

ARTICLE

Post-introduction evolution of a rapid life-history strategy in a newly invasive plant

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Abstract

A central question in invasion biology is whether adaptive trait evolution following species introduction promotes invasiveness. A growing number of common-garden experiments document phenotypic differences between native- and introduced-range plants, suggesting that adaptive evolution in the new range may indeed contribute to the success of invasive plants. However, these studies are often subject to methodological pitfalls, resulting in weak evidence for post-introduction adaptive trait evolution and leaving its role in the invasion process uncertain. In a common-garden glasshouse study, we compared the growth, life-history, and reproductive traits of 35 native- and introduced-range *Polygonum cespitosum* populations. We used complementary approaches including climate-matching, standardizing parental conditions, selection analysis, and testing for trait–environment relationships to determine whether traits that increase invasiveness adaptively evolved in the species' new range. We found that the majority of introduced-range populations exhibited a novel trait syndrome consisting of a fast-paced life history and concomitant sparse, reduced growth form. Selection analysis confirmed that this trait syndrome led to markedly higher fitness (propagule production) over a limited growing season that was characteristic of regions within the introduced range. Additionally, several growth and reproductive traits showed temperature-based clines consistent with adaptive evolution in the new range. Combined, these results indicate that, subsequent to its introduction to North America over 100 generations ago, *P. cespitosum* has evolved key traits that maximize propagule production. These changes may in part explain the species' recent transition to invasiveness, illustrating how post-introduction evolution may contribute to the invasion process.

KEYWORDS
 biological invasion, clinal variation, common garden, lag phase, *Persicaria longiseta*, plant introduction, *Polygonum cespitosum*, propagule pressure, range comparison, rapid evolution

INTRODUCTION

When species are transported beyond their original geographic distributions, most fail to colonize their

newfound environments, yet some spread aggressively (Blackburn et al., 2011; Richardson & Pyšek, 2006; Richardson & Pyšek, 2012; Williamson & Fitter, 1996). Since Herbert Baker (1965) first listed the features that

would characterize an “ideal weed”, numerous studies have sought to identify traits that confer invasive success in introduced plants (Davidson et al., 2011; Funk, 2008; Godoy et al., 2011; Grotkopp & Rejmánek, 2007; Montesinos & Callaway, 2018; Perglová et al., 2009). Several meta-analyses and multispecies comparisons agree that invasive plants generally show faster developmental timing, increased vegetative growth, and higher propagule production compared with their noninvasive relatives (Blumenthal & Hufbauer, 2007; Moravcová et al., 2010; Pyšek & Richardson, 2007; Rejmánek & Richardson, 1996; Schlaepfer et al., 2009; van Kleunen et al., 2011, 2015; van Kleunen, Weber, et al., 2010). Yet the origin of these traits in introduced-range populations is seldom known: debate persists as to whether invasive-related traits accompany a species’ initial introduction or evolve later in the new range (probably over a “lag phase”), although these alternatives need not be mutually exclusive (van Kleunen, Weber, et al., 2010; Withgott, 2004). Adaptive evolution, in particular, may be central to the invasion process if selective change in response to introduced-range conditions leads to trait changes or novel traits that enhance a species’ ability to spread across new sites and habitats (Blair & Wolfe, 2004; Blumenthal & Hufbauer, 2007; Bossdorf et al., 2005; Buswell et al., 2011; Felker-Quinn et al., 2013; Hodgins et al., 2018; Maron et al., 2004; Mooney & Cleland, 2001; Oduor et al., 2016; Prentis et al., 2008; Sultan et al., 2012; Whitney & Gabler, 2008; Williams et al., 2016).

In evaluating trait evolution of invasive species, direct evolutionary comparisons of introduced-range populations with ancestral source ones are possible only in rare cases in which precise colonization history is known (Brandenburger et al., 2019; Hernández et al., 2019; Montesinos & Callaway, 2018; Turner et al., 2013). Instead, common-garden comparisons of broadly sampled native- and introduced-range plants are a central approach to identify distinctive traits of plant invaders and evaluate their origin (Colautti et al., 2009; Moloney et al., 2009). Congeneric and intraspecific comparisons showing trait differences between invasive taxa and noninvasive relatives may identify key traits underlying invasiveness (Hulme & Bernard-Verdier, 2017; van Kleunen, Dawson, et al., 2010). Comparing populations from an invasive plant’s native and introduced ranges can additionally provide indirect evidence as to whether such traits likely accompanied the species’ introduction or adaptively evolved thereafter. Although between-range comparisons are frequently made to determine both invasion-related traits and whether they have adaptively evolved since introduction, such studies can be inconclusive due to several shortcomings (van Kleunen et al., 2018).

First, range comparisons may show spurious differences when within-range population variation is high

and population sampling is limited (Colautti & Lau, 2015). Invasive species often span broad climatic distributions in both their native and introduced ranges. When native- and introduced-range populations are sampled from climatically distinct subregions of the two ranges, trait differences may not represent genuine range differences but rather within-range patterns of local adaptation to climate (Colautti et al., 2009; Rosche et al., 2019). Second, many between-range comparisons are based on growing experimental plants from field-collected seed yet, in doing so, parental effects from the various source population environments may distort trait differences among populations (Bischoff & Müller-Schärer, 2010; Galloway & Etterson, 2007; Moloney et al., 2009). Finally, although robust trait differences between an invasive species’ native and introduced ranges can provide strong (albeit indirect) evidence for post-introduction evolution, they do not necessarily result from natural selection. Instead, range differences may arise from neutral diversification processes during introduction and colonization such as genetic drift and founder effects (Dlugosch & Parker, 2008; Hodgins et al., 2018; Kliber & Eckert, 2005). Studies have often lacked sufficient evidence indicating whether evolved traits among introduced-range populations are actually adaptive (van Kleunen et al., 2018).

The interpretive value of between-range comparisons can be strengthened through targeted experimental approaches addressing these issues. To ensure that range differences are genuine, numerous populations can be sampled from large, climate-matched portions of the native and introduced ranges, a practice that both reduces sampling error and accounts for the effects of local climate (Bossdorf et al., 2005; Colautti et al., 2009; Colautti & Lau, 2015; Moloney et al., 2009). Prior to the comparison, plants may be grown under uniform conditions for at least one generation; this standardizes the parental environment such that any trait variation reliably indicates underlying genetic variation (Brandenburger et al., 2019; Hernández et al., 2019; Montesinos & Callaway, 2018; Turner et al., 2013). Last, alongside testing for between-range trait differences, testing for environmentally associated trait clines and performing selection analysis can support the interpretation that range differences arose specifically from adaptive evolution (Colautti & Barrett, 2013; Colautti & Lau, 2015; Hulme & Barrett, 2012; Wadgymar et al., 2017). In particular, introduced-range trait clines that recapitulate those in the native range are considered to be some of the “best evidence” of post-introduction adaptive evolution (Bock et al., 2015).

To more rigorously determine whether plant traits that promote invasiveness may adaptively evolve following a species’ introduction, we combined these approaches in a common-garden comparison of native- and

introduced-range populations of the colonizing annual plant *Polygonum cespitosum*. This species was introduced to the eastern United States from East Asia over a century ago and has only recently become invasive in the region, providing an example of an invasion in progress (Matesanz et al., 2015; Mehrhoff et al., 2003; Paterson, 2000; Sultan & Matesanz, 2015). We drew on a large sample of 35 East Asian and eastern North American populations from climate-matched areas within the native and introduced ranges to test for potential between-range differences in growth, life-history, and reproductive traits. We grew the parents of experimental plants under uniform conditions to standardize any inherited environmental effects on trait expression. To assess potential adaptive evolution in the introduced range, we tested for climate-associated trait clines and conducted phenotypic selection analysis. The study addressed the following questions: Do native- and introduced-range *P. cespitosum* plants differ in growth, life-history, and/or reproductive traits expected to promote invasiveness in the introduced range? If so, is there evidence that traits in this newly invasive plant have been shaped by adaptive evolution following introduction? More specifically, (a) are between-range trait differences associated with changes to fitness, and (b) do traits vary clinally in relation to source population climate?

METHODS

Study system

Polygonum cespitosum s.l. (= *Persicaria longiseta*) is a primarily self-fertilizing annual plant distributed throughout East Asia, where it is native, and eastern North America, its introduced range (eFloras, 2008; GBIF.org, 2018; USDA NRCS, 2021). When *P. cespitosum* was first introduced to North America (in c. 1910–1940), its initial occurrences were limited to the mid-Atlantic and north-eastern USA (Paterson, 2000). Since then the species has spread throughout the eastern USA and into more ecologically diverse habitats; it was declared invasive in 2003 (Figure 1a; Matesanz et al., 2015; Mehrhoff et al., 2003).

Native- and introduced-range population sample

To create a climate-matched sample of populations from *P. cespitosum*'s native and introduced ranges, 17 introduced-range populations were first sampled from natural and managed areas in the eastern USA (October 2008 and September 2014; Figure 1a; Appendix S1:

Table S1). Areas within the species' native Asian range were then targeted for sampling based on climatic similarity to introduced-range sample populations (please refer to "Climate-matching native- and introduced-range sample populations" section for details). The resulting native-range sample included 18 populations from the Tōhoku and Hokkaido regions of Japan (October–November 2014; Figure 1a; Appendix S1: Table S1). Native-range populations overlapped with introduced-range populations both latitudinally and climatically (Figure 1a,b). All sample populations contained at least 100 individuals covering an area of $\geq 75 \text{ m}^2$; for each population, achenes (single-seeded fruit diaspores) were collected from 15–60 randomly selected individuals spaced $\geq 1 \text{ m}$ apart. Achenes were air dried and stored at 4°C.

Climate-matching native- and introduced-range sample populations

Principal components analysis (PCA) was performed on bioclimatic data to characterize the climate of *P. cespitosum*'s introduced range (Broennimann et al., 2007; van Boheemen et al., 2019). Temperature and precipitation data were extracted from WorldClim (Hijmans et al., 2005) for sample populations ($N = 17$) and additional introduced-range localities ($N = 432$). The additional localities were (herbarium) specimen occurrences retrieved from Global Biodiversity Information Facility (GBIF; GBIF.org, 2018). Specimens lacking latitude/longitude coordinates were georeferenced according to locality descriptions (provided that the radius of uncertainty was $< 15 \text{ km}$); duplicate localities were excluded. Correlation matrix-based PCAs were performed on either temperature (Appendix S1: Figure S1a, Table S2) or precipitation (Appendix S1: Figure S1b, Table S3) variables. To identify climate-matched areas in the native range suitable for population sampling, the climates of native-range localities ($N = 1434$) were projected onto two-dimensional climatic space (Crawley, 2007). (Native-range locality and bioclimatic data were obtained from GBIF and WorldClim in the same manner as introduced-range localities and climates). Native-range localities falling within the climatic envelope of introduced-range populations were identified as candidate collection sites (Appendix S1: Figure S2a,b). Regions within Japan were ultimately targeted for population sampling based on strong latitudinal overlap with, and climatic resemblance to, introduced-range sample populations.

Between native- and introduced-range sample populations, the ranges did not differ with respect to temperature, either annually or during the growth season (Student's *t* tests for annual temperature $t(33) = -0.59$, $p = 0.56$ and warmest

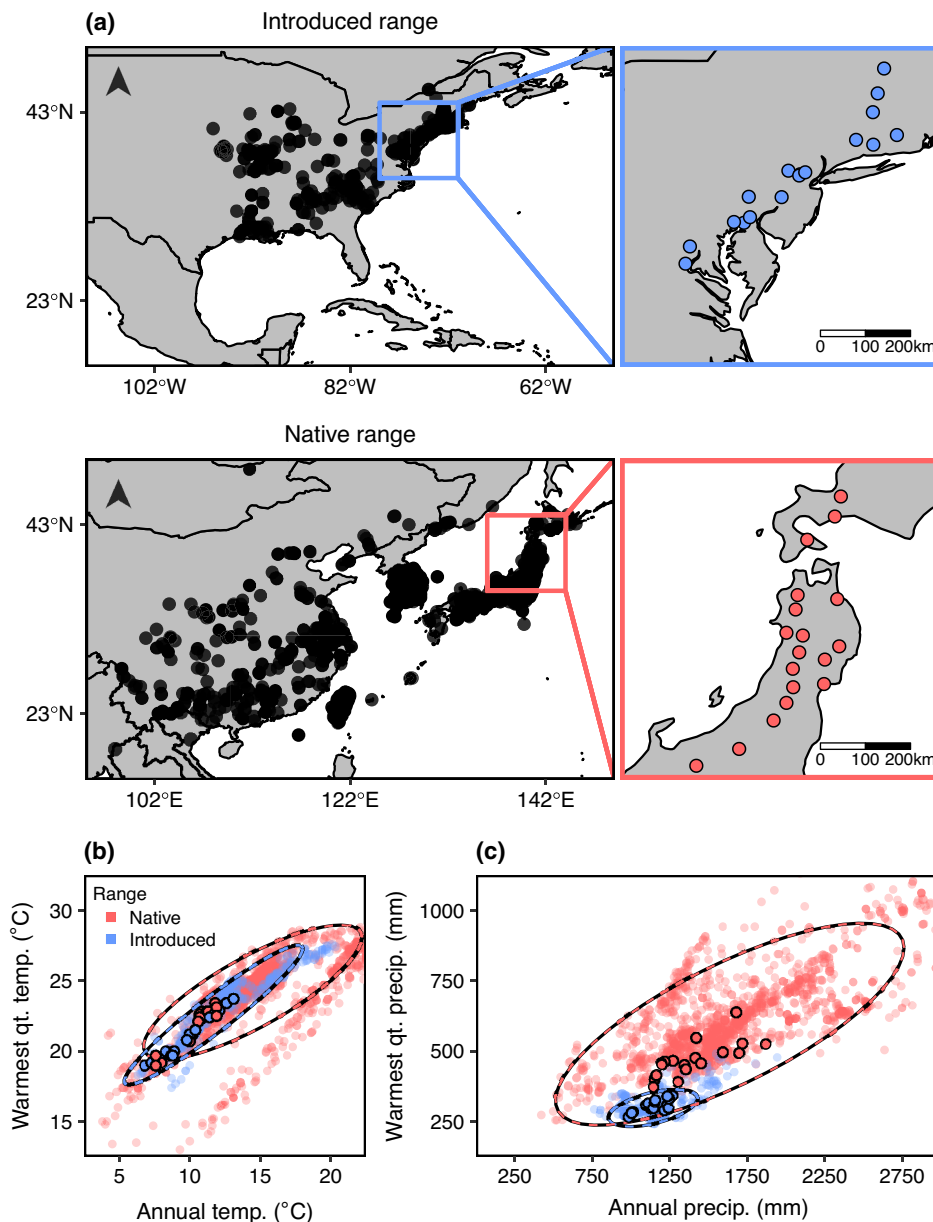


FIGURE 1 Sample populations in the context of *Polygonum cespitosum*'s geographic and climatic distributions. (a) *P. cespitosum*'s distribution in eastern North America (introduced range) and East Asia (native range) is shown according to all known specimen-based localities (black points) retrieved from GBIF (GBIF.org, 2018); insets show locations of sample populations (colored points). Sample populations (points with black outlines) and GBIF localities (points without outlines) are also plotted according to (b) temperature and (c) precipitation variables (qt., quarter). The 95% ellipses define each range's climatic distribution; axes are scaled to include the middle 95% of the data. Native- and introduced-range sample populations were matched according to latitude and temperature (note overlapping distributions), but not precipitation, as East Asia generally receives more precipitation than eastern North America.

quarter temperature $t(33) = -1.15$, $p = 0.26$; Figure 1b). Native-range sample populations, however, received more precipitation compared with introduced-range sample populations, both annually and during the growth season (Student's t tests for annual precipitation $t(33) = -4.09$, $p < 0.001$ and warmest quarter precipitation $t(33) = -10.58$, $p < 0.001$; Figure 1c). These precipitation differences reflected whole-range differences intrinsic to the species' distribution: *P. cespitosum* receives more precipitation in its

native range of East Asia than in eastern North America (Figure 1c; Appendix S1: Figure S1b).

Producing experimental material from sampled populations

From field-collected achenes, plants were grown to reproductive maturity under uniform glasshouse conditions,

producing inbred (selfed, full-sib) genetic lines (hereafter “genotypes”) with shared parental growing conditions. For each population, a maximum of 35 field parents were randomly selected for sowing, with seven achenes per field parent stratified (>4 weeks at 4°C) and sown into vermiculite flats (21–22 May 2015); of the 887 field parents, 814 (92%) produced at least one seedling. One seedling per field parent from a maximum of 20 field parents per population was randomly selected for transplanting ($N = 681$). Seedlings were transplanted at first true-leaf stage into 1-L clay pots filled with Metro-Mix 360 (Sun-Gro Horticulture; Agawam, MA; 15–17 June 2015). Plants were kept in a full-sun glasshouse, maintained at field capacity moisture, and given (in total) 350 ml of fertilizer solution (Jack’s Classic 20:20:20, JR Peters; Allentown, PA). Achenes were collected from each selfed parent plant (2–3 October 2015), air dried, and stored at 4°C . For four of the total 35 populations (ARM, BRL, JAM, and WAD), genotypes had an additional generation of uniform-environment inbreeding.

Common-garden comparison

Experimental sample

For each field-sourced inbred genotype, seven achenes (produced by glasshouse parents; please refer to “Producing experimental material from sampled populations” section) were stratified and sown into vermiculite flats (2–3 April 2016). At least one seedling germinated in 96% of genotypes. The final sample included one plant from each of 660 genotypes (13–20 genotypes per population \times 35 populations, for a total of 334 native- and 326 introduced-range genotypes). Experimental individuals were haphazardly selected for transplanting and grown to maturity as in the previous generation ($N = 660$).

Data collection

Several growth, life-history, and reproductive traits were measured for all plants during development and upon a destructive harvest. These traits are known to be variable and have a strong genetic basis in the species (Matesanz et al., 2012, 2013; Matesanz & Sultan, 2013). Growth and morphological traits were measured nondestructively from digital images taken 10 weeks after transplant (7–9 July 2016). Overhead (Figure 2) and side-view (Appendix S1: Figure S3) images were analyzed using Easy Leaf Area v.2 (Easlon & Bloom, 2014) and ImageJ v.1.49 (Schneider et al., 2012) software to quantify the

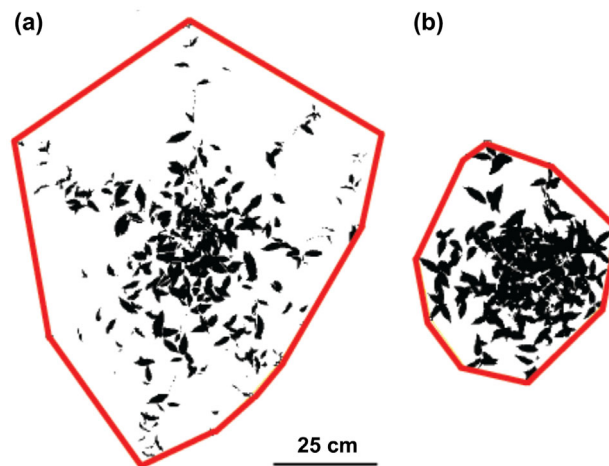


FIGURE 2 Plant growth-form variation. Binarized, overhead images of plants illustrate variation in spread area, the area of the convex hull (i.e., the smallest convex polygon) enclosing the plant (shown in red); canopy area, a plant’s total leaf area as viewed aerially (shown in black); and sparseness, with sparseness index calculated as spread area divided by canopy area. A plant’s sparseness index (SI) cannot be <1 . Plants (a) ALA09 (from the introduced range) and (b) MIN19 (from the native range) possessed similar canopy areas (816 vs. 827 cm^2), but ALA09 had a greater spread area (6022 vs. 1925 cm^2) and therefore a sparser growth form (7.4 vs. 2.3 SI).

following traits: height (see Appendix S1: Figure S3), (single) leaf area (area of the most recent fully expanded leaf), canopy area, spread area, and sparseness (latter traits defined in Figure 2). Reproductive onset (no. days to first flower) was recorded via daily censuses. Reproductive tissue (i.e., achenes) was nondestructively collected over the plant’s total lifetime. More specifically, achenes, which are gravity dispersed, were collected as they matured weekly to biweekly via gentle rubbing of the plants’ infructescences. Such a sampling method left the remaining flowers and immature achenes intact, allowing them to continue developing.

Plants were destructively harvested on a rolling basis 81 ± 3 days after individual reproductive onset (rolling harvest 128–237 days post-sowing, 9 August to 25 November 2016), giving all plants ample time for reproduction despite pronounced variation in flowering time. At harvest, reproductive tissue (i.e., remaining achenes and reproductive stalks) was separated from aboveground vegetative tissue. Aboveground vegetative tissue was oven dried (100°C for ≥ 1 h then 65°C for >48 h) and weighed (shoot biomass). Note that vegetative growth in *P. cespitosum* plateaus c. 105 days after sowing (Appendix S1: Figure S4), whereas the first plants harvested were done so at 128 days post-sowing. Differences in shoot biomass should therefore

reflect differences in maximal growth, not varying harvest dates.

All reproductive tissue was air dried (>2 weeks) and then weighed. Short-season (S-S) reproductive output was measured as total reproductive mass produced from sowing until 5 August, a fixed period of 124–125 days. Extended-season (E-S) reproductive output was measured as total reproductive mass produced from sowing until individual harvest. Because all plants had stopped achene production and were senescent by individual harvest (on average, 71% of a plant's leaves showed signs of senescence), E-S reproductive output predicts lifetime fitness provided unlimited time for reproduction. For instance, the last plant harvested experienced a 237-day growing season similar to that of the warmest, southernmost introduced-range sample population (WIL) where the 50-year mean freeze-free period is 210 days (NRCC, 2021). By contrast, S-S reproductive output indicates lifetime fitness under the constraints of a limited growing season comparable with the coldest, northernmost introduced-range sample population (AST) where the 50-year mean freeze-free period is 121 days (NRCC, 2021). Allocation to reproduction was calculated as $100 \times (\text{E-S reproductive output} / [\text{shoot biomass} + \text{E-S reproductive output}])$.

Analysis

All statistical analyses were performed in R v.3.6.1 (R Core Team, 2021). Use of nonbase R packages is indicated when applicable. When necessary, data were transformed to meet linear model assumptions. Alternatively, probability values were estimated using nonparametric permutation tests instead (5000 iterations; *lmPerm* package) (Kabacoff, 2011). To correct for multiple testing, probability values were adjusted using Holm's method (Holm, 1979).

One-way ANCOVA with type I sum of squares was used to test for trait differences between native- and introduced-range plants while accounting for the effect of source population temperature. Annual temperature and warmest quarter temperature were highly correlated (Pearson's $r = 0.97$, $p < 0.001$), and ANCOVAs using either variable produced the same results. We report models with warmest quarter temperature as a covariate. Due to nonoverlapping precipitation regimes between the ranges, source population precipitation was not included in ANCOVA. ANCOVAs were performed on population means.

To assess multi-trait variation between native- and introduced-range plants, correlation matrix-based PCA was performed on traits: height, spread, leaf area, shoot biomass, sparseness, reproductive onset, allocation to reproduction, S-S reproductive output, and E-S

reproductive output. (Canopy area was not included in the PCA due to a high correlation with shoot biomass; Pearson's $r = 0.78$, $p < 0.001$). After dimensional reduction using PCA, *k*-means clustering (*factoextra* package) was performed on the first four principal components using both the elbow and average silhouette methods to determine the optimal number of clusters (Hartigan & Wong, 1979; Kaufman & Rousseeuw, 2009). The optimal number of clusters ($k = 2$), as well as cluster identities, remained the same irrespective of whether the first two, three, or four principal components were used (cumulatively 67%, 82%, or 90% of the total variance, respectively).

Multiple linear regression with type III sum of squares was used to determine whether traits varied clinally in response to source population climate. Models estimated the effects of warmest quarter temperature and precipitation on plant traits. Native- and introduced-range plants were analyzed separately. Analyses were conducted on population means.

Phenotypic selection analysis was used to measure direct and indirect selection on traits (Lande & Arnold, 1983). Selection differentials (S), which measure total selection (i.e., direct and/or indirect selection), were estimated as the regression coefficients of relative fitness regressed on individual traits. Selection gradients (β), which measure direct selection, were estimated as the partial regression coefficients of relative fitness regressed on multiple traits. Native- and introduced-range plants were analyzed together, but separate selection analyses were performed using two different metrics of fitness: S-S and E-S reproductive output. S-S reproductive output represents fitness over a limited growing season, whereas E-S reproductive output represents fitness provided unlimited time for reproduction. Relative fitness was calculated for both fitness measures as absolute reproductive output divided by mean reproductive output (Stinchcombe, 2005). Growth and life-history traits were standardized by the standard deviation of the trait mean (mean = 0, variance = 1). One growth trait (canopy area) was excluded due to multicollinearity (i.e., variance inflation factor > 10) (Chong et al., 2018). Selection gradients and differentials were estimated using linear terms only.

RESULTS

Climatic comparison of native and introduced ranges

PCA of bioclimatic data showed that *P. cespitosum* encountered a greater range of climatic conditions across its native range than in its introduced range. In temperature-based space, the native range fully enveloped the introduced

range (Appendix S1: Figure S1a), allowing for a climate-matched population sample with respect to temperature. In precipitation-based space, there was little overlap between the ranges, with the native range occupying more space, receiving more precipitation, and having greater precipitation seasonality (Appendix S1: Figure S1b).

Trait differences between native- and introduced-range plants

Native- and introduced-range plants differed significantly (range $p < 0.001$; Appendix S1: Table S4) and substantially (17%–165% difference) for all traits measured except plant

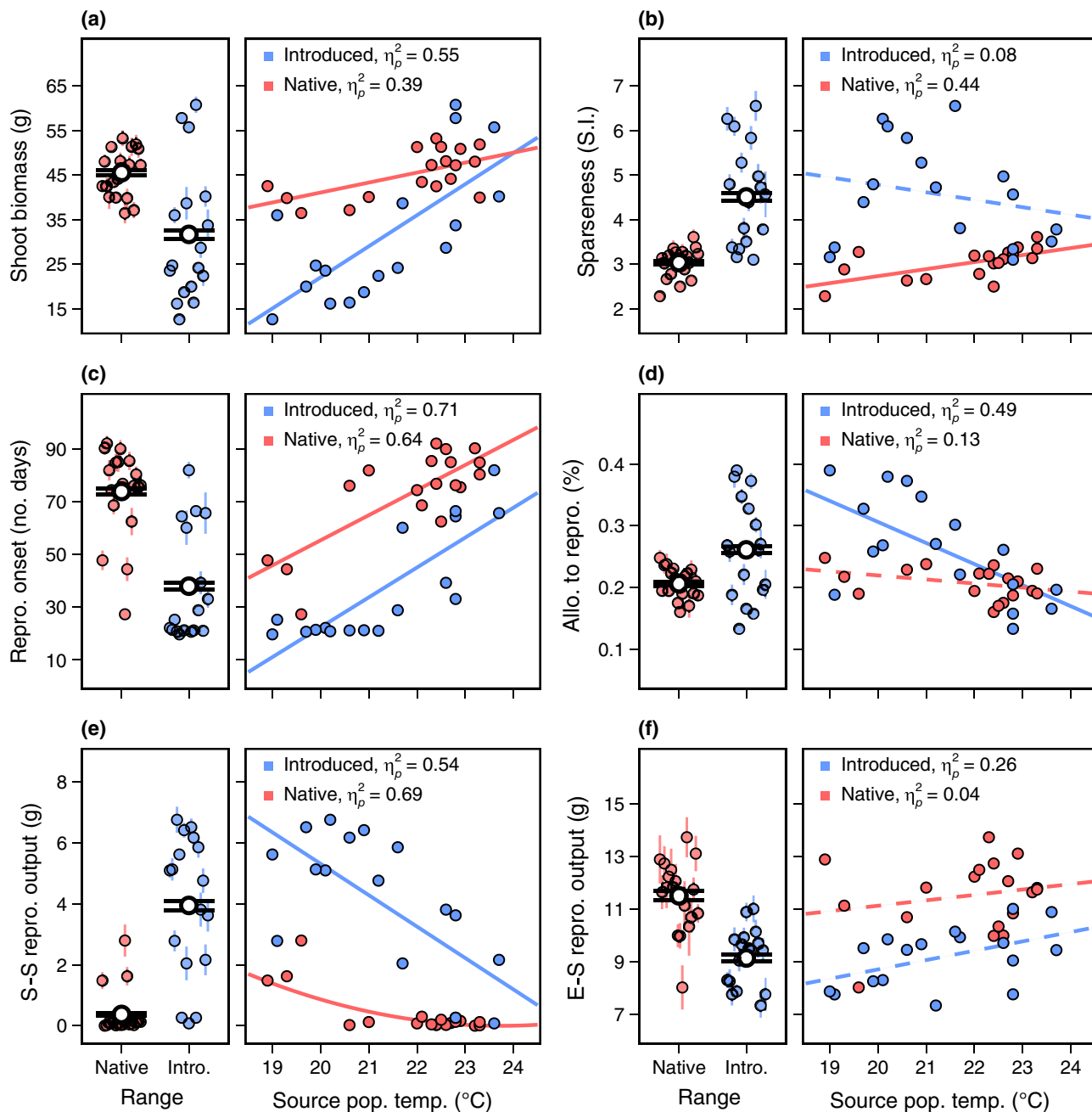


FIGURE 3 Between-range trait differences and temperature-based within-range clinal trait variation. For (a, b) growth, (c, d) life-history, and (e, f) fitness traits, left panels show population means in addition to native and introduced (Intro.) range means \pm SE (details are given in Appendix S1: Table S4); right panels show native- and introduced-range population means (points) plotted by source population temperature. Solid lines indicate significant trait-temperature relationships ($p < 0.05$); dashed lines indicate nonsignificant ones (details in Appendix S1: Table S7). Partial η^2 is reported for model term source population temperature. Transformed traits are shown back transformed. Some traits are labeled with the abbreviations: repro. onset, reproductive onset; allo. to repro., allocation to reproduction; S-S repro. output, short-season reproductive output; E-S repro. output, extended-season reproductive output.

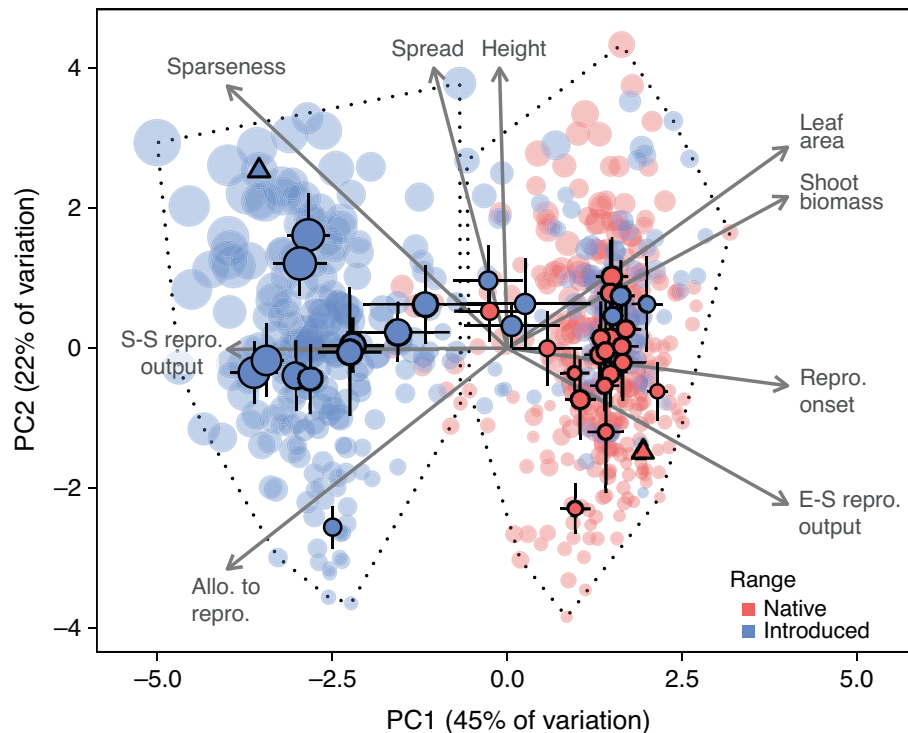


FIGURE 4 A novel, “fast-paced” syndrome among introduced-range plants. *k*-means clustering of multivariate phenotypic space revealed two contrasting trait syndromes: one “fast-paced” (left cluster enclosed with dotted line) and one “slow-paced” (right cluster enclosed with dotted line). Population means (points with black outlines) \pm 95% confidence interval and individual plants (points without outlines) are shown for introduced- and native-range plants with the size of each point corresponding to plant sparseness (i.e., larger points indicate sparser plants). Two representative plants, ALA09 and MIN19 (see Figure 2), are shown (triangles with black outlines) to demonstrate how variation in growth form projects onto phenotypic space. Principal components analysis (PCA) vectors (gray arrows) are shown for each trait. Some vectors are labeled with abbreviations: Repro. onset, reproductive onset; Allo. to repro., allocation to reproduction; S-S repro. output, short-season reproductive output; E-S repro. output, extended-season reproductive output. PCA details in Appendix S1: Table S5. *k*-means clustering details PCA in Appendix S1: Table S6.

height (Appendix S1: Figure S5a). On average, native-range plants grew more, producing larger canopies (\bar{x} = 1068 vs. 900 cm²; Appendix S1: Figure S5b) and more shoot biomass (\bar{x} = 45.5 vs. 31.7 g; Figure 3a). Conversely, introduced-range plants had sparser growth forms (\bar{x} = 4.5 vs. 3.0 sparseness index; Figure 3b) with more expansive canopies (spread \bar{x} = 3893 vs. 3253 cm²; Appendix S1: Figure S5c) and smaller leaves (\bar{x} = 7.4 vs. 9.1 cm²; Appendix S1: Figure S5d). With respect to life history, introduced-range plants flowered faster on average (\bar{x} = 38.0 vs. 73.8 days; Figure 3c), allocated more biomass to reproduction (\bar{x} = 26 vs. 21%; Figure 3d), and reproduced \sim 10-fold more over a shorter growing season (\bar{x} = 3.94 vs. 0.37 g; Figure 3e). However, over an extended growing season, native-range plants had \sim 26% greater lifetime reproductive output (\bar{x} = 11.51 vs. 9.15 g; Figure 3f).

PCA of plant traits (Appendix S1: Table S5) and *k*-means clustering of phenotypic space (Appendix S1: Table S6) revealed two distinct clusters: one characteristically “fast-paced” and the other “slow-paced” (Figure 4). Plants

belonging to the “fast-paced” cluster flowered faster and allocated more biomass to reproduction, but grew less and produced sparser canopies; plants belonging to the “slow-paced” cluster delayed reproductive onset, but grew more and produced denser, larger-leaved canopies (Figure 4). Although plants in the “slow-paced” cluster reproduced more over an extended growing season, plants in the “fast-paced” cluster reproduced more over a shorter growing season. Both native- and introduced-range populations occupied the “slow-paced” cluster, but only introduced-range populations occupied the “fast-paced” cluster. Moreover, most introduced-range populations (11/17), especially more northern ones (with the exception of AST), belonged to the “fast-paced” cluster.

Clinal trait variation in response to source population climate

Within both ranges, several traits exhibited clinal variation in response to source population temperature. Plants from colder populations flowered faster (Figure 3c) and

TABLE 1 Phenotypic selection analyses for plant growth and life-history traits based on two different measures of fitness: short-season (S-S) and extended-season (E-S) reproductive output.

Trait	Selection differentials				Selection gradients			
	<i>N</i>	<i>R</i> ²	<i>S</i> (SE)	<i>p</i>	<i>N</i>	<i>R</i> ²	β (SE)	<i>p</i>
S-S repro. output								
Height ^a	618	0.00	0.07 ...	1.000ns	612	0.91	−0.01 (0.02)	1.000ns
Spread ^a	616	0.07	0.34 ...	<0.001***			0.10 (0.04)	0.288ns
Leaf area	618	0.28	−0.66 (0.04)	<0.001***			−0.04 (0.02)	0.944ns
Shoot biomass	617	0.66	−1.02 (0.03)	<0.001***			−0.13 (0.04)	0.007**
Sparseness ^a	614	0.46	0.85 ...	<0.001***			0.18 (0.04)	0.002**
Repro. onset	618	0.71	−1.05 (0.03)	<0.001***			−0.69 (0.02)	<0.001***
Allo. to repro.	619	0.50	0.88 (0.04)	<0.001***			0.41 (0.03)	<0.001***
E-S repro. output								
Height	618	0.00	−0.01 (0.01)	1.000ns	612	0.77	0.04 (0.01)	<0.001***
Spread	616	0.00	−0.01 (0.01)	1.000ns			0.04 (0.01)	0.277ns
Leaf area	618	0.06	0.07 (0.01)	<0.001***			0.00 (0.01)	1.000ns
Shoot biomass	617	0.05	0.06 (0.01)	<0.001***			0.26 (0.01)	<0.001***
Sparseness	614	0.03	−0.05 (0.01)	<0.001***			−0.05 (0.02)	0.026*
Repro. onset	618	0.28	0.15 (0.01)	<0.001***			0.11 (0.01)	<0.001***
Allo. to repro.	619	0.06	0.07 (0.01)	<0.001***			0.36 (0.01)	<0.001***

Note: For each model, sample size (*N*), adjusted *R*², regression (*S*) or partial regression (β) coefficients for relative fitness on traits, standard error of the coefficient (SE), Holm-corrected *p*, and significance levels (ns, not significant; ⁺*p* < 0.10; **p* < 0.05; ***p* < 0.01; ****p* < 0.001) are shown with significant *p* values (*p* < 0.05) in bold. Some traits are labeled with abbreviations: Repro. onset, reproductive onset; and Allo. to repro., allocation to reproduction.

^aNonparametric permutation test was used.

reproduced more under the constraints of a shorter growing season (Figure 3e), whereas plants from warmer populations grew more overall (Figure 3a). For every 1°C decrease in source population temperature, introduced-range plants flowered 11.3 days earlier (*p* < 0.001; Appendix S1: Table S7) and reproduced 1.03 g more (*p* < 0.001; Appendix S1: Table S7) whereas native-range plants flowered 9.5 days earlier (*p* < 0.001; Appendix S1: Table S7) and reproduced 0.25 g more (*p* = 0.004; Appendix S1: Table S7). For every 1°C increase in source population temperature, native- and introduced-range plants grew more by 2.2 g (*p* = 0.031; Appendix S1: Table S7) and 7.0 g (*p* = 0.004; Appendix S1: Table S7), respectively.

Some temperature-based trait clines were specific to native- or introduced-range plants. For instance, introduced-range plants from colder populations allocated proportionately more biomass to reproduction (Figure 3d): for every 1°C decrease in source population temperature, reproductive allocation increased by 3% (*p* = 0.010; Appendix S1: Table S7). Among native-range plants, sparseness showed a statistically significant relationship with source population temperature (*p* = 0.015; Appendix S1: Table S7), although

native-range plants exhibited little variation in sparseness overall (Figure 3b).

No traits varied in response to source population precipitation except for sparseness (Appendix S1: Figure S6). Sparseness was positively associated with precipitation among introduced-range plants (*p* = 0.031; Appendix S1: Table S7), but this relationship was not evident along the broader precipitation continuum: plants from introduced-range populations were drastically sparser than plants from much wetter, native-range populations (Appendix S1: Figure S6).

Phenotypic selection analysis

Patterns of selection differed by growing season length (i.e., S-S vs. E-S reproductive output). Under the constraints of a shorter growing season (i.e., when S-S reproductive output was the fitness measure), selection favored rapid flowering, smaller leaves, and a reduced, sparser growth form (Table 1). (Note that for reproductive onset, a negative selection gradient or differential indicates selection for earlier flowering.) However, over an extended growing season

(i.e., when E-S reproductive output was the fitness measure), patterns of selection were reversed: selection favored delayed flowering, bigger leaves, and a larger, denser (i.e., less sparse) growth form (Table 1). Measures of total (S) and direct (β) selection were consistent for all aforementioned traits except leaf area, which was not under direct selection (Table 1). When S-S reproductive output was the fitness measure, selection gradients and differentials were generally bigger, indicating a stronger selection over a shorter growing season (Table 1). Whether selection favored taller plants or plants with more expansive spreads depended on both the growing season length and measure of selection, although these traits were never selected against (Table 1). Higher allocation to reproduction was always favored by selection (Table 1).

DISCUSSION

Introduced-range plants differ significantly from native-range plants in key growth and life-history traits

In a common-garden comparison, native- and introduced-range *P. cespitosum* plants differed substantially (and highly significantly) for nearly all growth and life-history traits measured. On average, introduced-range plants produced canopies with greater spatial spreads that were much sparser in form (i.e., greater spread area per unit canopy leaf area), whereas native-range plants had larger leaves and were generally larger in terms of both biomass and canopy area. Importantly, with respect to invasion potential, life-history traits also differed dramatically: introduced-range plants flowered faster, allocated relatively more biomass to reproduction, and reproduced more over a shorter growing season. Native-range plants, however, reproduced more provided an extended growing season.

Trait differences between a species' native and introduced ranges may indicate underlying genetic differentiation between the ranges, whether adaptive or neutral. Alternatively, these trait differences may be artifacts of limited population sampling and/or sampling populations from climatically distinct regions within each range (Colautti et al., 2009; Colautti & Lau, 2015; Rosche et al., 2019). Improving on earlier comparative work, the present study used rigorous experimental approaches to ensure that the between-range differences were genuine. To reduce the likelihood of detecting spurious range differences, our study used a relatively large genotypic sample (35 populations \times 13–20 genotypes/population) in which native- and introduced-range sample populations were matched according to latitude and local climate. To further account for the effects of local climate,

source population temperature was included as a covariate in comparing the traits of native- and introduced-range plants. Historically, including certain aspects of climate variation in experimental design may not have been feasible, but freely accessible climatic and species distribution data (e.g., GBIF.org, 2018; Hijmans et al., 2005) now permit this type of approach. The parental environment of experimental plants was also standardized to avoid confounding genetic and environmental sources of trait variation (Brandenburger et al., 2019; Griffith & Sultan, 2012; Matesanz et al., 2012).

Introduced-range plants show a novel, fast-paced life-history strategy that promotes propagule production in a shorter growing season

When traits were considered collectively (using PCA and k -means clustering), two contrasting life-history strategies emerged: one “fast-paced” and one “slow-paced”. The fast-paced life-history strategy was characterized by smaller plants that flowered earlier, allocated more biomass to reproduction, and reproduced more over a shorter growing season. An additional defining feature of this fast-paced strategy was a distinct growth habit: canopies with more expansive, although sparser, spreads consisting of smaller leaves. By contrast, the slow-paced life-history strategy was characterized by larger plants with denser (less sparse), larger-leaf canopies that delayed reproductive onset and reproduced more over an extended growing season. Both strategies were found in the introduced range, although the fast-paced strategy was predominant (found in 11, more northern, populations of the 17 populations sampled). Introduced-range plants that exhibited the slow-paced strategy resembled native-range plants in both their delayed life history and their larger, nonsparse growth form. Interestingly, none of the 18 native-range populations exhibited the fast-paced strategy or the associated sparse, reduced growth form. The aforementioned trait differences were not subtle mean differences, but rather stark differences with little overlap between the trait distributions. The fast-paced life-history strategy and concomitant small, sparse growth form therefore appear to be a novel trait syndrome found only in introduced-range populations.

This fast-paced life-history strategy may be facilitating *P. cespitosum*'s invasive spread in parts of the introduced range where growing season length is limited. Selection analysis confirmed that, when the growing season was relatively short, traits characteristic of the fast-paced strategy—fast reproductive onset, reduced biomass, sparse growth form, and high allocation to

reproduction—were associated with higher propagule production (i.e., lifetime fitness). Increased propagule production is considered a key driver of invasiveness (Lockwood et al., 2005; Pyšek et al., 2015; Pyšek & Richardson, 2007; Simberloff, 2009; van Kleunen, Weber, & Fischer, 2010) and has been associated with greater seedling recruitment, establishment success, and population persistence (Cassey et al., 2018; Holle & Simberloff, 2005; Hovick & Whitney, 2019; Jongejans et al., 2006; Maron, 2006). It is important to note, however, that the novel, fast-paced life-history strategy of most introduced-range plants was associated with increased propagule production (i.e., fitness) only in the context of a shorter growing season, such as that found in cooler regions of the introduced range (e.g., New England region). By contrast, over an extended growing season, the slow-paced strategy (found in some introduced-range populations but universal among native-range plants) was associated with higher propagule production. These results provide clear evidence that an invasive plant can evolve to outperform native relatives in a new range, but such a fitness advantage may be context dependent rather than universal.

Similarly, in a number of other systems, performance differences between invasive plants and noninvasive relatives have been found to depend on developmental environment (Daehler, 2003; Felker-Quinn et al., 2013; Hierro et al., 2005; Kumschick et al., 2013; Montesinos & Callaway, 2018; Pal et al., 2020; Williams et al., 2008). This context-dependence complicates the search for invasiveness traits and may, in part, explain the mixed support found for Blossey and Nötzold's (1995) influential "EICA" hypothesis—that because introduced plants are freed from native enemies, they evolve "increased competitive ability" furthering their invasive spread (Blumenthal & Hufbauer, 2007; Felker-Quinn et al., 2013; Parker et al., 2013; Rotter & Holeski, 2018). Future studies that test for between-range performance differences across multiple environments (e.g., reciprocal transplant experiments) will reveal more precisely the conditions in which introduced-range *P. cespitosum* plants have evolved to outperform native-range counterparts.

The accelerated life-history strategy probably reflects post-introduction adaptive evolution

The role of post-introduction evolution in species invasions can be difficult to determine. Even when differences between native- and introduced-range plants are well documented, inferring their cause requires a

substantial caveat: without a known colonization history permitting introduced-range populations to be compared with their precise source (i.e., ancestral) populations, range differences offer indirect, rather than direct, evidence for post-introduction evolution. This caveat applies to the great majority of published range comparisons, as multiple introductions of a given species are common and source populations rarely known (Bossdorf et al., 2005). However, complementary approaches including selection analysis and testing for trait-by-environment correlations can support the interpretation that introduced-range traits have adaptively evolved post-introduction (Bock et al., 2015; Colautti & Barrett, 2013).

In *P. cespitosum*, selection analyses support an adaptive explanation by revealing a fitness trade-off between size and age at reproductive onset: either plants flowered faster but grew less, thereby maximizing short-term fitness (i.e., the "fast-paced" life-history strategy), or plants grew more, but delayed flowering, maximizing longer term fitness (i.e., the "slow-paced" life-history strategy). Similar life-history trade-offs are well known in both annual and perennial plants (Chen et al., 2021; Colautti et al., 2010; Dorn & Mitchell-Olds, 1991; Griffith & Watson, 2005; Mitchell-Olds, 1996). In the invasive plant *Lythrum salicaria*, such a trade-off has led to the post-introduction evolution of earlier flowering in which smaller, earlier-flowering plants expressed a fitness advantage in the context of a shorter growing season (Colautti & Barrett, 2013). Similarly, in *P. cespitosum*, a trade-off between size and age at reproduction along with selection for early flowering appears to have resulted in the evolution of smaller, sparser, fast-paced plants in the shorter-season parts of the introduced range.

Selection analysis strongly indicates that the entire "fast-paced" trait syndrome endemic to the introduced range is indeed adaptive. (Despite the striking sparse morphology, the significance of this growth habit in itself is unknown. Sparseness may be simply the developmental by-product of a rapid life history or an allocational shift from vegetative to reproductive tissue; possibly it has some undetermined adaptive function.) Although many range comparisons of invasive plants have documented trait shifts between the native and introduced ranges, comparatively few have provided sufficient evidence to infer that these trait differences have resulted from post-introduction natural selection (Blair & Wolfe, 2004; Blumenthal & Hufbauer, 2007; Bossdorf et al., 2005; Buswell et al., 2011; Felker-Quinn et al., 2013; Hodgins et al., 2018; Maron et al., 2004; Mooney & Cleland, 2001; Oduor et al., 2016; Prentis et al., 2008; Sultan et al., 2012; Whitney & Gabler, 2008). This study provides robust evidence of distinctive traits in

introduced-range populations that is linked to increased propagule production (i.e., fitness), indicating that adaptive evolution in the introduced range has been integral to the species' success as an invader. Comparatively rapid evolution in this annual species was also found in a “resurrection” study showing that introduced *P. cespitosum* populations evolved adaptive functional changes and higher propagule production under novel ecological conditions in only 11 generations of natural selection (Sultan et al., 2012).

Multiple selective forces could be driving the evolution of an accelerated life cycle among introduced-range plants. In annual plants, a fast-paced life-history strategy may be advantageous if it helps to evade local disturbance (including mowing or tilling), herbivores, competitors, end-of-season drought, and/or frost (Alexander & Levine, 2019; Griffith & Watson, 2006; Lee & Gelembiuk, 2008; Mitchell-Olds, 1996; Stearns, 1992). Although fast-paced life histories are generally expected to evolve in response to colder climates with shorter growing seasons (Alexander, 2010; Etterson et al., 2016; Lustenhouwer et al., 2018; Montague et al., 2008; Stinchcombe et al., 2004; Woods et al., 2012), temperature variation should not underlie the observed major life-history differences between native- and introduced-range plants, as sample populations were matched according to temperature variables. Instead, *P. cespitosum* receives much less precipitation in its introduced range and perhaps this reduced precipitation has selected for the “fast-paced” suite of traits characteristic of introduced-range plants. In other herbaceous species, drought and water-limiting conditions have been shown to shorten the growing season and select for faster life histories (Alexander, 2013; Franks et al., 2007; Franks & Weis, 2008; Lowry et al., 2008; Wu et al., 2010). Further manipulative experiments could test the apparent role of drought in promoting the evolution of a faster-paced life history in introduced-range *P. cespitosum* populations.

Biogeographic trait clines further support post-introduction adaptive evolution

Clinal patterns among introduced-range populations provide further indirect evidence for adaptive evolution of *P. cespitosum* following its introduction to North America. Although the native- and introduced-range samples overlapped in temperature distribution, there was considerable temperature variation among populations that evidently influenced patterns of trait variation within each range. For both native- and introduced-range plants, plants from colder, more northern, populations grew less, but flowered earlier and reproduced more, given a shorter growing

season than plants from warmer, more southern populations. Uniquely among introduced-range plants, plants from colder populations allocated relatively more biomass to reproduction than plants from warmer populations. Similar clines in phenology, growth, and reproduction have been well documented in other plant invaders (e.g., Helsen et al., 2020; Kollmann & Bañuelos, 2004; Liu et al., 2020; Maron et al., 2004; Montague et al., 2008; Sun & Roderick, 2019); this clinal trait variation—especially the rapid recapitulation of native-range clines—is considered to be strong albeit indirect evidence for adaptive post-introduction evolution in response to climate (Bock et al., 2015; Endler, 1977; Huey et al., 2005; Hulme & Barrett, 2012).

Biogeographic trait clines can also arise via neutral processes as part of species introduction and expansion (e.g., spatial sorting, isolation-by-distance, founder events of pre-adapted genotypes) (Colautti & Lau, 2015; Hodgins et al., 2018; Keller et al., 2009; Vasemägi, 2006). However, neutral explanations for the clinal trait variation observed in the present case seem unlikely for two reasons. First, previous microsatellite analysis of introduced-range populations showed no indication of isolation-by-distance (i.e., no relationship between genetic and geographic distance) (Matesanz et al., 2014). Second, selection analysis showed that the direction of the trait clines among introduced-range populations was consistent with local adaptation to climate, as plants exhibited a “home-site advantage” (sensu Kawecki & Ebert, 2004): plants from colder, more northern populations had greater fitness given a shorter growing season, whereas plants from warmer southern populations had a slight fitness advantage when allowed an extended growing season. Barring the improbable scenario that each population was founded by native-range genotypes that were specifically pre-adapted to each respective local climate, the introduced-range trait clines indicate adaptive evolutionary change in *P. cespitosum* following its introduction to North America.

CONCLUSION

A growing number of common-garden studies has reported trait differences between native- and introduced-range populations and concluded that rapid adaptive evolution in situ has enhanced invasiveness in these species. Yet, many comparative studies are subject to experimental shortcomings that reduce their interpretive value, leaving in question the role of post-introduction adaptive evolution in the invasion process. We drew on experimental approaches that targeted these shortcomings (i.e., climate-matched populations, standardized parental growing conditions,

selection analysis, and trait clines) to investigate the role of post-introduction evolution in a newly invasive annual plant. We documented major differences in the growth, life-history, and reproductive traits of native- and introduced-range populations of this species to identify a novel fast-paced life-history strategy characteristic of the species' introduced range. By linking trait variation to increased propagule production and identifying within-range climatic drivers of selection, selection analysis and biogeographic trait clines provide strong indirect evidence that these novel traits adaptively evolved following the species' introduction. These findings suggest that, by rapidly shaping traits that enhance invasiveness, adaptive evolution in a species' new range can play a central role in the transition to invasiveness.

AUTHOR CONTRIBUTIONS

Ellen C. Woods and Sonia E. Sultan designed the experiments. Ellen C. Woods conducted the experiment. Ellen C. Woods carried out the statistical analyses and interpreted the results. Ellen C. Woods and Sonia E. Sultan co-wrote the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Polygonum cespitosum trait data (Woods, 2022b) and bioclimatic data (Woods, 2022a) are available at <https://doi.org/10.5061/dryad.rfj6q57cf> and <https://doi.org/10.5061/dryad.rv15dv493>, respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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