



Phenotypic differentiation among native, expansive and introduced populations influences invasion success

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Funding information

USDA Forest Service, Grant/Award Number: 19-DG11083150-006; Basque Government, Grant/Award Number: IT936-16; USDA Animal and Plant Health Inspection Service, Grant/Award Number: P37-19-02283

Handling Editor: Daniel Chapman

Abstract

Aim: Humans influence species distributions by modifying the environment and by dispersing species beyond their natural ranges. Populations of species that have established in disjunct regions of the world may exhibit trait differentiation from native populations due to founder effects and adaptations to selection pressures in each distributional region. We compared multiple native, expansive and introduced populations of a single species across the world, considering the influence of environmental stressors and transgenerational effects.

Location: United States Gulf and Atlantic coasts, United States interior, European Atlantic and Mediterranean coasts, east coast of Australia.

Taxon: *Baccharis halimifolia* L. (eastern baccharis).

Methods: We monitored seed germination, seedling emergence, survival and early growth in a common garden experiment, conducted with over 18,200 seeds from 80 populations. We also evaluated the influence of environmental stress and maternal traits on progeny performance.

Results: Introduced European Atlantic populations had faster germination and early growth than native populations. However, this was not the case for the more recently naturalized European Mediterranean populations. Introduced Australian populations

grew faster than native populations in non-saline environments but had lower survival in saline conditions commonly encountered in the native range. Similarly, expansive inland US populations germinated faster than coastal native populations in non-saline environments but grew and germinated more slowly in saline environments. Maternal inflorescence and plant size were positively related with seed germination and seedling survival, whereas flower abundance was positively correlated with seedling early growth and survival. However, maternal traits explained a much lower fraction of the total variation in early demographic stages of *B. halimifolia* than did distributional range.

Main conclusions: Phenotypic differentiation could allow *B. halimifolia* to adapt to different biotic and abiotic selection pressures found in each distributional range, potentially contributing to its success in introduced and expansive ranges.

KEYWORDS

Baccharis halimifolia, common garden experiment, distributional ranges, founder effects, introduced species, local adaptations, maternal traits, selection pressure

1 | INTRODUCTION

The native distributional range of species is shaped over millions of years by natural dispersal mechanisms (e.g. wind, animals and water) and biogeographical barriers (e.g. mountain ranges and oceans; Robinson et al., 2017). However, over the last few centuries, humans have greatly influenced species distributions by modifying the environment and by dispersing species beyond their natural ranges (Essl et al., 2019; Lucardi et al., 2020; Pyšek et al., 2004; Vitousek et al., 1997). As a result, many species now have populations throughout the world, each with different historical trajectories (e.g. changes in population size and genetic variation) and variable selection pressures that can drive adaptation to local conditions. These novel combinations of evolutionary forces can result in phenotypic differentiation among populations in different distributional ranges. For example, phenotypic changes among populations could be attributed to the evolution of geographic clines due to different biotic and abiotic conditions present in each of the species' distinct modern distributional ranges (e.g. climate, soil, pathogens, herbivores; Maron et al., 2004; Rundle & Nosil, 2005).

Within this general context of phenotypic divergence between native and introduced ranges, numerous specific mechanisms have been demonstrated for introduced species around the world. For example, species may be released from their natural enemies when introduced into new distant ranges, which can promote a shift in resource allocation from enemy defence to increased growth and/or reproduction; the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold, 1995; Colautti et al., 2004). Species may also change their morphology in response to differences in resource availability or climate between native and introduced ranges (Brandenburger et al., 2019; Maron et al., 2004). Phenotypic changes in isolated founder populations may also be caused by the loss of allelic variation that accompanies the founding of a new population

from a very small number of individuals (Emlen & Zimmer, 2019). Genetic drift and inbreeding depression can exacerbate the loss of allelic diversity and can, therefore, increase phenotypic change (Emlen & Zimmer, 2019). Time since introduction and naturalization (i.e. formation of a self-sustained population) of a species into a new region can also contribute to phenotypic changes. This may result from the species initially being poorly adapted to the novel environmental conditions of the introduced region and taking some time to undergo genetic differentiation and demographic explosion (Crooks, 2005; Müller-Schärer & Steinger, 2004). Once populations increase in size, selection can have a stronger effect on allele frequencies and phenotypes (Emlen & Zimmer, 2019).

Mechanisms that drive phenotypic change in introduced ranges may be different from those that act on expanding populations that follow human-induced environmental changes near the historic native range. Range expansions are usually driven by a small number of individuals occurring along the leading edge of the native range. These individuals are often less genetically diverse than those in the central part of the range (founder effect) but could be pre-adapted to the environmental conditions of the nearby expansive range (Essl et al., 2019; Excoffier et al., 2009; Pujol & Pannell, 2008). In contrast, populations introduced to new geographic regions can include individuals drawn from genetically different source populations, allowing novel admixtures of genetic material (Shirk et al., 2014; Essl et al., 2019; but see Hagenblad et al., 2015). These changes in genetic diversity, along with variation in both biotic and abiotic selection pressures affecting populations, can greatly affect the phenotypes of species throughout their global distributions.

Common garden experiments, in which individuals from different distributional ranges are grown together in a common environment, are critical to study what ecological traits may be promoted by underlying genetic variation in different populations. The genetic basis for phenotypic variation might become evident if the offspring



from different populations differ significantly in the ecological characteristic(s) of interest when subjected to identical environmental conditions (Bossdorf et al., 2005). Therefore, a common garden experiment can reveal whether observed phenotypic variation among populations is more closely correlated with environmental factors or genetic variation among those populations, by minimizing environmental variation among the experimental units (Leger & Rice, 2003). It is important to note that parental traits can also influence offspring phenotypes (Baskin & Baskin, 1998; Lázaro-Lobo et al., 2020; Sletvold, 2002; Wulff, 1995). Thus, common garden experiments should either choose offspring from similar parental individuals or account for parental traits.

In this study, we asked whether populations of *Baccharis halimifolia* have undergone phenotypic differentiation in germination and early growth across its present distributional range. *Baccharis halimifolia* is a coastal North American shrub that is expanding its native range northwards into interior areas of the United States (US) and has been widely introduced in Europe and Australia. We focused on germination and early growth/survival because they are key survivorship life phases and early mortality usually outstrips mortality at adult stages (Augspurger, 2013; Osland et al., 2015; Sakai & Larcher, 1987). Therefore, a strategy of rapid germination and faster growth is widely considered beneficial for range expansion and successful invasions of new areas (Erfmeier & Bruehlheide, 2005; Hirsch et al., 2012). Previous research conducted at local spatial scales demonstrated profound impacts on *B. halimifolia* germination and early growth from environmental stress (e.g. shade and salinity) and transgenerational effects (Calleja et al., 2019; Caño et al., 2016; Lázaro-Lobo et al., 2020; Tolliver et al., 1997; Young et al., 1994). However, this is the first study, to our knowledge, conducted with any single species that compares multiple native, expansive and introduced populations across the world, considering environmental stressors that mediate trait differentiation as well as transgenerational effects.

To evaluate our overarching hypothesis that *Baccharis halimifolia* has undergone phenotypic differentiation among populations across its present distributional range, we carried out a common garden experiment with plants from native, expansive and introduced populations of *B. halimifolia*. Our test of this central hypothesis was accomplished via a suite of observational and experimental assessments of maternal and environmental influences on progeny performance. Because the historic/native distribution of *B. halimifolia* comprises maritime coastal environments, we evaluated the influence of distributional range on offspring performance under different salinity levels as well as the effect and relative importance of maternal traits on progeny performance. The specific hypotheses that we tested in these analyses were that:

- Germination and early growth/survival of offspring from introduced and expansive populations would differ from native populations due to founder effects and adaptations to different biotic and abiotic selection pressures in their respective distributional ranges. We expected that (a) offspring from the expansive and introduced distributions would exhibit faster growth rates

(potentially as a result of selection on individuals capable of faster invasion), and (b) expansive inland populations would have lower tolerance to salinity than native coastal populations (potentially due to adaptation to inland environments with low soil salinity).

- Maternal traits would have a significant influence on early demographic stages of *B. halimifolia*, but a lesser influence than distributional range of origin, because genetic histories associated with distributional range of origin are expected to exert their influence at a broader spatiotemporal scale than maternal traits. We expected that offspring from larger maternal shrubs with larger inflorescences and more flower heads would germinate faster and show faster growth due to higher resource acquisition and higher resource allocation into reproductive effort.

2 | MATERIALS AND METHODS

2.1 | Study species

Baccharis halimifolia is a facultative halophytic shrub that can grow in a wide range of environmental conditions, which allows it to colonize multiple ecosystems such as wetlands, forests, prairies and roadsides (Lázaro-Lobo et al., in press). This species is especially adapted to pioneer stages of succession and benefits from natural and anthropogenic disturbances (Westman et al., 1975). Previous research has documented the numerous ecological, economic and social impacts that *B. halimifolia* causes in the invaded areas, including interference with human resource provision and alterations of ecosystem composition and function (Campos et al., 2004; Fried et al., 2016; Lázaro-Lobo et al., in press). Thus, *B. halimifolia* is considered a very deleterious invasive plant for native ecosystems (Fried et al., 2016; Herrera et al., 2017).

Baccharis halimifolia was first cultivated in Europe in different botanic gardens during the 1600s and 1700s (Caño et al., 2013). However, it was not until the 1800s that *B. halimifolia* was widely introduced in Europe for ornamental use, soil stabilization and windbreaks (Caño et al., 2013; Fried et al., 2016). In the European Atlantic coast, *B. halimifolia* became naturalized (i.e. formation of self-sustaining populations) during the early 1900s (1900–1920) and it was already considered as locally invasive and spreading rapidly in the 1940s, except for the North Sea coast where it started spreading in the 1990s (Fried et al., 2016; Rappé et al., 2004). However, *B. halimifolia* did not become naturalized along the European Mediterranean coast until the early 1980s (Fried et al., 2016). In Australia, *B. halimifolia* was introduced in 1888 and became naturalized in coastal areas of southeastern Queensland by the 1930s (Bailey, 1899; Sims-Chilton & Panetta, 2011). Then, *B. halimifolia* spread both northwards and southwards in the 1970s (Sims-Chilton & Panetta, 2011), suggesting that it had overcome the 'lag phase', if it had one, of the theoretical invasion process by that time. However, 14 biological control agents (including pathogens and insects) have been released into Australia since 1969, and seven have successfully established in that range (Sims-Chilton et al., 2009). *Baccharis*

halimifolia has declined in abundance over the past 60 years in the Australian range, possibly due to the early action of biological control agents and a decrease in the climatic suitability of the invaded areas (pers. obs.; Sims-Chilton et al., 2010).

2.2 | Plant material

We selected a total of 80 *Baccharis halimifolia* populations from areas along the Gulf of Mexico and Atlantic coasts of the US (native range), the interior of the US (Tennessee and northern parts of Mississippi, Alabama, and Georgia; expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges; Figure 1). We divided the native range into two parts (Gulf and Atlantic coasts of the US) because they have different environmental conditions (e.g. climate and biotic communities; Soltis et al., 2006) and *B. halimifolia* is deciduous in the cooler parts of its distributional range (Sims-Chilton & Panetta, 2011), which could impact offspring phenotype. For each *B. halimifolia*

population, we collected morphological data and achenes from two shrubs with different basal stem diameter (<50 and >70 mm) to introduce maternal trait variation, except for a few instances where all female shrubs with achenes in the population had similar basal stem diameter (seven populations). We measured height, canopy width and basal stem diameter of the mother shrubs as surrogates of maternal shrub size. Age was estimated by stem node counts in the longest branch of the shrubs, as shown in previous research (Caño et al., 2014; Lázaro-Lobo et al., 2020). We also randomly selected a maximum of 12 inflorescences in the mother shrubs to measure inflorescence length and width and count the number of flower heads per inflorescence as well as the number of seeds within a maximum of 24 intact flower heads, depending on the number of inflorescences and flower heads available. Data collection was conducted in 2019, during the seed production period in autumn, which occurred during May–June in Australia and October–December in the US and Europe.

We air-dried and stored the collected seeds in paper bags at room temperature (18–25°C) until 1 week before sowing. Then, the

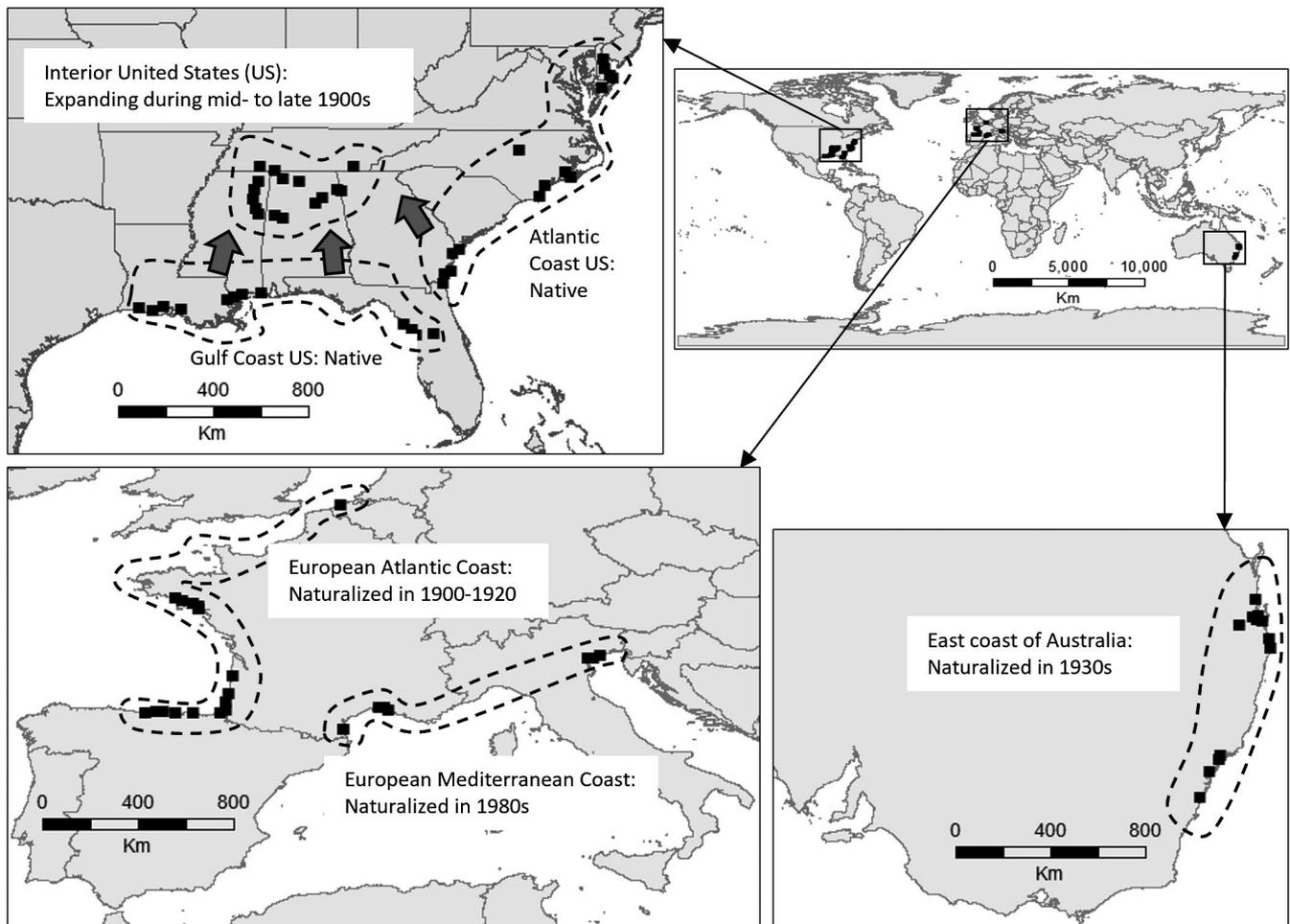


FIGURE 1 Location of the surveyed *Baccharis halimifolia* populations (indicated with black squares). For each population, we collected morphological data and achenes of the selected mother shrubs. Distributional ranges include the Gulf and Atlantic coasts of the United States (US; native range), the interior of the US (expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges). The world map shapefiles are projected in WGS 1984 and were extracted from the GADM database (www.gadm.org), version 3.4, April 2018



seeds were cold stratified at 5°C for a week to obtain maximum germination rates (Westman et al., 1975). The common garden experiment was carried out for 3 months, between 8 April and 8 July 2020, at Mississippi State University. As a result, the Australian seeds were stored approximately 6 months longer than those for the US and Europe.

2.3 | Seed germination and seedling emergence experiments

A total of 18,240 seeds were sown to evaluate offspring germination and emergence under non-saline (0 g NaCl L⁻¹) and saline conditions (10 g NaCl L⁻¹). The concentration for saline conditions was based on results from our previous work with this species (Lázaro-Lobo et al., 2020). Saline conditions were created using Instant Ocean® synthetic sea salt, which simulates natural seawater. We used microplates that contained 16-mm diameter wells to carry out the experiment and used six wells per mother shrub and treatment. We placed 10 seeds in each well on filter paper (Whatman® qualitative filter paper, Grade 1) at equal distances apart. The microplates were randomly placed in a growth chamber (Lab-Line Instruments, Inc.) and subjected to a regime of 16 h of light (10–12 μmol m⁻² s⁻¹), a day/night temperature of 24/18°C, and a relative humidity of 20%. We then re-randomized the microplates daily and added deionized water in the wells that lost water by evaporation to maintain the initial water levels. Microplates were inspected every 5 days to count germinated and emerged seeds over one month. Seeds were considered germinated if at least 2 mm of radicle was present and the criterion of emergence was the appearance of the hypocotyl or stem (Lázaro-Lobo et al., 2020).

2.4 | Early seedling growth experiment

Two to 3 weeks after the initiation of germination and emergence experiments, we transplanted up to 12 seedlings per mother shrub and treatment into germination trays containing six cells that measured 3.8 × 3.8 × 5.7 (deep) cm. The cells had drainage holes at the bottom and were filled with a soil substrate (Sta-Green Potting Mix) that contained necessary nutrients for plant growth for up to 9 months. The germination trays were randomly placed in the greenhouse and subjected to a regime of 16 h of light (19–21 μmol m⁻² s⁻¹), a day/night temperature of 21–32/16°C and a relative humidity of 70%. The positions of germination trays were re-randomized every week to avoid greenhouse position effects. Seedlings were subjected to the same salt solutions as in the previous experiment. Saline conditions (10 g NaCl L⁻¹) were now created by watering the germination trays twice per week until the water drained through the drainage holes to maintain similar concentrations of salinity throughout the experiment. Soil salinity was checked every 2 weeks using a conductivity metre (Apera Instruments®) to verify that salinity levels were stable over time.

We sampled the seedlings at 2 and 3 months from the beginning of the germination and emergence experiments. We measured survival of the transplanted seedlings at month 2 and left one seedling per cell to evaluate seedling height, width (at their greatest extent) and leaf number. At month 3 we evaluated survival of the seedlings left in at month 2, as well as height, width, number of leaves and above- and below-ground dry biomass of the survivors.

2.5 | Statistical analyses

All statistical analyses were conducted using the program R (version 3.6.1; R Core Team, 2020). We used generalized linear mixed models (GLMMs) to evaluate the effect of distributional range, maternal traits and salinity on seed germination, seedling emergence, survival and early seedling growth. Mother shrubs were nested within their population of origin for the analyses and were treated as a random effect. We also considered microplate ID as a random effect in the germination and emergence experiments. We used the 'glmmTMB' R package (Magnusson et al., 2017) with the appropriate data distribution for each response variable to build the GLMMs, following the guidelines for mixed models (Zuur et al., 2009). Seed germination, seedling emergence and survival were tested using the binomial distribution, whereas leaf number was evaluated with the Poisson distribution. Seedling height, width and above- and below-ground biomass were examined with gamma distribution because, due to the skewness of their data distributions, the model residuals were not normally distributed and we obtained lower AIC values when compared to the models with Gaussian distribution.

We analysed response variables at each sampling time. We also conducted repeated-measure analyses with time as a fixed factor to account for observations of germination and emergence at multiple periods of time. For the analysis regarding distributional range of origin, we conducted post-hoc comparisons of estimated marginal means calculated using the 'emmeans' R package (Lenth et al., 2020) with Bonferroni's adjustment, which is appropriate to declare statistical significance ($p < 0.05$) in multiple comparison testing analyses (Cabin & Mitchell, 2000). Before conducting the GLMMs, we tested collinearity among maternal traits with Spearman's correlations, and retained those variables that were not highly correlated with each other; Spearman's $r < 0.5$, sensu Dormann et al. (2013). We excluded those maternal traits that were less important to explain offspring performance (e.g. age and basal stem diameter), based on previous research (Lázaro-Lobo et al., 2020). Lastly, we conducted variation partitioning analyses to evaluate the fraction of the variance explained by distributional range alone, maternal traits alone and their joint effects (Legendre & Legendre, 2012). We used the `varpart()` function of the `vegan` package for variation partitioning analyses (Oksanen et al., 2019) because it considers adjusted R-squared values. We included all the evaluated maternal traits in these analyses because collinear variables do not have to be removed prior to partitioning (Oksanen et al., 2019).

3 | RESULTS

3.1 | Effect of distributional range on offspring performance

Introduced European Atlantic populations had faster germination rates than native coastal US populations and all the other introduced populations, especially in non-saline environments ($p < 0.05$; Figure 2, Figure A1, and Table A1). Progeny from introduced populations growing along the European Mediterranean coast had the lowest germination and emergence values (~15%). Offspring from expansive interior US populations yielded the highest germination and emergence (~70%) when subjected to a non-saline environment.

Seedling survival of introduced European Mediterranean populations in non-saline environments was ~45% lower ($p < 0.02$) than the rest of distributional ranges at month 2, whereas nearly all the seedlings left in month 2, across all distributional ranges, survived until the end of the experiment (Figure 3 and Table A1). Seedlings from introduced European Atlantic populations in non-saline conditions also were ~1 cm taller ($p < 0.03$) by the end of the study than individuals from the rest of distributional ranges, except for Australia, which were ~0.4 cm taller than the native coastal US and the expansive inland US populations ($p < 0.02$; Figure 4, Figure A2, and Table A1).

Offspring from introduced European Atlantic populations had ~0.4 cm wider width than other distributional ranges ($p < 0.03$), and Australian seedlings had ~0.15 cm wider width than native seedlings ($p < 0.02$). Offspring from introduced European Atlantic and Australian populations also produced ~1 more leaf than plants originated from the native coastal US and expansive inland US ranges ($p < 0.03$). Seedlings from introduced European Atlantic populations had ~5 mg more above-ground biomass and ~7 mg more below-ground biomass at the end of the experiment than seedlings from native and expansive populations ($p < 0.001$; Figure 5 and Table A1). Introduced Australian seedlings also had ~4 mg more below-ground biomass than native and expansive US populations, while

above-ground biomass was ~3 mg higher in the Australian seedlings than native US Gulf coast and expansive US populations ($p < 0.05$).

Under saline conditions, expansive inland US populations had lower germination percentages than native coastal US and introduced European Atlantic populations during the first days after sowing ($p < 0.02$; Figure 2 and Table A1). As time since sowing under saline conditions passed, offspring from different distributional ranges reached similar germination and emergence percentages (~35%), except for the seeds from introduced Mediterranean Europe (~12%). This region consistently had lower germination than native, expansive and introduced European Atlantic populations. In saline environments, introduced Australian populations had ~40% lower seedling survival than introduced European Atlantic and expansive inland US populations at month 2, and at month 3 had ~30%–60% lower survival values than all the other ranges, except for expansive inland US ($p < 0.03$; Figure 3 and Table A1). Offspring from expansive US populations also had ~30% lower survival than those from the native US Atlantic coast and introduced Atlantic Europe at month 3 ($p < 0.03$).

As for early growth in saline environments, seedlings from expansive inland US were ~0.25 cm shorter than seedlings from the other distributional ranges, except for Mediterranean Europe ($p < 0.002$; Figure 4, Figure A2, and Table A1). However, seedlings were significantly wider when grown from seeds produced by the introduced European Atlantic populations, compared to expansive inland US populations (~0.2 cm wider; $p < 0.03$). Introduced populations from Atlantic Europe also were ~0.2 cm wider than introduced Mediterranean populations at month 2 ($p < 0.009$). Moreover, seedlings from introduced Atlantic Europe and native coastal US produced ~1 more leaf than seedlings from expansive inland US at month 2 ($p < 0.007$). Expansive populations also had ~1–3 mg lower above-ground biomass and ~0.5–1.5 mg lower below-ground biomass than the rest of the populations, except for Mediterranean Europe, which had similar above-ground biomass values ($p < 0.001$; Figure 5 and Table A1). Below-ground biomass was also ~1 mg higher

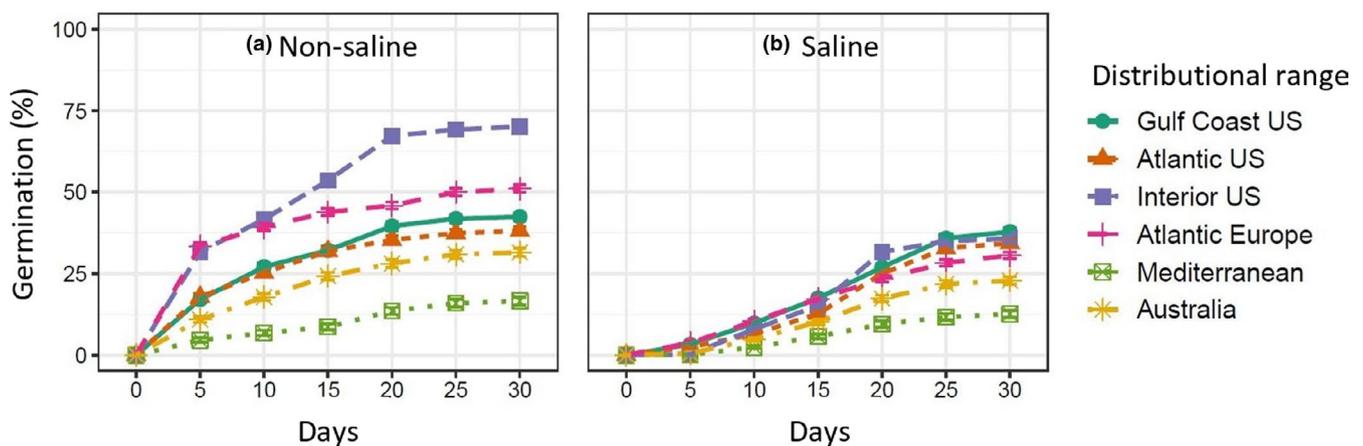


FIGURE 2 Mean percentage of cumulative seedling germination among distributional ranges over time under non-saline and saline (10 g NaCl L⁻¹) conditions. Distributional ranges include the Gulf and Atlantic coasts of the United States (US; native range), the interior of the US (expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges). See Table A1 for statistical differences among distributional ranges

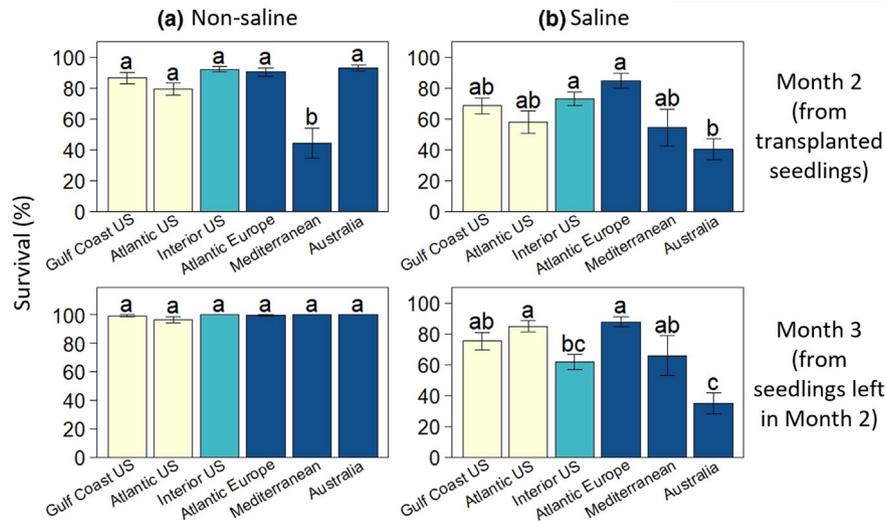


FIGURE 3 Mean percentage seedling survival 2 and 3 months after sowing, among distributional ranges and under non-saline and saline (10 g NaCl L^{-1}) conditions. Survival at month 2 was measured from the seedlings initially transplanted for the early growth experiment, whereas survival at month 3 was measured from those seedlings left in at month 2. Different letters indicate statistically significant differences among distributional ranges (Bonferroni-adjusted p -value < 0.05). Error bars represent standard errors (SE). Distributional ranges include the Gulf and Atlantic coasts of the United States (US; native range), the interior of the US (expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges)

in all the introduced populations (European Atlantic, Australian, Mediterranean) than in native US Gulf coast populations ($p < 0.001$).

3.2 | Effect of maternal traits on offspring performance

Maternal characteristics had a significant influence on early demographic stages of *B. halimifolia*. Inflorescence traits had a greater effect than shrub size on the evaluated variables. Inflorescence size had a positive effect on seed germination and seedling emergence in both saline and non-saline environments, whereas the number of flower heads per inflorescence was negatively associated with germination and emergence under saline conditions ($p < 0.05$; Table A2). However, we found the opposite pattern for early seedling growth in non-saline environments. We found that seedlings from shrubs with shorter inflorescences and more flower heads were significantly taller, wider, produced more leaves and above- and below-ground biomass ($p < 0.05$). In saline environments, seedling survival was also significantly higher for individuals that came from larger maternal plants with more flower heads per inflorescence.

3.3 | Relative importance of distributional range maternal traits on offspring performance

The distributional range of origin explained a larger fraction of total variation (14% on average) than maternal traits (0.7% on average) in all the evaluated variables, except for survival at month 3 under non-saline conditions (Table A3). Maternal traits alone did not explain a

significant fraction of the variance ($p > 0.05$) in any variation partitioning models. However, joint effects of distributional range and maternal traits significantly contributed to explain total variation in most of the models and accounted for the highest proportion of the variation in early seedling growth (21%–37%) in non-saline environments.

4 | DISCUSSION

Our results from this common garden experiment show that distributional range of origin, transgenerational effects and environmental stress have complex and profound effects on early demographic stages of *B. halimifolia*, influencing seed germination, seedling growth and seedling survival. Distributional range of origin (native, expansive or introduced) was more influential than maternal traits on seed germination and early seedling growth, suggesting that the genetic history of introduced populations can have persistent effects on individual responses of invasive species to local environmental variation. Furthermore, salinity highly influenced the relative performance of offspring from these different distributional ranges. This study emphasizes the need to compare trait change and response to environmental stressors among multiple native, expansive, and introduced populations to provide insights into the invasion process and local adaptations.

Native populations from the Gulf and Atlantic coasts of the US displayed similar patterns in their early demographic stages and response to salinity, which suggests little variation in germination and early growth of *B. halimifolia* in both saline and non-saline environments across the native distributional range. However, we found high variability in the performance of *B. halimifolia* offspring among the expansive and introduced ranges. Counter to predictions, not all introduced

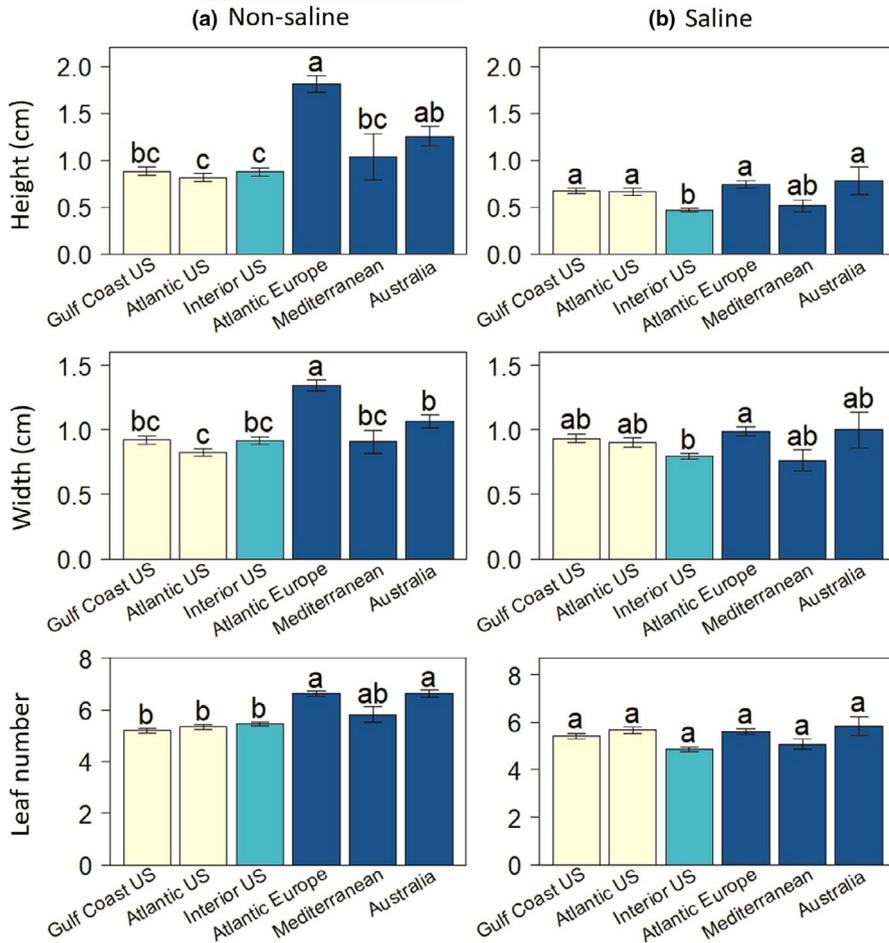


FIGURE 4 Mean seedling height, width and leaf number at 3 months after sowing, among distributional ranges and under non-saline and saline (10 g NaCl L⁻¹) conditions. Different letters indicate statistically significant differences among distributional ranges (Bonferroni-adjusted *p*-value < 0.05). Error bars represent standard errors (SE). Distributional ranges include the Gulf and Atlantic coasts of the United States (US; native range), the interior of the US (expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges)

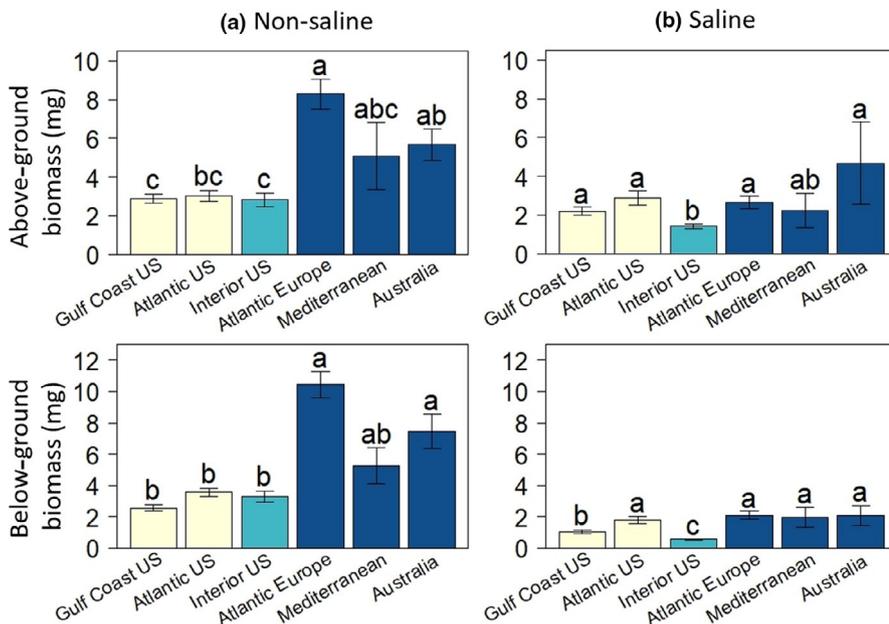


FIGURE 5 Mean above- and below-ground biomass of seedlings at 3 months after sowing, among distributional ranges and under non-saline and saline (10 g NaCl L⁻¹) conditions. Different letters indicate statistically significant differences among distributional ranges (Bonferroni-adjusted *p*-value < 0.05). Error bars represent standard errors (SE). Distributional ranges include the Gulf and Atlantic coasts of the United States (US; native range), the interior of the US (expansive range), the Atlantic and Mediterranean coasts of Europe and the east coast of Australia (introduced ranges)

populations showed faster rates of germination and growth than native populations. European Atlantic populations had greater above- and below-ground biomass and faster germination, emergence and growth when compared to the native populations. Australian populations grew faster and accumulated more biomass than native populations in non-saline environments but had lower survival in saline conditions.

However, populations from Mediterranean Europe had lower germination, emergence and survival rates than native populations.

Phenotypic changes in *B. halimifolia* could be due to founder effects in introduced populations, as well as due to adaptations to different biotic and abiotic selection pressures that occur in their respective distributional ranges. Introduced populations may need time to adapt to



the novel environmental conditions of the introduced range prior to expanding their distributions; the so-called 'lag time' or 'lag phase' (Crooks, 2005; Müller-Schärer & Steinger, 2004). The populations from Atlantic Europe and Australia became naturalized much earlier than those from Mediterranean Europe, thus, they have experienced more time to overcome possible founder effects and adapt to local conditions. The suggested adaptation to local conditions in introduced European Atlantic and Australian populations could have increased the germination and growth rates, compared to native populations, as shown in previous research conducted with other species (e.g. Caño et al., 2008; Erfmeier & Bruelheide, 2005; Jakobs et al., 2004; Leishman et al., 2014; Siemann & Rogers, 2001). Such shifts towards faster growth have frequently been attributed to the enemy release hypothesis and EICA, which predict that the absence of coevolved enemies in the new introduced range will promote a shift in resource allocation from defence to increased growth, reproduction and competitive ability. Competitive ability at the stage of seed germination and seedling early growth can strongly determine species abundance (Gurevitch et al., 2002; Howard & Goldberg, 2001). Thus, the evolution of increased competitive ability of *B. halimifolia* in introduced European Atlantic and Australian populations could have increased its invasion success across these distributional ranges. We have preliminary evidence, discussed below, to suggest this process may also be occurring in the expansive range.

Expanding populations from the interior US had superior germination and emergence rates than coastal native populations in non-saline environments, but lower biomass production and slower germination, emergence and growth than native populations in saline environments. This finding suggests selection for individuals adapted to non-saline conditions in this region of relatively rapid expansion out of the historic native range, corroborating the results from previous research conducted at a much smaller scale (Lázaro-Lobo et al., 2020). Anthropogenic disturbances such as reductions in tree canopy cover and increases in edge habitat have facilitated the range expansion of *B. halimifolia* towards interior areas of the US during the last century (Duncan, 1954; Ervin, 2009; Estes, 2004). The favourable climatic conditions of this region of the world, such as warm temperatures and abundant rainfall, allow the colonization of competitive early-successional species in disturbed areas (Oswalt et al., 2015). Competition with other fast-growing species could have driven selection for faster germination rates of *B. halimifolia* in the expansive range, at the expense of reduced tolerance to salinity. Considering its expansion into the interior US, the loss of tolerance to salinity is expected and consistent with our initial prediction.

In addition to the potential for expansive populations to have exploited opportunities arising from human disturbances, escape from herbivore enemies also may have contributed to the success of *B. halimifolia* in the expansive, interior US range. In a separate pilot study (Lázaro-Lobo, unpublished data), densities of seed-eating insects (*Ochrimnus mimulus*) were measured from inflorescences collected in the interior of the US, versus those collected from native coastal habitats. *Ochrimnus mimulus* (Lygaeidae) is a seed predator that shows preference for *Baccharis* spp. (its principal host) and its phenology is closely tied to that of *Baccharis* spp. in its native range,

maximizing access to abundant nutrition within *Baccharis* seeds (Gould & Sweet, 2000). Densities of *O. mimulus* per inflorescence were 99.9% lower in the expansive range than in the native range. We noted that seed production in *B. halimifolia* occurs a month earlier in the native US coastal range than in the interior expansive range. This mismatch in the host and parasite phenologies could explain the lower occurrence of *O. mimulus* in the expansive range.

Our results suggest that maternal traits, especially those related to inflorescences, had a significant influence on early demographic stages of *B. halimifolia*, as shown by previous research (Lázaro-Lobo et al., 2020). However, maternal traits explained a much lower fraction of the total variation in germination, early growth and survival than distributional range, which suggests that phenotypic differences in early demographic stages of *B. halimifolia* are driven by genetic histories associated with distributional range of origin, rather than maternal effects. Even so, inflorescence and plant size were positively related with seed germination and seedling survival, respectively, possibly because larger plants and inflorescences attract more pollinators and can access more above- and below-ground resources (Baskin & Baskin, 1998; Lázaro-Lobo et al., 2020; Sletvold, 2002; Wulff, 1995). Seed size/mass (unmeasured variables) could have also explained early-stage growth traits, as shown in previous research (Velooso et al., 2017). We found that offspring from maternal shrubs with a higher number of flower heads per inflorescence resulted in lower germination percentages, but higher survival and growth rates. This suggests that maternal plants that allocate more resources to reproductive effort increase the survival and competitive potential of their offspring, but the proportion of fertilized flower heads may be reduced with increasing number of flower heads (Lázaro-Lobo et al., 2020). *Baccharis halimifolia* is a dioecious shrub; thus, pollen travelling from male to female shrubs could be retained in the most exposed flower heads, preventing its access to the less exposed flower heads.

5 | CONCLUSIONS

Our results demonstrate that there are significant phenotypic differences in germination and early growth, which affect seedling survival, among native, expansive and introduced *B. halimifolia* populations. Counter to predictions, not all introduced populations showed faster germination and growth rates than native populations. Populations that became naturalized earlier showed higher growth rates than the rest of populations. Furthermore, we found evidence of phenotypic differentiation consistent with adaptation to local conditions. Maternal traits explained a much lower fraction of the total variation in early demographic stages of *B. halimifolia* than distributional range, which suggests that phenotypic variation at the spatial scale examined in this study is driven more by underlying genetic differentiation among populations than by maternal effects on offspring.

ACKNOWLEDGEMENTS

We thank Precious Cornejo and Akshita Singh for their help with the common garden experiment. We are also grateful to Dr. Bridget

Lassiter, Eamonn Leonard, Luc Devos, and Jacob Hockensmith for their help with field sampling. This research was supported in part by USDA Forest Service grant 19-DG11083150-006 and Basque Government grant IT936-16. Seeds were imported into the United States under permission from the USDA Animal and Plant Health Inspection Service (permit #: P37-19-02283). The authors are also grateful for many helpful suggestions provided by Dr. F. Dane Panetta and another anonymous reviewer. The findings and conclusions in this report are those of the author(s) and should not be construed to represent any official USDA or US Government determination or policy.

CONFLICT OF INTEREST

The authors declare that this research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCH

Adrián Lázaro-Lobo is interested in understanding how species traits, biotic interactions, abiotic factors and landscape characteristics affect species distributions at multiple spatial scales. This work represents a component of his PhD work at Mississippi State University on plant invasions. He and the other authors are broadly interested in the ecology, biogeography and evolution of invasive species.

Author Contributions: A.L.-L. and GNE conceived the ideas and designed methodology. All authors collected field data; A.L.-L. conducted the common garden experiment, analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Lázaro-Lobo, A., Moles, A. T., Fried, G., Verloove, F., Antonio Campos, J., Herrera, M., Goñi, E., Bioret, F., Buffa, G., Fantinato, E., Sentinella, A., Zalucki, M. P., Mayfield, M., Smith, T., Catling, A., Zalucki, J. M., Lucardi, R. D., Shoemaker, C. M., Mason, D. S., & Ervin, G. N. (2021). Phenotypic differentiation among native, expansive and introduced populations influences invasion success. *Journal of Biogeography*, 00, 1–12. <https://doi.org/10.1111/jbi.14252>