.5 m area and rhizosphere soil (as above) to characterize community composition, productivity, soil edaphic properties, and AM fungal communities. These adjacent, non-*Conyza* communities matched the *Conyza* communities in slope, aspect, apparent disturbance regime, and in their cover of grasses, forbs, and bare ground (Fig. S3 and Table S3). Recognizing population as the level of replication, we pooled the roots and soil per population for a total of 34 *Conyza* roots, 34 *Conyza* rhizosphere, and 34 non-*Conyza* rhizosphere samples. Roots and soil were transported in a cooler to the lab.

At the lab, *Conyza* roots were rinsed with tap water to remove soil and rapidly dried with desiccant (Drierite, W.A. Hammond Drierite Company Ltd., Xenia, OH, USA). A subset of soil was also dried with desiccant for DNA extraction. Another subset was put into 50 mL centrifuge tubes and shipped on ice to the University of Montana, where it was analyzed for available NO_3^- and NH_4^+ following 2M KCl extractions [47]. The remainder was air-dried and sent to Ward Laboratories (Kearney, NE, USA) for routine analyses involving pH, soil organic matter (SOM), $P_{Merlich}$, K, S, Zn, Fe, Mn, Cu, Ca, Mg, Na, and CEC (Table S4). All aboveground biomass was dried at 65 °C and weighed. A subset of desiccated fine roots was rehydrated, cleared, and stained with trypan blue [48] to quantify AM fungal colonization using the magnified intersection method based on approximately 50 intercepts per sample [49]. AM fungi were identified based on arbuscules, coils, vesicles, and dichotomous branching patterns of mostly non-septate hyphae [18].

Site-specific climate and soil characteristics

Climate data for all sites were obtained from Worldclim 2.1 [50] at a 0.5′ scale using the R package raster 3.3–13 [51] in R 4.1.0 [52]. Nineteen "Bioclim" variables were derived representing annual and seasonal temperature and rainfall means and extremes. To quantify climatic differences among sites, we used the R package vegan 2.5–7 [53] to perform a standardized and centered principal component analysis (PCA) with the Bioclim variables (Fig. S1). We extracted the site scores of the Climate PCA of the first two axes (CPC1 & CPC2), which corresponded with gradients in temperature and aridity, respectively. Our PCA scores integrating temperature and precipitation only approximate evapotranspiration, but CPC2 provides a reasonable gradient in increasing aridity [38].

To quantify differences in soil properties among populations, we performed a PCA (Fig. S2). The first axis, SPC1, represented gradients in fertility while SPC2 mainly correlated with P, SOM, and some heavy metals. We tested whether CPC1, CPC2, SPC1, and SPC2 differed between native vs. non-native ranges and for SPC1 and SPC2 also whether they differed between the adjacent non-*Conyza* vs. *Conyza* communities. We found that none of our environmental variables were significantly affected by range or community type (see legends of Figs. S1 and S2 for details).

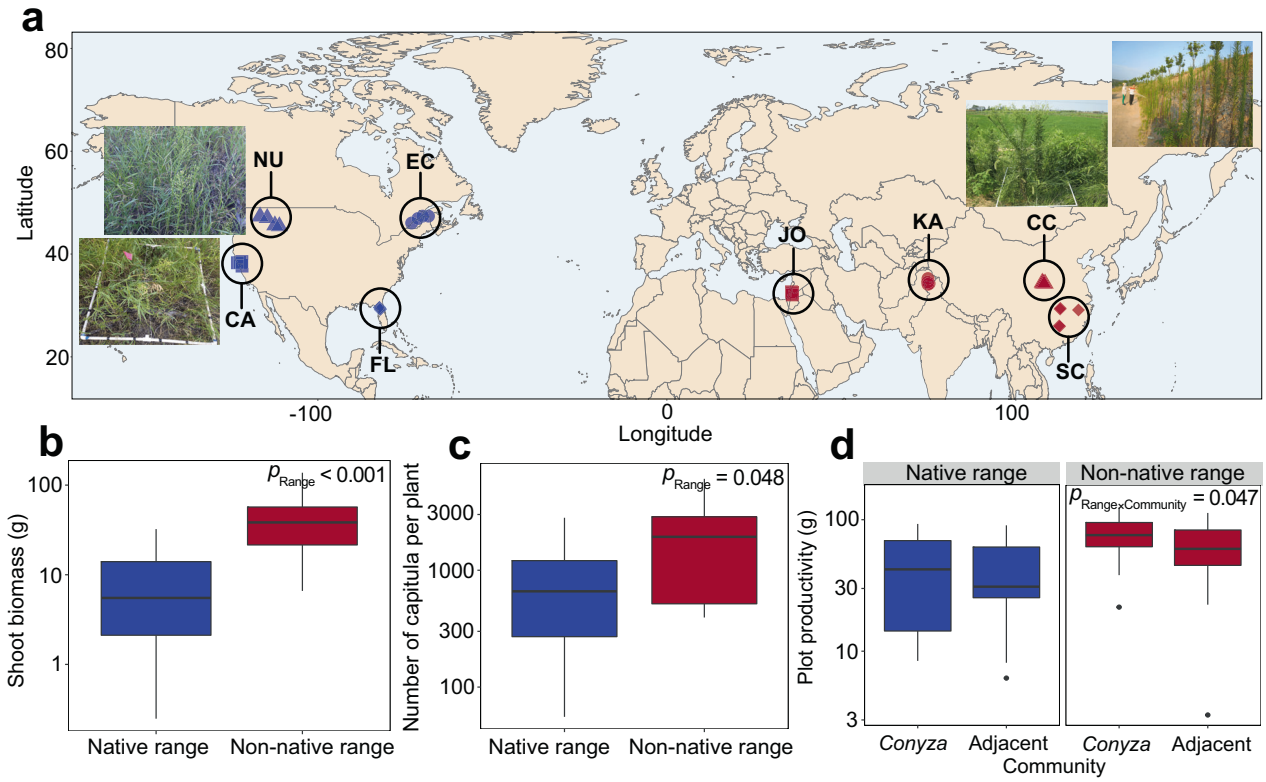


Fig. 1 Geographical distribution and field performance of the studied *Conyza* populations. a Locations of the 17 native (blue) and 17 non-native (red) populations. **b** *Conyza* shoot biomass in native vs. non-native ranges. **c** Number of capitula per *Conyza* plant in native vs. non-native ranges. **d** Interactive effects of range and communities (*Conyza* vs. adjacent) on plot productivity. Abbreviations in **a** refer to four native and four non-native regions: CA California ($n = 4$); NU North West US ($n = 4$); FL Florida ($n = 5$); EC East Canada ($n = 4$); JO Jordan ($n = 4$); KA Kashmir ($n = 4$); CC Central China ($n = 4$); SC South China ($n = 5$). Symbols refer to macroclimatic conditions: square = Mediterranean, triangle = continental, diamond = subtropical, circle = temperate (see Fig. S1). Details on the populations including mean values for shoot biomass, number of capitula per *Conyza* plant and plot productivity are presented in Table S1. Details on the linear mixed-effects models for **b**, **c** and **d** are in Tables S5 and S6.

DNA extraction, amplification, and bioinformatic analyses

DNA was extracted from 10 g silica dried soil and 25 mg of silica dried roots using PowerSoil DNA and MO BIO PowerPlant Pro-htp DNA isolation kits (MO BIO Laboratories Inc., Solana Beach, CA, USA), respectively, following the manufacturer's instructions. The small subunit rRNA (SSU rRNA) region was amplified to characterize AM fungal communities using the primer pairs WANDA-AML2 [54, 55]. Two-step PCR amplification was performed in duplicate as outlined in Bullington et al. [56]. Amplicons generated during PCR1 were diluted 1:10 for use as template for barcode addition in PCR2. PCR2 amplicons were purified using AMPure XP beads (Beckman Coulter Genomics, Brae, CA, USA), and pooled based on band strength prior to sequencing. Sequencing was done at the Genomics Core facility at the University of Montana. Amplicon libraries were sequenced using a MiSeq v2 kit (500 cycles) on an MiSeq sequencing platform (Illumina Inc., San Diego, CA, USA).

Processing of raw sequence data was performed using "Quantitative Insights Into Molecular microbial ecology 2" (QIIME2 2018.4, https://qiime2.org/) [57]. Sequence reads were first demultiplexed using the q2-demux plugin (https://github.com/qiime2/q2-demux). Only forward reads (trimmed to 210 bases) were used as they cover the informative region [55], and the overlap between forward and reverse reads was too small to pair without causing significant sequence loss. All sequences were quality filtered and de-replicated using the q2-dada2 plugin [58] which uses nucleotide quality scores to produce amplicon sequence variants (ASVs) with 100% similarity (for simplicity referred to as taxa) representing the estimated true biological variation within each sample. We assigned taxonomy using the *MaarjAM* database [59] and the QIIME2 q2-feature classifier (https://github.com/qiime 2/q2-feature-classifier) with a confidence threshold of 0.9. We also removed all ASVs that did not match with at least 85% similarity and 85% coverage to *MaarjAM* sequences. We rarefied sequences from the field to a resampling depth of 3200 and the greenhouse to 2647 sequences per sample. These sampling depths resulted in saturation of sequencing rarefaction curves produced in QIIME2 (Figs. S4 and S5). Two field samples collected from the adjacent communities (FL3 and SC1) and one greenhouse sample (FL3) were lost at this sequencing depth due to poor amplification. Raw amplicon sequence data and associated meta-data is available at NCBI Sequence Read Archive (PRJNA831567).

The AM fungal richness (ASV count), Shannon index, and beta diversity were analyzed based on the rarefied ASV table with the vegan package. Shannon index was calculated using the diversity() function, and distances to within-group centroids based on weighted UniFrac dissimilarities were calculated using the betadisper() function. The weighted UniFrac dissimilarities were calculated using the GUniFrac() function from the R package GUniFrac 1.1 [60]. The nearest taxon index (NTI) [61] within each sample was calculated using the R package picante 1.8.2 [62]. Representative sequences from each ASV were aligned using MAFFT [63] (Multiple Alignment using Fast Fourier) via the QIIME2 alignment plugin. An Ascomycota sequence from GenBank (MH014976), was used as an outgroup, and an approximately-maximum-likelihood phylogenetic tree was constructed using the FastTree [64] plugin in QIIME2. Phylogenetic trees were displayed using the ggtree() function from the R package ggtree 2.0.4 [65].

Greenhouse experiment

We grew seedlings from seeds collected from the five focal *Conyza* plants from 29 of the 34 populations. We did not obtain viable seeds from FL2, FL5, NU2, and SC1, and FL3 was lost due to low sequence numbers. On 8 May 2019, seeds were surface sterilized by an immersion into 70% EtOH for 2 min followed by five rinses in sterile, distilled H_2O and then germinated in a Miracle Gro Seed Starting Potting mix (Marysville, OH, USA) devoid of AM fungi. On 29 May, seedlings were transplanted into an autoclaved 2:1:1 soil:sand:turface mix (pH = 6.6, 1 ppm NO_3^-, and 12 ppm $P_{Merlich}$) and

inoculated with 20 mL of soil collected from a native community close to Missoula, MT, USA, where *Conyza* was absent, to simulate a new colonization (pH=6.8, 1.6 ppm NO_3^-, and 18 ppm $P_{Merlich}$). Plants were grown in ambient light in the greenhouse (25/18 ± 5° C day/night) and watered daily with tap water. To address nitrogen limitations indicated by a yellowing of leaves, plants were fertilized on July 3 and July 22 with 20 mL of 20-2-20 (N-P-K) Peters Professional fertilizer (JR Peters, Inc., Allentown, PA, USA). After four months, plants were harvested, AM fungal root colonization was quantified as outlined above, and rhizosphere soils were collected for DNA extraction, amplification, and bioinformatic analyses as outlined above. Root and shoot biomass was dried at 65 °C until constant weight. To quantify plant functional traits, we calculated leaf mass area and shoot/root ratios and recorded the average root diameter with WinRHIZO 2012a (Regent Instruments Inc., Quebec, Canada) using pooled, rehydrated root samples from each population.

Statistics

To assess the drivers of among-population variation in plant community productivity, plant cover, plant performance, plant functional traits, AM colonization (percentage of root intercepts), and descriptors of AM fungal community (diversity and phylogenetic dissimilarity), we conducted linear mixed-effects models using the R package lme4 1.1–26 [66]. We applied stepwise backward model selection based on likelihood ratio tests to identify minimal adequate models (i.e., removing non-significant fixed effects if $p > 0.05$). Transformations of variables were based on visual inspection of normality of residuals and variance homogeneity in model plots. We used arcsine square root transformations for estimates of plant cover and AM colonization. Performance data were $\log_e$-transformed. Random effects were region, or population nested within region. The latter we used in analyses that included samples from both *Conyza* and adjacent communities (productivity estimates) or from both *Conyza* roots and *Conyza* rhizosphere (field AM community estimates). All models included the fixed effects of range and four covariates to account for within-range variation in climate and soil gradients: CPC1, CPC2, SPC1, and SPC2. Further fixed effects were the interaction of range with either community type (productivity estimates from *Conyza* vs. adjacent non-*Conyza* plots; AM fungal community estimates from *Conyza* roots vs. rhizosphere), or with plant functional traits (to test their effect on AM root colonization), or with AM root colonization (to test their effect on plant performance). The full model structures can be found in the Supplementary data (Tables S3 and S5–S14).

To explore determinants of the AM fungal community composition in the field, we performed two distance-based redundancy analyses (db-RDAs) with the capscale() function from the vegan package, using two data sets. The first data set included only *Conyza* samples which were collected from two sampling types (root vs. rhizosphere). The second data set included only rhizosphere samples from the adjacent plant communities. We performed this second db-RDA to assess whether any between-range differences observed for *Conyza* were indeed due to altered AM interactions between the ranges or instead due to general differences between the sites sampled in either range. Tested predictors of the db-RDAs included range in interaction with sampling type for the first data set or only range for the second data set, respectively, plus in both cases, the covariates (CPC1, CPC2, SPC1, SPC2). We applied forward selection to add predictors that significantly ($p < 0.05$) improve model fit [67]. To assess whether determinants of AM fungal community composition in the greenhouse were similar to those in the field, we performed the same db-RDA analysis for the greenhouse AM community data.

Since differences in AM fungal community composition may stem from differences in location or dispersion, we tested for both. We tested for significant difference in the distances to within-group centroids and between native vs. non-native ranges and between root vs. rhizosphere communities using the TukeyHSD() function, and corrected for multiple hypothesis testing using the Benjamini and Hochberg method [68]. We found differences in dispersion among groups, and because this can affect outputs of compositional analyses, we also used PERMANOVA—known to be relatively robust against differences in dispersion [69]—to test for differences in location on the weighted GUniFrac distance using the adonis() function. As before, we controlled for multiple hypothesis testing. These PERMANOVA analyses supported outputs from the db-RDA. We conducted the same PERMANOVA on soils collected from the adjacent communities across ranges.

To assess whether AM fungal community composition in the field was related to that in the greenhouse, two Procustes tests were conducted comparing the PCoA plots of AM fungal beta diversity (weighted GUniFrac distance) in the field and in the greenhouse, separately for each range. Moreover, Mantel testes were carried out to explore correlations between pairwise weighted GUniFrac distances in the field and in the greenhouse, again separately for each range.

To explore which taxa occurred more frequently in the native and non-native ranges, we conducted differential abundance analyses for both the field and greenhouse data using the R package DESeq2 1.30.0 [70]. Taxa were considered to differ significantly between native vs. non-native ranges at a significance level of $p < 0.05$ after Benjamini and Hochberg adjustment [68]. Moreover, the relationships between differentially abundant taxa with shoot biomass and number of capitula for the field data, shoot biomass, root biomass and shoot/root ratios for the greenhouse data were also analyzed with the DESeq2 package (significance level: $p < 0.05$ after Benjamini and Hochberg adjustments).

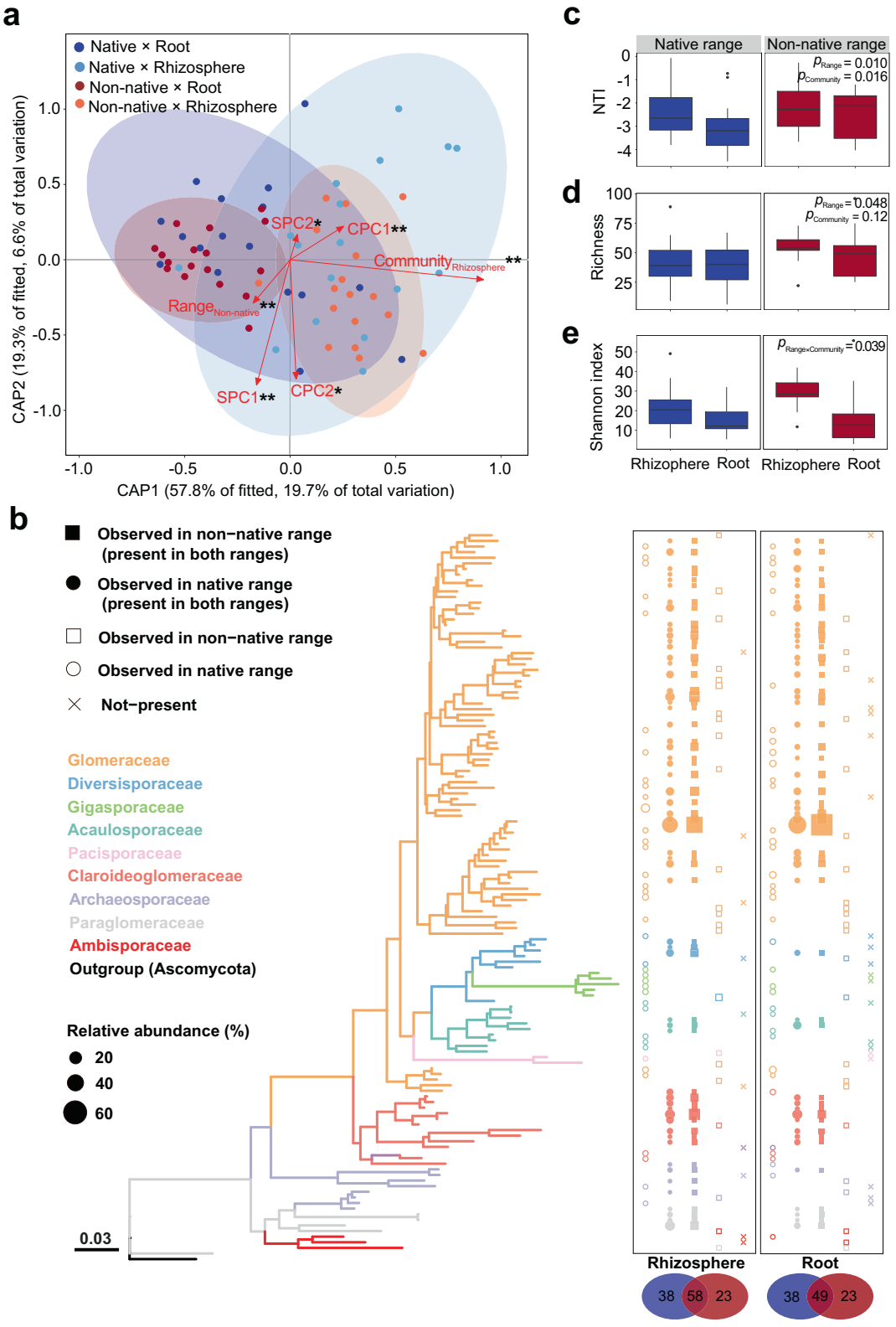
RESULTS

Field survey

Conyza *biomass and plot productivity*. *Conyza* plants in the non-native range had similar cover (Fig. S3 and Table S3) but were three times larger ($p < 0.001$, Fig. 1b) and more than twice as fecund ($p = 0.048$, Fig. 1c, Tables S1, S5) as plants in the native range. In the non-native range, productivity was higher in plots with *Conyza* than plots without *Conyza*, but in the native range, plots with *Conyza* did not differ from adjacent plots without *Conyza* ($p_{Range \times Community} = 0.047$, Fig. 1d, Table S6). *Conyza* shoot biomass increased with the mean annual temperature (CPC1) of sites across ranges ($p = 0.045$, Fig. S6, Table S5), but no other environmental site variables correlated with differences in performance or productivity.

AM associations in the native and non-native range. *Conyza* plants in most populations were highly colonized by AM fungi, and average colonization did not differ between the native (75%) and non-native (71%) ranges ($p = 0.23$, Tables S1, S7). However, colonization varied along environmental gradients across ranges and decreased with increasing aridity ($p_{CPC2} = 0.013$), soil P-availability, soil organic matter, and heavy metal concentration ($p_{SPC2} = 0.005$, Fig. S7, Table S7).

Despite similar AM fungal abundance in *Conyza* roots across ranges, the db-RDA indicated that native and non-native *Conyza* plants associated with different AM fungal communities ($p = 0.005$, Fig. 2a), a pattern that was also supported by PERMANOVA (Table S8). *Conyza* encountered novel fungal taxa in the non-native range, although abundant taxa occurred across both ranges (Fig. 2b). *Conyza* roots in the non-native range were mostly colonized by taxa in the Glomeraceae family, whereas *Conyza* roots in the native range harbored more divergent communities that included more taxa in the Claroideoglomeraceae, Acaulosporaceae, and Paraglomeraceae families (Fig. S8). This resulted in tighter clustering of AM fungal communities among non-native populations ($p < 0.001$, Fig. S9). In addition, co-occurring taxa were more closely related within sites in the non-native range as suggested by a less negative Nearest Taxon Index (NTI [61], $p = 0.01$, Fig. 2c, Table S9). Non-native *Conyza* plants also associated with a richer AM fungal community than native *Conyza* plants ($p = 0.048$, Fig. 2d, Table S9). We observed greater differences in fungal diversity between rhizosphere and roots in non-native than in native *Conyza* populations ($p_{Range \times Community} = 0.039$), which reflects a lower evenness and perhaps a greater "selectiveness" in non-native *Conyza* roots relative to native *Conyza* roots. No differences were observed in richness ($p = 0.073$), Shannon index ($p = 0.75$), AM fungal community composition ($p = 0.18$), dispersion ($p = 0.93$) or NTI ($p = 0.61$) between the adjacent native and non-native communities where *Conyza* was absent (Table S10), suggesting that community attributes associated with *Conyza* were not mediated by differences in regional species pools.



AM fungal communities varied across environmental gradients of soil fertility ($p_{SPC1} = 0.005$), soil organic matter, and heavy metal concentration ($p_{SPC2} = 0.025$), temperature ($p_{CPC1} = 0.005$), and aridity ($p_{CPC2} = 0.025$, Fig. 2a, S10, and Table S9). Richness also declined with aridity, as did Shannon index and NTI in the adjacent communities (Fig. S11 and Table S10).

Relationships between Conyza *performance and AM associations.* Biomass decreased with increasing AM colonization in the native range but showed no relationship in the non-native range ($p_{Range \times AM} = 0.048$, Fig. 3a, and Table S11). Fungal taxa that were more abundant or existed exclusively in the non-native range often correlated positively with shoot

Fig. 2 AM fungal communities associated with *Conyza* roots and rhizosphere in native and non-native populations in the field survey. **a** Relationship between environmental variables and composition of AM fungi in the native (blue) and non-native (red) ranges for both the roots (darker hues) and rhizosphere soils (lighter hues) of *Conyza*. Significance levels based on the db-RDA results: *$p < 0.05$; **$p < 0.01$. **b** Phylogenetic tree of AM fungal taxa (ASVs, representing identical sequences) color coded by AM fungal families. Open circles refer to taxa that only occurred in the native range and open squares indicate taxa that only occurred in the non-native range for both roots and rhizosphere samples. Filled circles and squares refer to the relative abundance of taxa that occurred in both ranges. This shows that while some taxa occurred in only one range, the more abundant taxa occurred across ranges. Venn diagrams at the bottom sum up the taxa specific to either range or shared between ranges. **c** Nearest taxon index (NTI), **d** richness (based on identical sequences, ASVs), **e** Shannon index in the native (blue) and non-native (red) ranges in roots and rhizosphere soils. Details on the linear mixed-effects models for **c**, **d** and **e** are in Table S9.

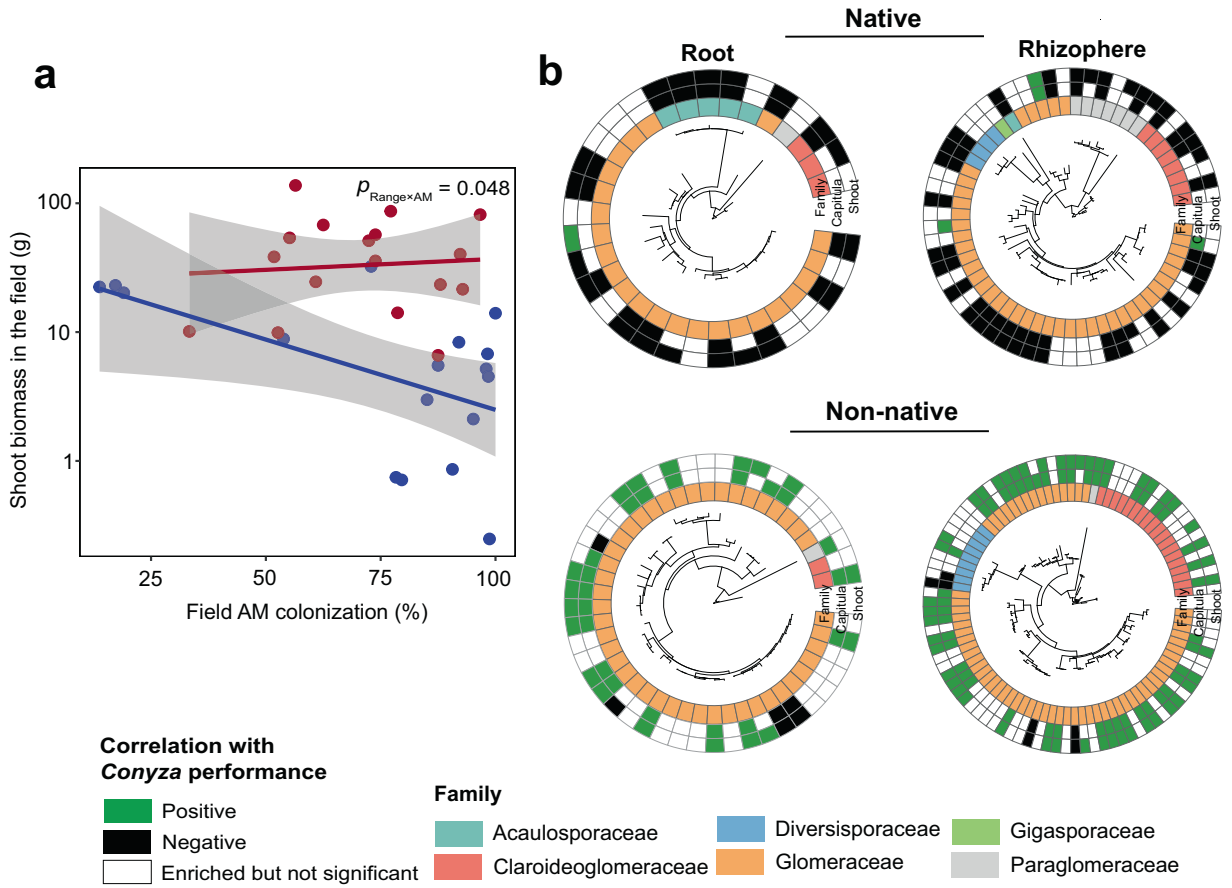


Fig. 3 Correlations between AM colonization, AM fungal taxa relative abundance, and *Conyza* field performance. **a** Relationship between field AM colonization and *Conyza* shoot biomass in native (blue) and non-native (red) populations. Details on the linear mixed-effects models can be found in Table S9. **b** Phylogenetic tree of taxa that were enriched in either the native or non-native ranges and their relationships with *Conyza* shoot biomass and capitula number (Wald test, $p < 0.05$ after multiple-comparison adjustment). Details on the assessments of enriched taxa are in Fig. S12.

biomass and fecundity across ranges, whereas AM fungal taxa that were more abundant or only occurred in the native range tended to correlate negatively with *Conyza* performance (Fig. 3b and S12). These patterns —albeit weaker—persisted when analyses were restricted to taxa that occurred in both ranges (Fig. S13), suggesting that *Conyza* may benefit from an improved function of the same taxa in the non-native range as well as encounters with novel taxa. The correlations between *Conyza* biomass and AM fungal taxa were not indirectly mediated by similar responses to environmental gradients (i.e., no pseudo correlations), because *Conyza* biomass only responded to temperature (CPC1), but temperature did not differ across ranges. Moreover, only 8% of the AM fungal taxa that correlated with *Conyza* performance also correlated with temperature.

Greenhouse experiment

Productivity and plant traits. Shoot biomass did not differ between native and non-native populations when grown in soils from the native range ($p = 0.56$), nor did we observe differences in average root diameter ($p = 0.61$), or leaf mass area (LMA, $p = 0.15$, Table S12). However, non-native plants produced less root biomass ($p = 0.049$, Table S12), indicating a shift in allocation patterns between native and non-native populations. Irrespective of range, populations originating from more arid sites had less shoot biomass ($p < 0.001$), greater root diameters ($p = 0.005$), and lower shoot/root ratios ($p = 0.003$, Table S12, Fig. S14).

AM associations in native and non-native populations and comparisons to field observations. Similar to the field measurements, overall AM colonization in the greenhouse was high and

did not differ among native (72%) and non-native (71%) populations ($p = 0.62$, Tables S2). However, native and non-native populations associated with different AM fungal communities when exposed to the same AM fungal species pool ($p = 0.005$, Fig. 4a). Abundant AM fungal taxa colonized both native and non-native populations, but native populations harbored a greater proportion of Diversisporaceae AM fungi, whereas non-native populations were dominated by taxa in the Glomeraceae family (Fig. 4b, S15). Non-native *Conyza* also harbored a richer ($p = 0.002$, Fig. 4c) and more diverse AM fungal community ($p = 0.002$, Fig. 4d, Table S13). Richness and Shannon index were also lower in populations from more arid sites (Fig. S16).

Comparing AM fungal communities in the field and greenhouse using Procrustes, we found significant relationships for the non-native ($p = 0.005$) but not for the native populations ($p = 0.44$, Fig. S17). Mantel tests supported this pattern: the correlation between pairwise distances of AM fungal communities in the field with pairwise distances of AM fungal communities in the greenhouse was not significant for the native populations ($r_M = -0.03$, $p = 0.54$) but highly significant for the non-native populations ($r_M = 0.29$, $p = 0.005$, Fig. S18). This does not mean that non-native plants were colonized by the same fungal taxa in the field and greenhouse, but that the non-native populations maintained comparable phylogenetic patterns in AM associations among populations in the field and greenhouse whereas associations among native populations appeared more random.

Relationship between Conyza *performance and AM associations*. Across ranges, plants with greater AM colonization were larger ($p = 0.012$) and had a higher shoot/root ratio ($p = 0.045$, Fig. 5a, Table S14). Non-native plants that were more colonized had less root biomass, but this was not the case for native populations ($p_{\text{Range x AM}} = 0.012$, Fig. 5a, Table S14). Also, AM fungal taxa that were more abundant in non-native *Conyza* correlated positively with shoot biomass, whereas taxa that were more abundant in native *Conyza* appeared more parasitic (Fig. 5b, S19). These patterns—albeit weaker—persisted when analyses were restricted to taxa that associated with both native and non-native plants (Fig. S20). This suggests the same taxa were more mutualistic with non-native plants, and that non-native plants associated with beneficial AM fungal taxa that native plants did not.

DISCUSSION

Differences in field performance was linked to shifts in AM associations

Similar to other invasive plant species [34, 38, 71, 72], *Conyza* plants in the non-native range grew bigger and were more fecund than conspecifics in the native range. This increased performance was not caused by more favorable environmental conditions in the non-native range because *Conyza* biomass correlated with temperature only, but temperature and other climate and soil abiotic properties were comparable across ranges. Also, productivity did not differ across ranges in the adjacent non-*Conyza* communities, suggesting that the increased productivity was associated with *Conyza*. However, whether *Conyza* caused the increased productivity or just colonized more productive sites in the non-native range is uncertain. Some invasive plants undergo genetic shifts between ranges toward high-performance genotypes [73], but this also seems an unlikely explanation for the increased performance, because climate was more important than range effects for the population genetic structure and greenhouse performance of *Conyza* in an earlier study [38]. This was supported here because non-native populations did not grow bigger in the greenhouse, and performance was more dependent on the history of aridity. Assuming there were no unmeasured variables that greatly influence productivity, the most parsimonious explanation for the increased *Conyza* size and fecundity in the non-native range is a change in biotic interactions.

Several patterns indicate that differences in AM associations across ranges may have contributed to *Conyza* performance. First, biomass decreased with increasing AM colonization in the native range, but not in the non-native range. Second, taxa that were more abundant or occurred exclusively in the non-native range often correlated positively with shoot biomass and fecundity across ranges, whereas taxa more abundant in the native range predominately showed negative correlations. The apparent shift from parasitism in the native range towards mutualism in the non-native range may result from the higher abundance of Glomeraceae taxa in the non-native range. Traits differ among AM fungal families [26] and this can affect the nature and degree of benefits provided to plants [27]. For example, Glomeraceae appear better at promoting overall growth [74], acquiring phosphorus, and protecting plants against pathogens than some other AM families [75], which may be related to a greater allocation of fungal biomass inside rather than outside roots by Glomeraceae fungi [74]. This high Glomeraceae abundance mirrors previous findings for an invasive palm [76] and raises the question of whether this is a common phenomenon among AM invaders, similar to what has been suggested for a particular group of ectomycorrhizal fungi enabling pine invasions into the Southern Hemisphere [77]. Moreover, the greater AM fungal richness associated with non-native *Conyza* both in the field and greenhouse might provide further benefits given that more species-rich fungal communities are related to increased plant productivity and community resilience [78, 79]. These shifts in AM associations were uniquely associated with *Conyza* because there were no differences in plant productivity and AM fungal community attributes in the adjacent non-*Conyza* communities. We cannot exclude the possibility that the increased performance of *Conyza* in the non-native range was also affected by an escape from pathogens, as this is known to be important for some other invasive plants [9]. Experimental inoculations with AM fungal indicator species from the native and non-native ranges are necessary to unequivocally assess if AM fungi drive the apparent increase in competitive ability of *Conyza* in the non-native range [44], as are comparisons of pathogen abundances and disease severity in the native and non-native range. Nonetheless, our results are consistent with a previous greenhouse experiment showing that *Solidago canadensis* changed AM fungal communities in the non-native range in ways that promoted its growth and enhanced its ability to compete with native species [80].

Community assembly patterns in the greenhouse reflected field patterns and suggest evolutionary shifts in AM associations

Both native and non-native *Conyza* were highly colonized by AM fungi in the greenhouse, indicating no evolutionary shift in host quality. This high colonization agrees with previous findings for this plant [41, 42]. Regardless of range, plants that were more colonized were bigger, but whether AM fungi promoted growth or merely benefitted from associating with larger plants [81] is unclear. Given that non-native populations appeared to select more beneficial fungi than native populations, it is noteworthy they were not bigger than native populations. We can think of at least three possible explanations for this. First, the benefits of AM fungi can take time to manifest [18], and differences might have become apparent had the experiment run longer, possibly even across generations, as AM fungal communities may continue to change with time. Second, non-native plants may have benefitted more had greenhouse conditions been less benign and better mirrored field conditions. Third and probably most important, we grew plants in soil from the native range that likely also harbored pathogens, and *Conyza* growth may reflect responses to both AM fungi and pathogens, which may differ among populations. For

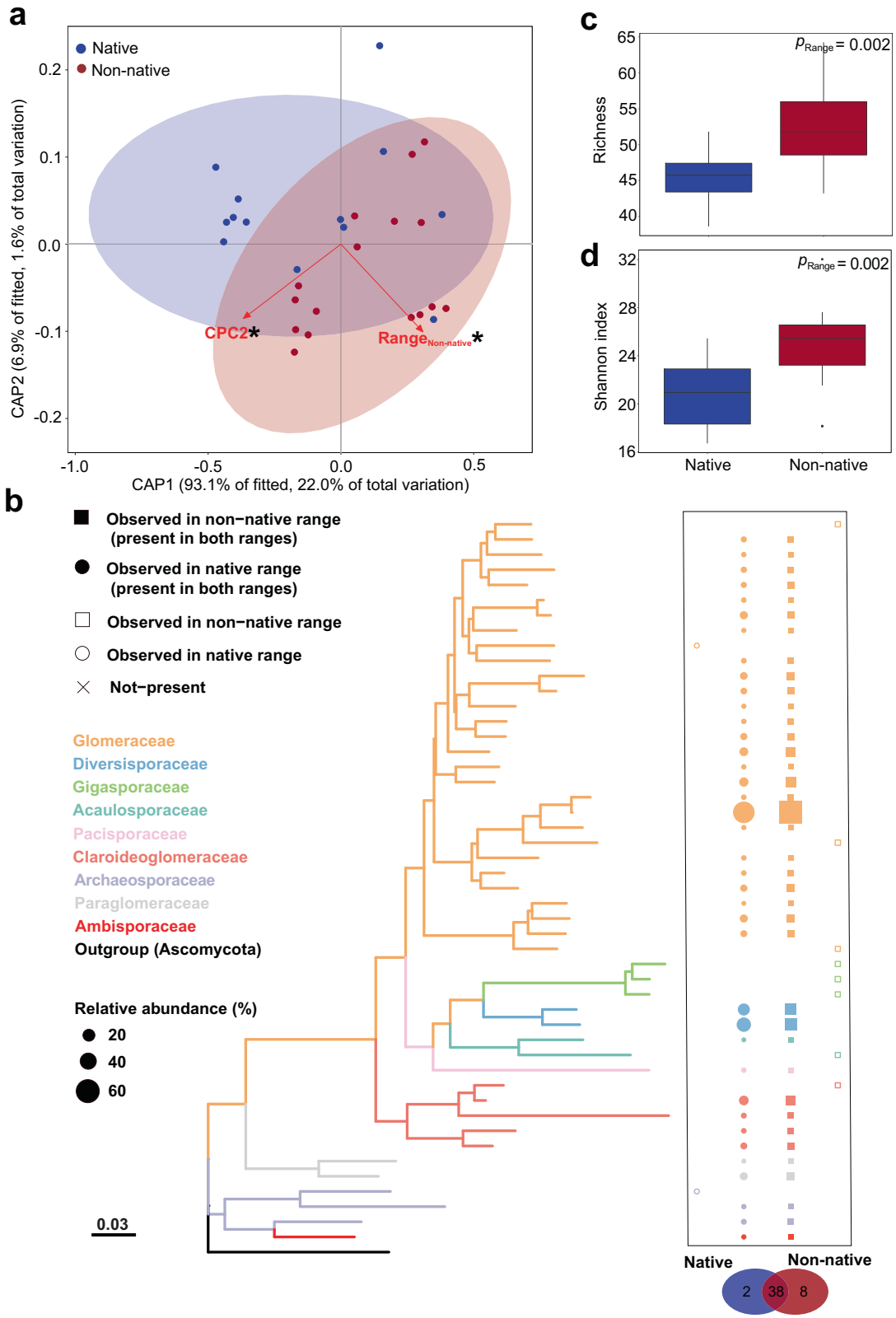


Fig. 4 AM fungal communities in rhizosphere soil of *Conyza* populations grown in the greenhouse. a Relationship between environmental variables and composition of AM fungal communities in the rhizospheres of native (blue dots, $n = 13$) and non-native (red dots, n=16) *Conyza* populations. Significance levels based on the db-RDA results: *$p < 0.05$. **b** Phylogenetic tree of AM fungal taxa (ASVs, representing identical sequences) color coded by AM fungal families. Open circles refer to taxa only found associating with *Conyza* from the native range and open squares refer to taxa only associating with *Conyza* from the non-native range. Filled circles and squares refer to the relative abundance of taxa that associate with both native and non-native *Conyza*, respectively. Venn diagrams at the bottom of panel sum up the number of taxa specific to either range or shared between ranges. **c** Richness in the native and non-native ranges, **d** Diversity (Shannon index) in the native and non-native ranges. Details on the linear mixed-effects models for Shannon index and richness can be found in Table S13.

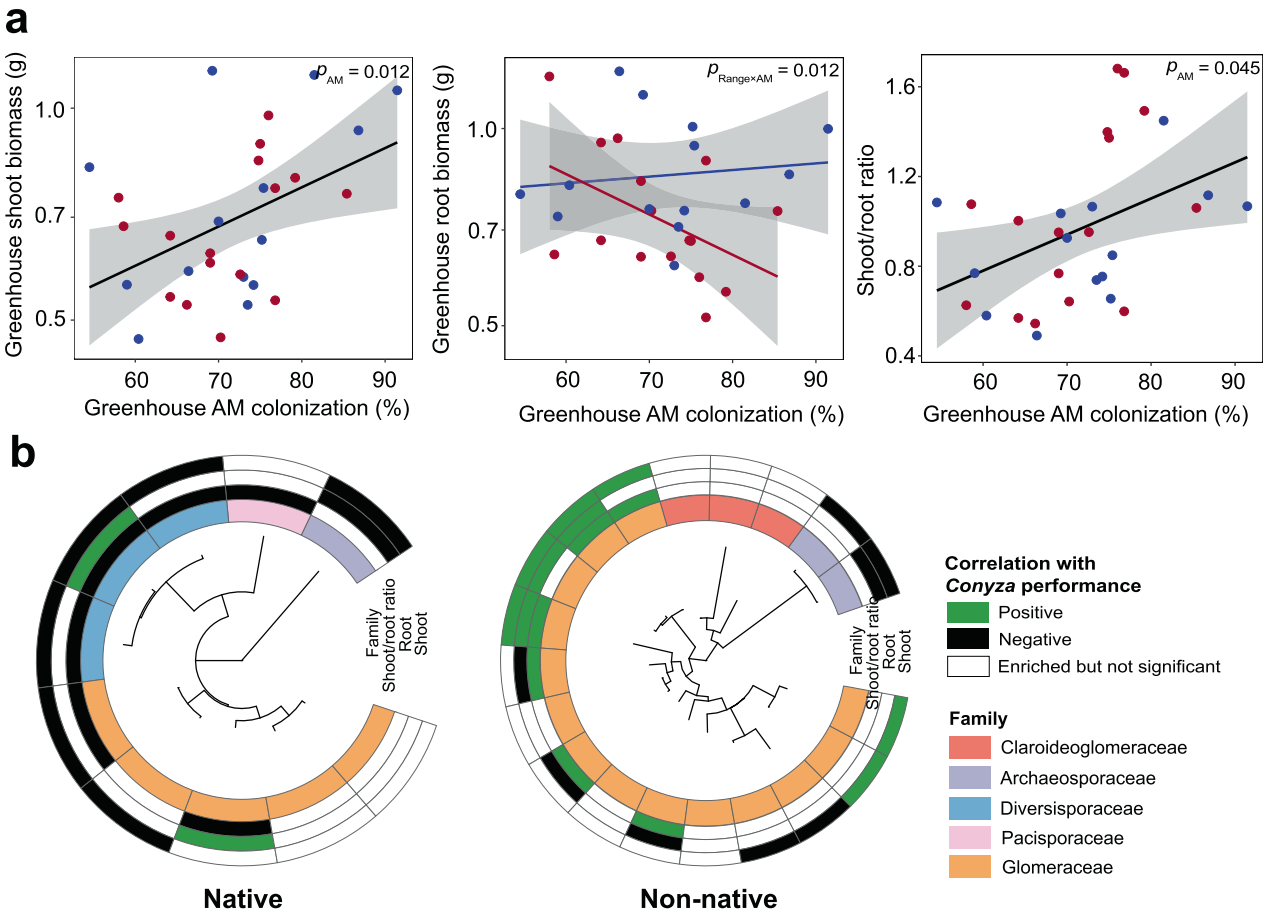


Fig. 5 Correlations between AM colonization, AM fungal taxa, and *Conyza* greenhouse performance. a Relationship between AM colonization and *Conyza* shoot biomass, root biomass, and shoot/root ratios in native (blue) and non-native (red) populations. Details on the linear mixed-effects models can be found in Table S11. **b** Phylogenetic tree of range enriched taxa and their relationships with *Conyza* shoot biomass, root biomass, and shoot/root ratio (Wald test, $p < 0.05$ after multiple-comparison adjustment), suggesting that interactions are more beneficial in the non-native than native ranges. Details on the assessments of enriched taxa in either range can be found in Fig. S19.

example, a recent study showed that greater performance by *Solidago canadensis* in the non-native range did not translate to greater performance in the native range [72], suggesting a process inherent to the native range reduced its growth potential.

While plants from non-native and native populations did not differ in size, they cultured different communities when exposed to a common AM fungal species pool in the greenhouse. Non-native populations harbored a richer and more diverse AM fungal community dominated by *Glomeraceae* compared with native populations. It is noteworthy that AM fungal communities associated with non-native populations also sorted themselves in a pattern similar to what we observed in the field, indicative of greater selectivity and "memory" in non-native than native *Conyza* populations. Differences in plant traits, such as life history and root architecture can influence AM associations [82, 83]. However, they seem an unlikely explanation here as we found no consistent difference in traits between ranges except root biomass, which was lower and more responsive to differences in AM colonization in non-native populations. This reduced root biomass may suggest general shifts in allocation, which is consistent with biogeographical comparisons between native and non-native *Hypericum perforatum* populations [84]. Variations in nutrient concentrations in roots have also been shown to correlate with differences in AM fungal associations in an Australian grassland [85], as have divergence of mycorrhizal-associated genes involved in strigolactone production and ammonium transporters in two sister palm species [86]. Also, a recent study showed non-native populations of *Triadica sebifera* had higher flavonoid concentrations in root exudates than native populations, and this promoted percent AM colonization and growth in a greenhouse experiment [87]. Comparing nutrient concentrations, exudation profiles, and gene expressions associated with AM formation and function [88] on *Conyza* might be fruitful avenues for future studies.

Our field survey and greenhouse experiment support the enhanced mutualism hypothesis [9]. Few mycorrhizal studies have addressed this hypothesis, and those that have tend to show mixed results [84, 89–92]. The eco-evolutionary processes whereby invaders encounter better mutualists in the non-native range are unclear, but are important to consider in the broader context of mutualism theory. Exploitation in mutualisms is not uncommon and can derive from an evolutionary defection to escape costs associated with mutualisms [93]. As such, exploitation can accumulate over time and may contribute to the apparent parasitism we observed in the native range where associations presumably are much older. However, a degradation of mutualisms over evolutionary time contradicts the notion that plants and fungi are able to identify and selectively reward more beneficial partners [94], which should stabilize cooperation. Selection could also favor enhanced cooperation if it results in a fitness advantage [89]. Benefits from AM fungi depend on plant life history strategy, where early successional and ruderal species often benefit less than late successional, more competitive plants [95]. *Conyza* may undergo a switch from a ruderal in the native range to a more competitive life history strategy in the non-native

range [44]. While this can help explain the apparent shifts in AM associations, it does not resolve if AM fungi caused, or simply responded to this shift. However, the potential for AM fungi to drive plant evolution has been shown recently and may be more common than expected [86]. In our study, population history in field AM associations appeared to trigger rapid evolution in biotic interactions, although maternal effects need to be removed to separate genetic and epigenetic differentiation. Based on this, studying invasive plants may be particularly fruitful to explore trajectories of mutualisms given the rapid evolution and altered biotic interactions that often accompany invasions.

Environmental effects on plants, AM fungal communities, and AM associations

In addition to addressing our primary objectives (i.e., to assess eco-evolutionary shifts in AM associations related to range shifts), our study design allowed us to assess the relative importance of environmental factors. We found that in many cases, their effect was just as strong, or stronger, than the effect of range, possibly due to longer evolutionary history and/or stronger selection pressures. For example, AM fungal communities varied across aridity gradients, and AM colonization decreased with increasing aridity, as did Shannon index and NTI, which agree with previous findings [96, 97]. In the greenhouse, richness and Shannon index were lower in populations from more arid sites, indicative of evolutionary shifts in AM association due to climate history. Unlike the range effect where we did not find differences in measured plant traits, altered AM associations among arid populations coincided with lower shoot/root ratios and thicker roots, which most likely reflect a selection toward a more conservative growth pattern in environments where water is limited. In the field, AM colonization also decreased, and community composition changed, with increasing P-availability, soil organic matter, and heavy metals, which conforms with findings for other plant species [18, 98]. Because AM fungi have the potential to reduce stressors related to heat, drought, nutrient limitation, heavy metal toxicity, and pathogens [99], future work should explore both the underlying mechanism(s) for the patterns detected here and their functional consequences.

The strong effects of environmental conditions underscore the need to sample a sufficient and representative number of populations across ranges and to control for potential differences in environmental conditions. Failure to do so may result in erroneous conclusions about range effects in cases where dissimilar environments are sampled between ranges, or conclusions of neutral range effects where within-range environmental variation is substantial but unaccounted for. Efforts to assess drivers of within-range variation among populations are rare in eco-evolutionary studies of biological invasions, and considering these aspects in future studies will allow for more robust between-range comparisons.

CONCLUSION

Our results show that: (1) native and non-native *Conyza* populations differed in how they interacted with AM fungi in ways that may have functional consequences; and (2) that these differences persisted when populations were exposed to a common AM fungal species pool in the greenhouse. Our findings add to a small but growing body of research [5, 11, 32, 84] indicating that biogeographical expansions of plants are often accompanied by altered interactions with soil biota. We provide data suggesting evolution of plant-AM fungal associations toward enhanced mutualism in non-native ranges. To what extent such novel relationships and rapid evolution of mutualisms contribute to the disproportionate abundance and impact of non-native plant species is unknown, but exploration of potential underlying mechanisms is imperative to better understand plant invasions specifically and the organization of communities generally.

DATA AVAILABILITY

Population means required to repeat analyses are available in the Supplementary Information for this paper.

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AUTHOR CONTRIBUTIONS

MS, CR, and YL conceived the idea of the study and all co-authors provided input on the design. MS and CR conducted all statistical analyses with input from YL and LB. YL, MS, and CR wrote the first draft. All co-authors were involved in either sampling or sample processing and provided edits to earlier drafts.

COMPETING INTERESTS

The authors declare no competing interests.

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