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Trait differences between and within ranges of an invasive legume species

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Abstract Novel ecological interactions can drive natural selection in non-native species and trait evolution may increase the likelihood of invasion. We can gain insight into the potential role of evolution in invasion success by comparing traits of successful individuals in the invasive range with the traits of individuals from the native range in order to determine which traits are most likely to allow species to overcome barriers to invasion. Here we used *Medicago polymorpha*, a non-native legume species from the Mediterranean that has invaded six continents around the world, to quantify differences in life history traits among genotypes collected from the native and invasive range and grown in a common greenhouse environment. We found significant differences in fruit and seed production and biomass allocation between invasive and native range genotypes. Invasive genotypes had greater fecundity, but invested more energy into belowground growth relative to native genotypes. Beyond the variation between ranges, we found additional variation among genotypes within each range in flowering phenology, total biomass, biomass allocation, and fecundity. We found

non-linear relationships between some traits and fitness that were much stronger for plants from the invasive range. These trait differences between ranges suggest that stabilizing selection on biomass, resource allocation, and flowering phenology imposed during or after introduction of this species may increase invasion success.

Keywords Evolution · Genetic variation · Life history traits · *Medicago polymorpha* · Rapid evolution

Introduction

Novel environments represent a multitude of challenges to which invading species must adapt, particularly when invaders are adapted to substantially different conditions in their native range (Parker and Gilbert 2007; Zenni and Nuñez 2013; Hui et al. 2016). Despite these challenges, potential invaders are often afforded clear advantages in new ecosystems, including naïve competitors or other natural enemies who may not be adapted to harm novel species and offer some release from antagonistic interactions relative to the native range (Keane and Crawley 2002; Lau and Strauss 2005; Maron et al. 2014). Although some invaders tend to invade habitats similar to the native habitat in which they evolved for long periods of time, many invaders spread to a variety of novel habitats with a range of climates and ecological

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interactions. The ability to spread to multiple habitat types depends on the ability of a species to cope with a variety of environmental conditions. Depending on the species, successful strategies can rely on phenotypic plasticity, selection on and evolution of inherited traits, or both (Davidson et al. 2011; Palacio-López and Gianoli 2011; Geng et al. 2016; Marchini et al. 2019).

Though evolution is often considered over very long time periods, there is extensive evidence that evolution often occurs on ecologically relevant time scales (Thompson 1998; Hairston et al. 2005; Schoener 2011). For invasive species, evolution on ecological time scales can be crucial for adaptation to a novel ecosystem (Maron et al. 2004; Lambrinos 2004). In one example, invasive St. John's wort (*Hypericum perforatum*) displayed changes in life history traits (size and fecundity) in response to environmental clines, indicating rapid evolution to new environments (Maron et al. 2004). Similarly, high genetic variation and repeated introductions of the invasive grass *Phalaris arundinacea* allowed for vegetative colonization ability and greater phenotypic plasticity to evolve in the invasive range (Lavergne and Molofsky 2007). Depending on the mode of introduction of a novel species, the invasion process may impose selection for greater dispersal, higher fecundity, larger size or competitive ability (defined here as the effect of an individual on its neighbors, as in Goldberg 1996), or other life history traits associated with invasion success (Jelbert et al. 2015).

Trait variation within a species has been recognized as an important driver of many ecological phenomenon, including niche selection and expansion, nutrient usage, competition, and community structure (Hughes et al. 2008; Agashe and Bolnick 2010). The spectrum between r and K life history strategies (MacArthur and Wilson 1967) is often considered to reflect differences among species, but is also relevant in considering differences among individuals within a species (Bolnick et al. 2011). Differences in life history strategies within a species may allow a species to fill more niche space—generalist species can be composed of a population of specialist individuals (Bolnick et al. 2003; Agashe and Bolnick 2010), as in the generalist American mink (*Mustela lutreola*) which specializes in local available prey (Sidorovich et al. 2001; Bolnick et al. 2003). Genetic diversity is also important for rapid evolution, as such diversity is required for natural selection to act upon. If high genetic diversity enables a population to respond to different types or strengths of species interactions (Vellend and Geber 2005) or utilize more resources and expand the range of the niche (Agashe and Bolnick 2010), we might expect some genotypes in the species to experience greater invasion success, or experience positive selection in a broader range of ecosystems.

Life history strategies have been shown to be important targets of selection in invasive species (Barrett et al. 2008), as adaptation to a new ecosystem requires considering evolution of linked and correlated traits in the community context in which invasion occurs (terHorst et al. 2018b). Because of ecological pleiotropy or genetically-linked traits, we must also consider selection on life history traits that promote invasion into a novel ecosystem. For example, an increase in fecundity, which is typically positively related to invasion success (Jelbert et al. 2015) may be selected for in an introduced population. However, if increased seed number is associated with decreased seed size, which decreases competitive ability, this presents a trade-off in life history strategies.

Medicago polymorpha, commonly known as burr clover or burr medic, is an invasive legume species that often competes with native species in its introduced range (Lau and Strauss 2005). *M. polymorpha* is endemic to the Mediterranean region, but has invaded six continents, predominantly spreading from its use in agriculture as a nitrifying cover crop (Porter and Simms 2014). Understanding *M. polymorpha* and the traits that facilitate invasion success can provide insight into how invasive plants shift from a native to invasive range and which traits lead to invasion success (Jelbert et al. 2015), and is important for limiting the spread of this invader into further habitats (Westbrooks 1998). Previous research has shown significant genetic variation in interactions between *M. polymorpha* and other species, including competitors, herbivores, and mutualists (terHorst and Lau 2015; Bayliss et al. 2017; Getman-Pickering et al. 2018; terHorst et al. 2018a). Such genetic variation, as well as the ability to experimentally replicate genotypes, presents the opportunity to compare genotypes of *M. polymorpha* that have been successful in the invasive and native ranges. We can use such comparisons to examine any differences in life history traits between

genotypes that were able to successfully establish in novel habitats and those genotypes successful in the native range. This can provide insight into potential evolutionary shifts that may have taken place during or after the invasion process and may have played a role in successful invasion by this species.

We used a greenhouse experiment to quantify differences in life history traits among and between genotypes from invasive and native ranges to examine extant variation in this species and consider a possible role of evolution in invasion success. In the absence of an adaptive radiation in the invasive range, we expected less trait variation among invasive range genotypes, assuming that seed stocks used in agricultural settings from which invaders have escaped around the world represent only a fraction of the genetic variation in the native range. However, it is possible that existing variation or new beneficial mutations in invasive range genotypes could have facilitated selection in response to a wider range of niche space in the invasive range relative to the Mediterranean climate experienced in the native range. Further, we expected invasive range genotypes to have greater overall biomass and fitness and earlier flowering phenology than native range genotypes, as these traits are often associated with invasion success in other species (Helliwell et al. 2018; Marchini et al. 2019). Finally, if invasive genotypes rely less on rhizobia mutualists and invest less in belowground growth, then we expected to see greater above:belowground biomass ratios in invasive range genotypes. Broadly, we hypothesized that we would see differences in mean traits and trait variation between invasive and native range genotypes of *M. polymorpha*.

Methods

Collection and rearing

We haphazardly selected 10 accessions of *Medicago polymorpha* from the native and invasive ranges of *Medicago polymorpha* (Bullitta et al. 1994), from the USDA Germplasm Resource Information Network collection, for a total of 20 genotypes (Table 1). Because these genotypes have been grown in greenhouses for several generations after collection from their natural environment, maternal effects should play little role in determining traits. As these plants are primarily selfing, which should result in homozygous clones after a few generations, we refer to each accession as a genotype.

We physically scarified seeds from each genotype and then planted them in 164 mL cone-tainers (Stuewe and Sons, Tangent, OR, USA) filled with low-nutrient soil (Sun-Gro Sunshine mix #5). Plants were grown in the greenhouse at California State University, Northridge. We planted three seeds in each cone-tainer and weeded the number of seedlings down to one per cone-tainer. This resulted in 240 total replicate cone-tainers (2 ranges × 10 genotypes × 12 replicates). Cone-tainers were randomly placed into racks and re-randomized periodically to ensure that no genotypes received uniform exposure to any conditions. Cone-tainers were watered every day for the first week and then every other day for the remainder of the experiment.

Halfway through the experiment, plants were fertilized once with Grow More fertilizer (Grow More Inc, Gardena, CA, USA; 20 N:20P:20 K) at 1/4 strength. During the experiment, we recorded the date

Table 1 USDA GRIN accession numbers for *Medicago polymorpha* with country of origin and range for each genotype

Genotype	Country of origin	Range	Genotype	Country of origin	Range
260270	Ethiopia	Invasive	170546	Turkey	Native
201206	Australia	Invasive	170547	Turkey	Native
197346	Russia	Invasive	170548	Turkey	Native
186329	Australia	Invasive	197345	Morocco	Native
186963	Uruguay	Invasive	197344	Malta	Native
186964	Uruguay	Invasive	198964	Cyprus	Native
197336	Australia	Invasive	206380	Cyprus	Native
197338	United States	Invasive	206695	Turkey	Native
197859	Uruguay	Invasive	239870	Morocco	Native
202809	Peru	Invasive	205428	Turkey	Native

on which each plant produced its first flower. We collected each fruit produced by each plant after fruits had ripened and quantified the number and weight of fruits per plant, as well as the number and weight of total seeds per plant. We harvested each plant when no fruits or flowers remained on the plant, which occurred between 140 and 169 days after planting. Plants that had not produced any flowers by this time were also harvested and noted to have not reproduced. Once harvested, we rinsed the soil from the roots of plants, separated aboveground and belowground portions, and placed them in a drying oven at 50 °C for two days. We then measured the total dry weight and the above:belowground biomass ratio.

Data analysis

We used generalized linear mixed models to test the fixed effects of range (native or invasive) and genotype (random effect nested within range) on several dependent variables in R (version 4.0.3). Our dependent variables were: survival to reproduction or the end of the experiment, time to first flower, fruit number, total fruit weight, seed number, total seed weight, total biomass, and above:belowground biomass ratio. For all variables except survival, data analyses were restricted to plants that survived. We tested each variable for normality and homogeneity of variances, and when possible, transformed the data to meet these assumptions and fit models using 'lmer' in the lme4 package. Biomass ratio was transformed by natural log and total biomass was transformed by inverse square root. When variables could not be transformed to meet assumptions, we fit appropriate error distributions using 'glmer'. Survival was analyzed using a binomial error distribution. Fruit and seed weight were analyzed with a Gaussian distribution with a log link. Fruit and seed number were analyzed using a zero-inflated distribution in the 'zeroinfl' package. We tested the significance of fixed effects using 'Anova' in the car package, with Type III sums of squares, and tested random effects using Likelihood Ratio Tests. We also calculated Cohen's d to determine effect size. To examine relationships between pairs of dependent variables, we used similar models with seed number as the dependent variable, but included each other dependent variable as a covariate in separate models. Using these models, we tested the linear and quadratic components of each pairwise

relationship with seed number, and examined whether these relationships differed between invasive and native ranges.

Results

Survival rate and time to flower

The survival of plants in the experiment was 67.5% across all ranges and genotypes. There was no significant effect of range on survival ($X^2 = 0.485$, df = 1, P = 0.486, d = 0.97), though there were significant differences among plant genotypes independent of range ($X^2 = 106$, df = 1, P < 0.001). One invasive genotype (186963 from Uruguay) experienced a 100% mortality rate, but six invasive genotypes and eight native genotypes experienced a 100% survival rate, with the remaining five genotypes showing intermediate survival. There was a marginally significant difference in flowering time between ranges ($F_{1,14} = 3.30$, P = 0.089, d = 2.56), with invasive genotypes tending to flower earlier than native genotypes. Though marginally significant, the effect size of genotype range was large (d = 2.56). However, there was also significant variation among genotypes within each range ($X^2 = 84.6$, df = 1, P < 0.001). There was more variation in flowering times among native genotypes—one native (239,870 from Morocco) and one invasive genotype (260270 from Ethopia) flowered earlier than any others, but two native genotypes were the last to flower (Fig. 1).

Mean total biomass and above:belowground biomass ratio

There were marginally significant differences in total biomass between native and invasive range individuals ($F_{1,15} = 4.21$, P = 0.058, d = 2.88), and significant differences among genotypes within ranges ($X^2 = 22.9$, df = 1, P < 0.001), with a large effect size of genotype range (d = 2.88). Despite significant variation within ranges, invasive genotypes tended to be smaller than native genotypes (Fig. 2A). Similarly, above:belowground biomass ratio was marginally significantly different between native and invasive ranges ($F_{1,160} = 3.17$, P = 0.07, d = 0.87). The difference in total biomass between ranges was due largely to differences in aboveground biomass, with invasive
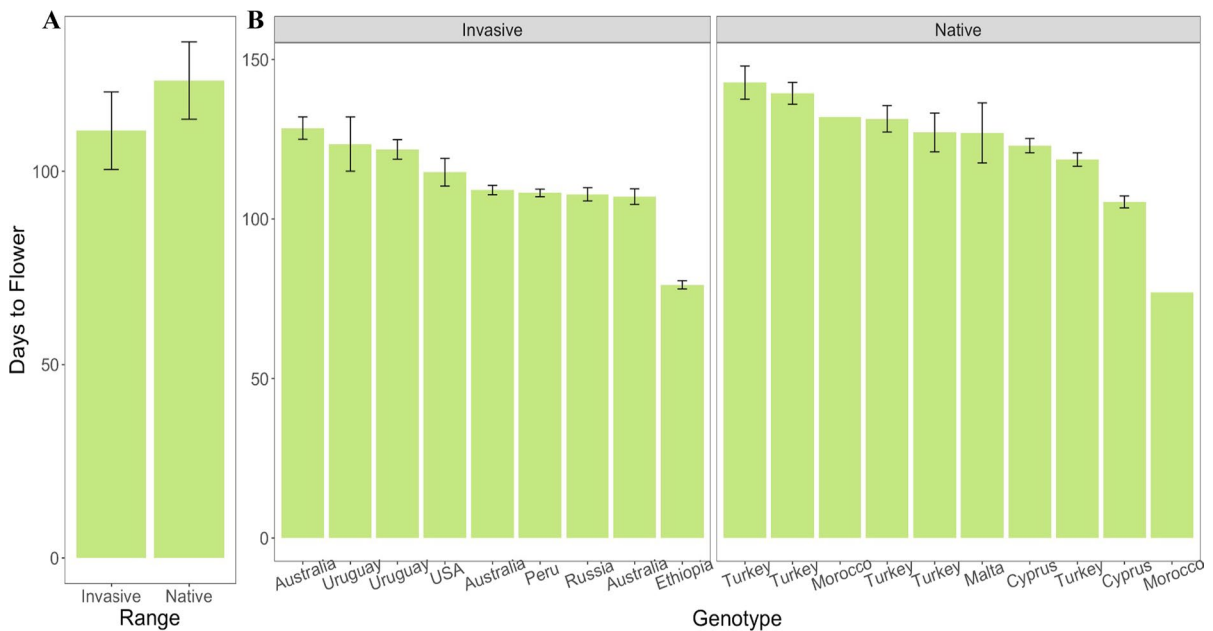
Fig. 1 Mean days to first flower ($\pm$ SEM) of **A** invasive and native range genotypes and **B** variation among genotypes within each range

genotypes investing relatively less in aboveground than belowground biomass compared to native range genotypes (Fig. 2B). As with total biomass, we observed significant difference among genotypes within ranges ($X^2 = 5.26$, df $= 1$, P $= 0.022$).

Fruit and seed production

Both fruit and seed number were significantly different between native and invasive ranges (Figs. 3, S1), with invasive genotypes producing more fruits ($X^2 = 10.2$, df $= 1$, P $= 0.001$, d $= 5.5$) and more seeds ($X^2 = 73.6$, df $= 1$, P < 0.001, d $= 14.04$). In addition to differences between ranges, genotypes also varied significantly in both fruit ($X^2 = 11.0$, df $= 1$, P < 0.001) and seed number ($X^2 = 76.4$, df $= 1$, P < 0.001). However, we found no significant differences in total fruit or seed weight between ranges (fruit weight: $X^2 = 1.14$, df $= 1$, P $= 0.286$, d $= 1.5$; seed weight: $X^2 = 1.97$, df $= 1$, P $= 0.161$, d $= 2.0$, Fig. S2). The disparity between quantity and quality of fruits and seeds does not seem to be due to a trade-off between number and size, as there is significant positive correlation between fruit number and weight ($F_{1,160} = 323$, P < 0.001) and between seed number and weight ($F_{1,160} = 1317$, P < 0.001). Rather, there

was more variability in weight than in number, resulting in decreased power to detect differences between ranges. There was significant variation among genotypes in fruit and seed number ($X^2 = 72.351$, df $= 1$, P < 0.001; Fig. 3).

Relationships among life history traits

We found only three cases in which the relationships between traits and fitness differed between the native and invasive range. All other relationships were non-significant (P > 0.05). There was a nonlinear relationship between seed number and total biomass ($F_{1,156} = 10.6$, P $= 0.001$), but the strength of that relationship differed among plants from the native and invasive ranges ($F_{1,156} = 53.2$, P < 0.001). Plants from the invasive range with intermediate biomass produced more seeds than plants with high or low biomass, but there was no such relationship for plants from the native range (Fig. 4A). Similarly, there was a significant non-linear relationship between seed number and above:belowground biomass ratio ($F_{1,156} = 11.9$, P < 0.001) that was stronger for plants from the invasive range ($F_{1,156} = 66.7$, P < 0.001). Invasive range plants with intermediate above:belowground ratios tended
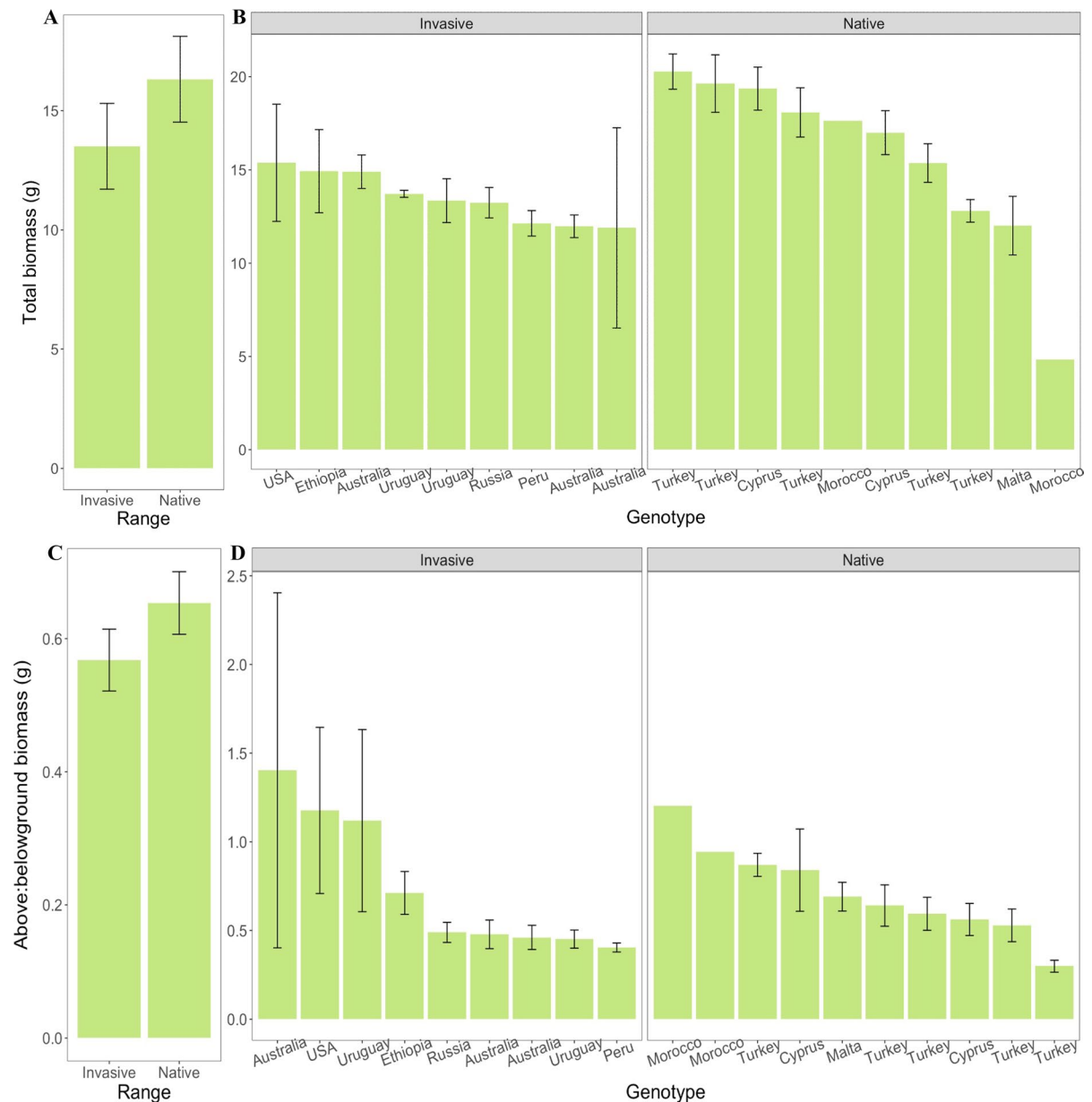
Fig. 2 Mean total biomass (± SEM) of **A** invasive and native range *M. polymorpha* genotypes and **B** variation among genotypes within each range. Mean above:belowground biomass ratios (± SEM) of **C** invasive and native range genotypes and **D** variation among genotypes within each range

to produce the most seeds, but this pattern was much weaker for genotypes from the native range (Fig. 4B). Finally, there was a significant non-linear relationship between seed number and flowering phenology, but the relationship differed depending on range ($F_{1,148} = 42.0$, $P < 0.001$). For invasive

range genotypes, plants that flowered at intermediate times produced the most seeds. However, for native range genotypes, the plants that flowered the earliest produced the most seeds (Fig. 4C).
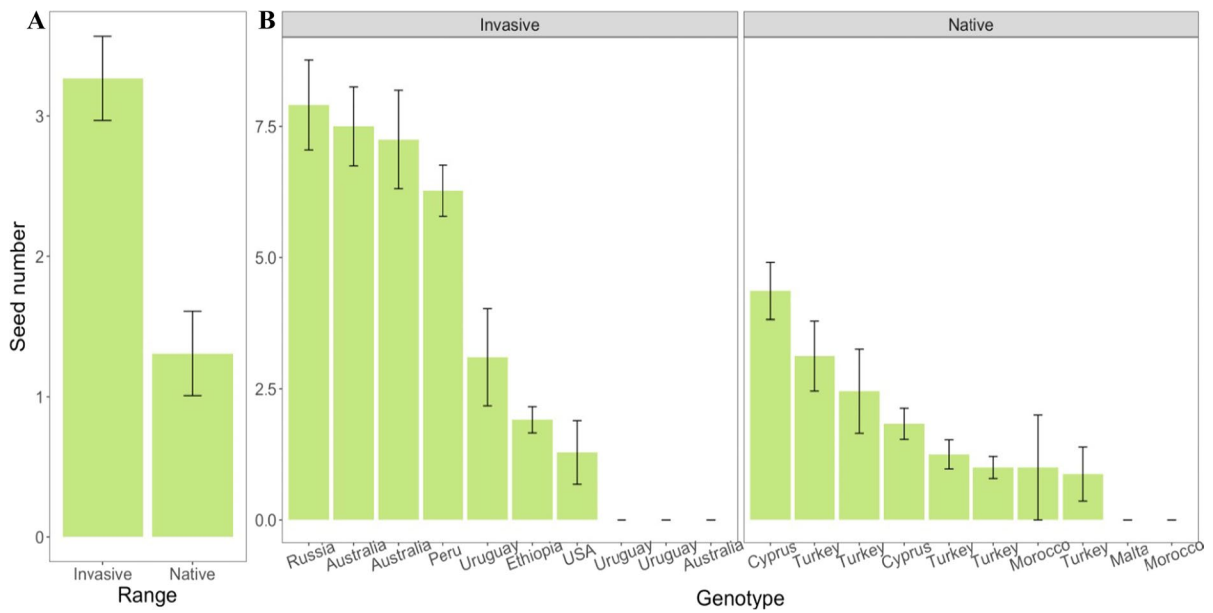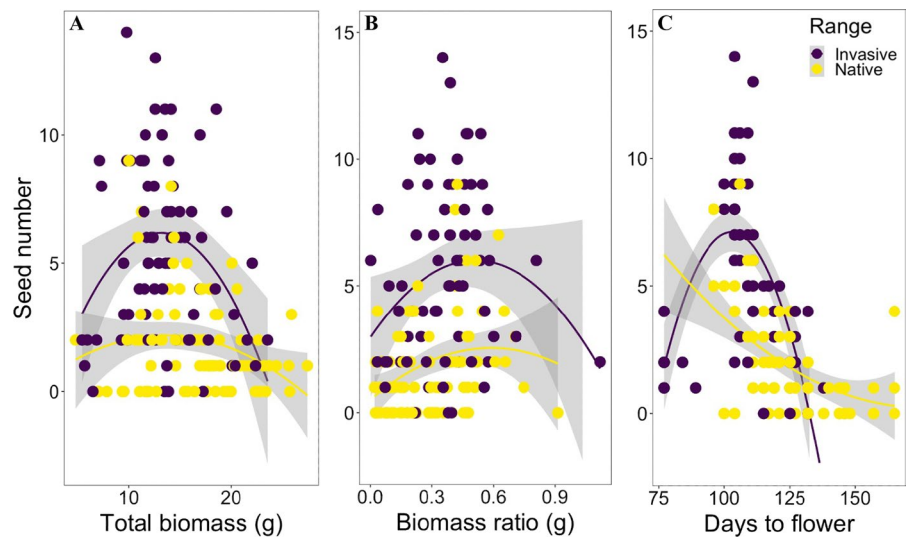
Fig. 3 Mean seed number (± SEM) of **A** invasive and native range genotypes of *M. polymorpha* and **B** variation among genotypes within each range

Fig. 4 Non-linear relationships between *M. polymorpha* seed number and **A** total biomass, **B** above:belowground biomass ratio, and **C** days to flower, for invasive and native range genotypes ± 95% CI

Discussion

We found differences in traits between genotypes collected from the native and invasive ranges of *Medicago polymorpha*. That all plants were grown in a common environment suggests that these traits are the result of genetic differences among native and invasive range plants that have evolved during or after the invasion process. Overall, invasive range genotypes tended to flower sooner, produced more fruits and seeds, and produced less biomass, primarily because of relatively less investment in aboveground growth relative to native genotypes. Such evolution could have occurred because of genetic drift if the introduction and success of individual genotypes in each collection location was random. However, consistent

differences between invasive and native genotypes from across the globe suggest that selection was more likely to have driven evolutionary changes. In addition to differences among ranges, we also found considerable variation within ranges, suggesting that both drift and selection could be important evolutionary forces during invasion at more local scales. Broadly, the traits that were consistently selected for in invasive genotypes regardless of geography, including fecundity, earlier flowering, and lower aboveground growth, may be traits that facilitate invasion into novel environments.

Invasive genotypes tended to have higher fecundity than native genotypes, producing greater numbers of fruits and seeds. Increased fecundity is often associated with increased invasion success because greater propagule pressure increases the likelihood of success by some of those propagules (Simberloff 2009; Lockwood et al. 2009). Jelbert et al. (2015) found that invasive plant species tended to be larger and had higher fecundity than closely related non-invasive plants, which has been demonstrated further in both invasive plant and animal species (Simberloff and Rejmanek 2011, 2020), though there are exceptions (Maron et al. 2004). The fitness advantages of producing more seeds are often limited if quantity trades off with quality, and higher quality seeds have a greater chance of germination or survival (Wen and Simons 2020). Although we did not observe such a trade-off between seed weight and seed number, we did observe more variation in seed weight than in seed number and the lack of a trade-off may other factors influencing the evolution of these two traits.

We found marginally significant differences in flowering time, biomass, and above:belowground biomass ratio between invasive and native ranges. These statistics suggest there is less than 10% chance that our null hypothesis of no differences between ranges is correct, so here we interpret these as real differences, but also note that these results should be interpreted with caution because of the variation within invasive and native ranges. Invasive genotypes tended to flower earlier than native genotypes, which may provide them with a reproductive advantage in highly seasonal environments where plants must reproduce quickly before conditions become unfavorable (Badri et al. 2016; Helliwell et al. 2018). Genotypes collected from the invasive range tended to be smaller than genotypes collected from the native

range, largely due to differences in aboveground size. This is contrary to many findings of increased size in the invasive range (Van Kleunen et al. 2010). Increased size in invasive plants is often thought to be a result of release from expensive investments in defense against natural enemies, and that energy can be reinvested into growth that confers increased competitive ability (Blossey and Notzold 1995). Although increased size is often used as a proxy for competitive ability, previous work on this species suggests that competitive ability is not well correlated with size (Getman-Pickering et al. 2018). Even if one assumed such a correlation, whether increased biomass confers greater competitive ability against native species in the introduced range would likely depend on whether competition occurs above or belowground. If competitors are indeed the agent of selection on size in the invasive range of *M. polymorpha*, then the increased investment in belowground biomass by invasive genotypes suggests that size is driven by competition for nutrients or rhizobia in the soil, rather than aboveground competition for light or space (Wang et al. 2017; Eisenhauer et al. 2017).

There may be still other agents of selection on belowground growth. The different strategies displayed by invasive and native genotypes may indicate that successful *M. polymorpha* invaders dedicate more resources to root growth, which may provide more nutrients to provision the highest possible number of fruits and seeds. If invasive genotypes rely less on rhizobia (terHorst et al. 2018a, b), they may need more extensive root growth to obtain nitrogen. This is in contrast to successful genotypes in the native range of *M. polymorpha*, which invest more resources into aboveground biomass production, perhaps at the cost of producing fewer fruit and seeds. Along a continuum between r and K life history strategies (MacArthur and Wilson 1967), native range *M. polymorpha* may be more like K-strategists, occupying a more stable ecosystem, and invasive genotypes may be more like r-strategists, moving between more unpredictable, potentially unstable ecosystems. Just as invasive species tend to fall more toward the r end of the r-K continuum (MacArthur and Wilson 1967; Devin and Beisel 2007), genotypes within a species that fall closer to the r end of the continuum may experience positive selection during invasion. Although this weedy strategy may give each individual seed a lower chance of survival, it may allow greater net fitness of

genotypes that cast a wider net across microclimates in novel environments.

In addition to the observed trait differences between invasive and native ranges of *M. polymorpha*, there were also large differences among genotypes within ranges. This confirms previous work in this species that documented different phenotypes among individuals, including plant height, trichome number, coloration, and fruit morphology (Bullitta et al. 1994; Graziano et al. 2009; Badri et al. 2016). In addition to the traits documented here, we observed differences in leaf pattern and color among genotypes that we did not quantify in this study. In addition to latitudinal clines in phenotypes in both the native and a portion of the invasive range, two distinct subpopulations of *M. polymorpha* have been identified in the native range (Helliwell et al. 2018), perhaps explaining some intra-range variation among genotypes. Additionally, there is likely to be some population structure within the invasive range, as many invasive range populations are isolated by large distances, but may also share the same source of introduction. Most genotypes in North and South America appear to have been introduced from the western Mediterranean region (Helliwell et al. 2018), but the origin of invasive genotypes on other continents is not yet known. Our results do not indicate that phenotypes in the broad invasive range are a subset of native range phenotypes, so it is possible that other continents have different origin sources. As most invasive populations are the result of escape from agriculture, knowing the source of cultivars in each location may explain some of this genotypic variation. Population structure will also likely depend on the time since the start of invasion and how long populations have been isolated from one another. Further, we do not see consistently greater variation among genotypes in either the invasive or the native range. Invasive genotypes showed more within-range variation in seed and fruit production, but less variation in days to flower and biomass than the native range genotypes. This gives an equivocal answer to whether trait variation is likely to have been driven by a population bottleneck in invasive populations or the result of adaptation to a range of ecosystems. Future exploration of selection on traits in specific populations of *M. polymorpha* in the invasive and native range, as well as identifying the original sources of various invasive populations, could help to explore these questions in greater depth.

We observed non-linear relationships between fitness (seed number) and three traits (biomass, biomass allocation, and flowering phenology), but these relationships were stronger in invasive range genotypes than in native range genotypes. For example, genotypes from the invasive range that flower too early or too late have lower fecundity, but for native range genotypes, only later flowering plants had lower fecundity. We must be cautious in inferring selection gradients from these patterns, as these genotypes were not collected from the same population and likely do not reflect variation within any single population (Kingsolver and Diamond 2011; Davidson et al. 2011). However, they were grown in the same environment in this study, albeit an artificial one. Taken at face value, these data suggest stabilizing selection in the invasive range, but either directional selection or no selection on the same traits in the native range. It would be useful to know if these patterns hold up in natural environments, and what, if any, the agents of stabilizing selection may be in those environments, and whether those agents of selection differ between native and invasive ranges (Kingsolver et al. 2001).

These trait differences between invasive and native ranges provide evidence of which traits may have allowed *M. polymorpha* to successfully invade non-native habitats. Understanding the traits that allow plants to become invasive can enhance strategies to limit or prevent invasion (Maron et al. 2004; Van Kleunen et al. 2010; Minoarivelo and Hui 2016). Differences in traits like flowering phenology, fecundity, biomass, and biomass allocation may have important implications for how to control invasion spread (Cannas et al. 2003; Eschtruth and Battles 2009). Moreover, our results suggest that understanding how these traits evolve during or after invasion may be critical to understanding how plants are able to initially colonize new environments, or proliferate after they have been introduced. The global differences we found between native and invasive range genotypes may reflect those traits that increase invasion success broadly, but it does not preclude that other traits may be just as or more important at the local scale. Future studies of selection on traits at individual locations may lead to greater understanding of how populations of this species adapt to specific biotic and abiotic conditions. Understanding these evolutionary changes

on ecological time scales in more invasive species will provide a broader understanding of the role of evolution in invasion dynamics.

Declarations

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