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An ideal weed: plasticity and invasiveness in *Polygonum cespitosum*

Sonia E. Sultan[1] and Silvia Matesanz[2]

[1]Biology Department, Wesleyan University, Middletown, Connecticut. [2]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, c/ Tulipán s/n, Móstoles, Spain

Address for correspondence: Sonia E. Sultan, Biology Department, Hall-Atwater Labs, Wesleyan University, Middletown, CT 06459-0170. sesultan@wesleyan.edu

The introduced Asian plant *Polygonum cespitosum* has only recently become invasive in northeastern North America, spreading into sunny as well as shaded habitats. We present findings from a multiyear case study of this ongoing species invasion, drawing on field environmental measurements, glasshouse plasticity and resurrection experiments, and molecular genetic (microsatellite) data. We focus in particular on patterns of individual phenotypic plasticity (norms of reaction), their diversity within and among populations in the species' introduced range, and their contribution to its potential to evolve even greater invasiveness. Genotypes from introduced-range *P. cespitosum* populations have recently evolved to express greater adaptive plasticity to full sun and/or dry conditions without any loss of fitness in shade. Evidently, this species may evolve the sort of "general-purpose genotypes" hypothesized by Herbert Baker to characterize an "ideal weed." Indeed, we identified certain genotypes capable of extremely high reproductive output across contrasting conditions, including sunny, shaded, moist, and dry. Populations containing these high-performance genotypes had consistently higher fitness in all glasshouse habitats; there was no evidence for local adaptive differentiation among populations from sunny, shaded, moist, or dry sites. Norm of reaction data may provide valuable insights to invasion biology: the presence of broadly adaptive, high-performance genotypes can promote a species' ecological spread while providing the fuel for increased invasiveness to evolve.

Keywords: plant invasion; genetic variation; rapid evolution; ecological generalists; range expansion; norm of reaction; population differentiation

Introduction

In an influential 1965 paper, Herbert G. Baker[1] listed the traits of a hypothetical ideal weed, expressing a botanist's reluctant admiration for the plants that most successfully colonize new ranges and displace other taxa (see also Ref. 2). When they spread into new geographic regions, often as a result of human-mediated introduction, such aggressively spreading species are termed *invasive plants*.[3] Understanding the "characteristics and modes of origin" of these taxa (to use Baker's phrase) and of other invasive organisms has become an even more urgent task as biological invasions increasingly alter and destabilize ecological communities.[4–7] Yet fundamental questions remain unanswered, particularly with respect to the possible role of evolutionary changes that may occur subsequent to a species' introduction.[8–18] As is well known, only a small subset of the many plant and animal species that are introduced to new geographic ranges becomes invasive in the new range, often after many generations as naturalized species.[1,8,19] What biological events occur during the lag phase that precedes aggressive spread, and how do these events contribute to the transition to invasiveness? What characteristics lead certain taxa to make this transition, and not others? Once established in a new range, what is the potential of an introduced species to evolve even greater invasiveness, and how may that potential vary among populations?

Baker[1,20] predicted that individual phenotypic plasticity would be among the key characteristics of successful invasives. Such plasticity confers broad environmental tolerance that, together with the

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resulting ability to reproduce in diverse conditions, permits existing genotypes to establish across multiple habitats.[21,22] This long-standing conceptual connection between plasticity and invasiveness[23,24] suggests that an *ecological development* approach to adaptive diversity—studying the phenotypes that a single genotype may express in response to different possible environments—may yield central insights into invasion dynamics. The essence of this approach is the *norm of reaction* experiment, in which replicates of individual genotypes are raised in alternative naturalistic conditions to determine their patterns of functional and fitness trait expression.[25]

Here, we present a multifaceted case study of a single species invasion in progress, that of *Polygonum cespitosum* (Blume) = (*Persicaria cespitosa*; Ref. 26). This body of work exemplifies how norms of reaction provide ecologically meaningful information about genotypic and population-level diversity. Although individual plasticity and evolutionary change are often viewed as alternative factors in invasiveness, we examine the interplay of these factors to consider how variation in plasticity patterns and selection may jointly shape a species' invasive trajectory. We first discuss the recent spread of *P. cespitosum* in its introduced range in northeastern North America, focusing on ecological range expansion in the field and concomitant change in adaptive plasticity patterns, as revealed by "resurrection" experiments.[27] We then characterize diversity for genotypic norms of reaction within and among introduced-range populations, as well as neutral molecular variation, to examine adaptive diversity, population-level factors in invasion dynamics, and evolutionary potential of this non-native plant to evolve even greater invasiveness in the region.

Background: *P. cespitosum* and its recent ecological expansion

P. cespitosum is a herbaceous plant introduced into North America approximately a century ago from its native range in temperate and subtropical Asia.[28–30] Like its closely related Eurasian congeners *P. lapathifolium*, *P. persicaria*, and *P. hydropiper*, species that were also introduced into North America following European settlement,[31,32] *P. cespitosum* has a mixed but predominantly self-fertilizing breeding system, an obligately annual life cycle, and indeterminate reproduction by means of small, single-seeded achenes.[32,33] In contrast to these close relatives, however, following approximately 100 generations in North America, *P. cespitosum* began to spread aggressively in the northeastern part of its introduced range, forming more numerous and extensive populations that often make up dense monocultures up to 250 plants/m^2.[34] The species' transition to invasiveness took place during the time between our initial field studies in the early 1990s, and the formal recognition of *P. cespitosum* as a regional invasive in 2003.[35] This scenario thus offers an exceptionally interesting window onto a biological invasion that is actively in progress.

P. cespitosum's newly aggressive spread in northeastern North America (an area also known as New England) has coincided with a recent expansion of its ecological range in this region: within the geographic area in which the species was already naturalized, it has recently begun to occupy a broader range of habitats.[34] Building on field studies that were fortuitously established before the species' switch to invasive behavior, we documented this change in ecological breadth within the existing, introduced geographic range over a recent 15-year period. We compared measurements of light (photosynthetically active radiation (PAR)) and soil moisture (scaled by soil field capacity) for a sample of field sites that were chosen—from initial samples of over 50 sites each year across an area of approximately 40,000 km^2—to represent the range of habitat conditions the species occupied in central New England in 1994 and 2009 (years with extremely similar patterns of precipitation). Hence, the final population sample for each year reflected, by design, the highest and lowest resource levels in which the species occurred that year, based on an initially large, random sample of field populations encompassing all annual plant habitats in the region (see Ref. 34 and its supplemental information for full details regarding field sampling strategy and locations). This type of structured sample captures the extremes of an environmental distribution, providing a more robust basis for characterizing the extent of a species' ecological range than a feasibly sized random sample of field sites.[36]

Comparison of these field data confirmed that, although initially restricted to moderately shaded habitats in New England,[36] *P. cespitosum* is now also found in sunnier, more open sites (Fig. 1). In 1994, mean available PAR at *Polygonum* canopy

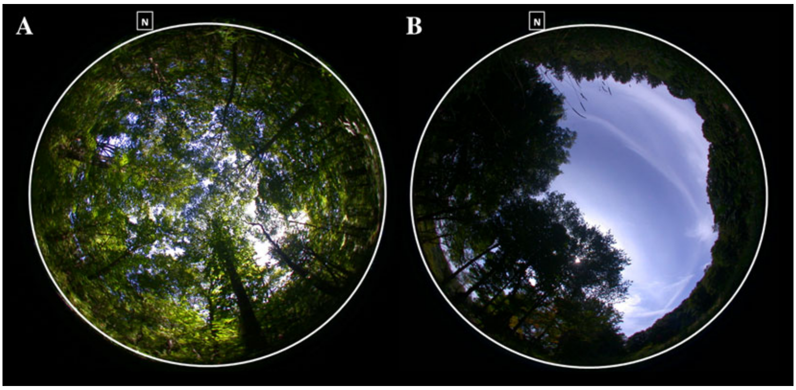

Figure 1. Ecological range expansion in North American *P. cespitosum*. Hemispherical canopy photographs can be used to quantify light conditions in field populations based on global site factor (GSF; the proportion of direct plus diffuse solar radiation received diurnally in a given site relative to a fully open site). In its introduced New England range, *P. cespitosum* was previously restricted to moderately shaded forest understory conditions (A), where GSF is low (0.1–0.2). Recently, this species has expanded its ecological range within the region to include sunnier habitats such as meadows (B; GSF 0.5–0.6). Photographs by S. Matesanz.

level was approximately 20% of full insolation, with the sunniest site averaging 32% of full PAR (Fig. 2A). As of 2009, the species' habitat range within the same geographic area included sites with mean PAR of 40–50% of full sun (Fig. 2A). The distribution of *P. cespitosum* plants in light microsites within local sites also changed during this time period: in 1994, 70% of plants occupied deeply shaded microsites (those with $<10\%$ PAR), with only 5% of plants found in open microsites (those with $>80\%$ PAR) (Fig. 2C). In 2009, plants still occurred in the very dark microsites, but the proportion occupying open microsites had tripled to 17% (Fig. 2C). This microsite shift within sites makes clear that the ecological expansion during this time period did not result from dispersal into different field locations. Rather, the altered microsite occupancy pattern reflects a change in the species' actual environmental distribution from shade-only to both shade and sun conditions.

We also found increased ecological breadth with respect to soil moisture. In 1994, mean soil moisture at the wettest population was ca. 60% of field capacity, and the species was not found in sites that included flooded microsites ($>100\%$ of field capacity); in 2009, the species occurred in much wetter sites with mean soil moisture up to 140% of field capacity (Fig. 2B). The distribution of *P. cespitosum* plants within field sites had also shifted: in 1994, about 80% of plant microsites had low soil moisture ($< 60\%$ of field capacity), while in 2009 more than half of the microsites occupied by *P. cespitosum* plants had soil moisture greater than 70% of field capacity (Fig. 2D).

A clear inference is that *P. cespitosum*'s recent ecological expansion into open and very moist as well as shaded New England habitats is a major factor in the species' newly aggressive spread in this region. In northeastern North America, low-light forest habitats are interspersed with open and often moist sites, such as meadows, agricultural areas, and suburbs. The ability to establish in both open and shaded sites increases both the total area available to the species and the connectivity among suitable habitat patches. Site connectivity can hasten a species' spatial spread[37,38] and promote gene flow among its populations.[39] Moreover, reproductive output is dramatically boosted in high light, so expansion into open microsites and habitat patches can be expected to increase propagule pressure in the region.[40,41] What biological changes underlie the expanded environmental breadth of *P. cespitosum* within the species' existing introduced range? Are such changes in environmental breadth a common feature of the lag time between a species' introduction and its transition to invasiveness?

The evolution of broader adaptive repertoires within the introduced range

A series of glasshouse resurrection experiments revealed a possible evolutionary explanation for *P. cespitosum*'s recent ecological range expansion.

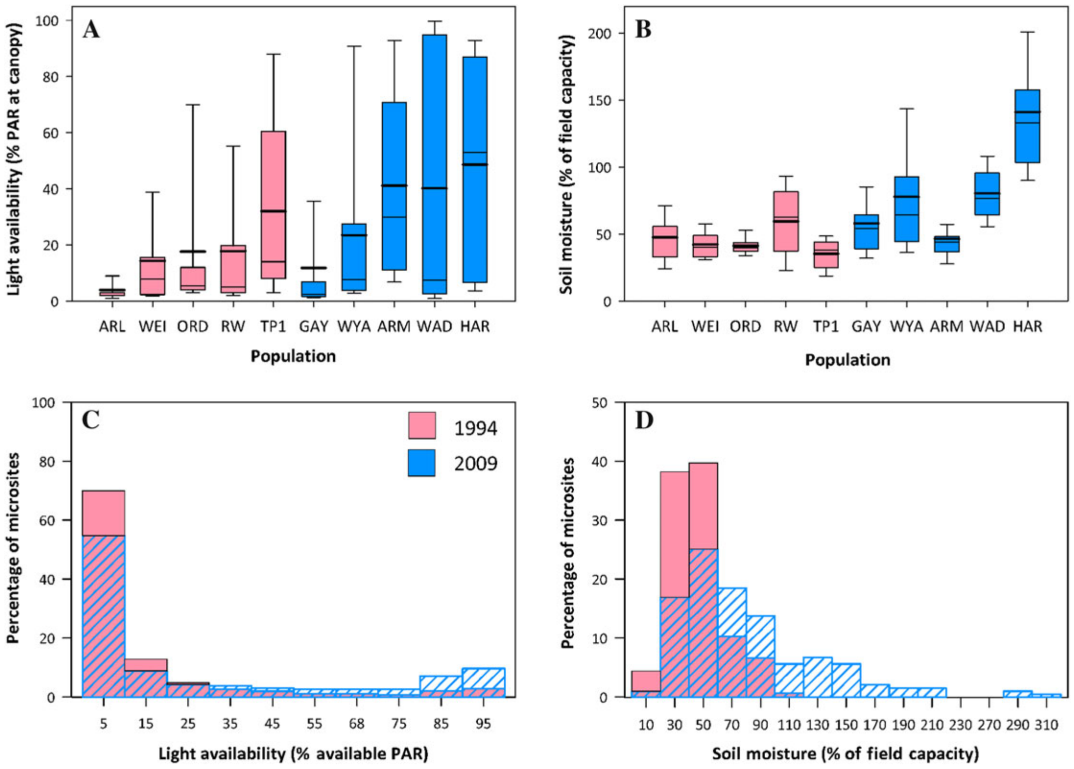

Figure 2. Recent expansion in moisture and light conditions occupied by *P. cespitosum* in its introduced range. Environmental data are shown from five populations representing the species' ecological range in northeastern North America in 1994 (pink) and in 2009 (blue). Box-and-whisker plots (10th, 25th, 50th, 75th, and 90th percentiles) and site means (dark lines) are given for (A) light availability at *Polygonum* canopy height and (B) soil moisture (pooled from 0 to 10 and 20 to 30 cm soil depths). Within field sites in each year, the percentage of (C) light microsites and (D) soil moisture microsites occupied by *P. cespitosum* individuals is shown. Figure modified from Ref. 34.

Resurrection experiments test directly for rapid evolutionary change, by re-sampling the same field populations across a time interval comprising several generations.[27,42,43] We compared environmental response patterns of field-collected *P. cespitosum* genotypes drawn from the same three geographically disjunct New England populations in 1994 and again in 2005.[44] This 11-generation time interval encompassed the species' shift to invasiveness in this part of its introduced range, and is roughly congruent with the change in ecological distribution described above. The three replicate populations occupied very similar habitats: spatially patchy, moderately shaded sites with mesic soil.[36,44] After a "refresher" inbreeding generation under uniform conditions (conducted in 2001 (1994 collections) and 2006 (2005 collections)) followed by dry storage at 4 °C, replicate individuals of 1994- and 2005-collected genotypes were raised in contrasting naturalistic glasshouse light and soil moisture treatments to determine norms of reaction for functional and fitness traits. (High germination rates (>70%) in all lines from both collection years, as well as equivalent day-10 biomass for their seedlings, confirmed the absence of any possibly confounding seed aging effects from 1 versus 5 years of storage; see Ref. 44 for full details.)

In all three populations, 2005 genotypes expressed greater adaptive plasticity in response to full sun conditions than genotypes collected in 1994. When grown in full sun with either moist or dry soil, replicates of the 2005 genotypes had significantly greater biomass allocation to root tissue per unit of leaf area compared with plants of 1994 genotypes (Fig. 3); 2005 plants also produced roots in dry soil that were longer and thinner. Such changes to

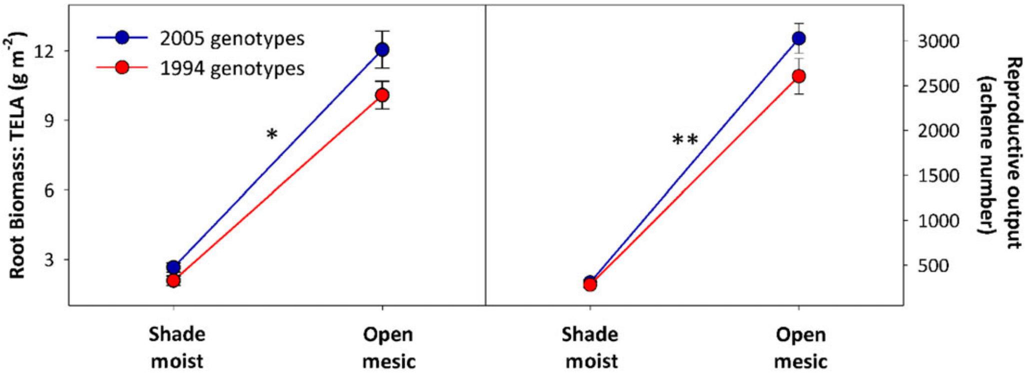

Figure 3. Rapid evolution of fitness and functional traits in introduced-range *P. cespitosum* populations. Under sunny, mesic glasshouse conditions, genotypes collected in 2005 showed increased root allocation (root mass per unit leaf area (whole-plant root biomass divided by total estimated leaf area, TELA); left) and greater lifetime reproductive output (total achene number; right) than those collected in 1994 from the same three field populations. Means are shown ±1 SE for 26–29 genotypes per collection year (pooled across populations); 1994 (red) versus 2009 (blue). Asterisks indicate significant effect of collection year in ANOVA; $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$. Figure modified from Ref. 44.

root allocation and morphology would maximize the supply of soil nutrients and water to actively photosynthesizing tissues, allowing for opportunistically high rates of carbon assimilation despite the increased transpirational demands of full-sun conditions. Accordingly, 2005 plants also showed significantly higher instantaneous photosynthetic rates under full-sun conditions in both moist and dry soil. Along with changed norms of reaction for these functional traits, 2005 genotypes produced significantly greater reproductive output than 1994 genotypes in full-sun treatments (Fig. 3; complete results in Ref. 44). Such very rapid adaptive evolution has been documented in many plants and animals, most often in response to sudden environmental changes, such as introduction to a new range or exposure to a novel contaminant.[16,18,45–56] The surprisingly fast pace of evolutionary change in these *Polygonum* populations (measured in *haldanes*, units of phenotypic change in standard deviations per generation) is similar to that found in other herbaceous plants exposed to strong new selection pressures (e.g., evolution of tolerance to road salt and heavy metals (Ref. 57 and references therein)), and falls within the published range for studies of mollusks, fish, and reptiles in novel conditions (reviewed in Refs. 58 and 59).

Alongside this shared, general pattern of increased functional plasticity and reproductive output in response to high light, the three populations differed in the degree of change from 1994 to 2005 in specific components of physiology and fitness, such as reproductive allocation and propagule size.[44] Mean among-population differences in absolute reproductive output in both shade and sun persisted across the sampling interval, consistent with the existence of population-specific genetic constraints on adaptive evolution (see section on among-population differences below).

Notice that there was no evidence for a functional or fitness trade-off in the altered *P. cespitosum* norms of reaction: the increased success of 2005 genotypes in full sun was not accompanied by reduced functional-trait plasticity or lifetime reproductive output in low light conditions. Genotypes collected in 2005 maintained or slightly increased the total number of achenes produced in low-light conditions compared with 1994 genotypes, whether light limitation was encountered as neutrally reduced quantity of PAR or as simulated shade (reduced PAR with reduced red: far-red ratio).[44] Repertoires of individual plasticity have evidently evolved in New England *P. cespitosum* populations that allow plants to maintain fitness in shade conditions and to exploit resource-rich, full-sun environments, even with limited moisture availability. Most notably, the rapid, recent evolution of these broadly adaptive genotypic norms of reaction coincided with the species' ecological expansion into open as well as shaded conditions in this part of its introduced North American range.

These resurrection data document the very recent evolution of broader repertoires of adaptive plasticity for physiological, developmental, and fitness traits in all three of the *P. cespitosum* populations we studied in the species' introduced northeast North American range. This finding is particularly intriguing because light conditions in the study populations did not change during the sampling interval (see Ref. 44). Hence, the evolution of adaptive plastic responses to high light appears not to have resulted from directional selection due to sunnier, more open site conditions. Instead, more broadly adaptive norms of reaction may have been selectively favored in the heterogeneous, disturbed sites the species inhabits in its introduced North American range. In annual plants, effective utilization of high PAR results in dramatically higher reproductive output; genotypes able to exploit the intense light encountered in open microsites or via intermittent sunflecks would be strongly favored in these patchy populations (see Ref. 60). Generally speaking, adaptive plasticity is predicted to be selectively favored in populations and metapopulations that encounter variable environments.[61–64]

This familiar point leads to an important insight regarding the evolution of introduced organisms. To the extent that invasive taxa occupy disturbed, variable habitats and/or encounter diverse conditions via high levels of dispersal into new sites, such taxa may be particularly likely to evolve greater adaptive plasticity following introduction.[64] Indeed, the evolution of more broadly adaptive norms of reaction may be a common event during the lag phase between a species' introduction and its transition to invasive spread.[44] Norm of reaction resurrection experiments can provide robust, direct tests for evolution of plasticity patterns in populations within a species' introduced range.

The nature of genotypic diversity in an invasive taxon: high-performance genotypes of *P. cespitosum*

A norm of reaction approach also suggests a way to study the genotype-level basis of an introduced species' ecological spread, as well as its quantitative-genetic potential to evolve greater invasiveness within a new range.[65] In his 1965 review, Baker speculated that invasive taxa might consist of broadly adaptive "general purpose genotypes" that allow such taxa to colonize diverse sites across a landscape (see also Ref. 23). By virtue of ample functional and developmental plasticity, such genotypes could survive, compete, and maintain high reproductive output in a variety of environments. The existence of such broadly adaptive, *high performance* genotypes could contribute to invasiveness in two distinct ways. First, these genotypes could promote a species' immediate spread across its introduced range because their broad environmental tolerance and consistently high reproductive output ("propagule pressure" *sensu* Ref. 40) would promote colonization of multiple, diverse sites.[66] Empirical studies have confirmed that ability to produce numerous offspring in diverse environments promotes invasiveness in both animals and plants.[40,41] Second, the existence of generalist, high-performance genotypes in introduced-range populations would fuel the selective evolution of greater invasiveness in the new range, since these genotypes would increasingly come to predominate due to their consistent fitness advantage. Accordingly, any populations that contained such genotypes could be expected to serve as the primary sources of both immediate and long-term invasiveness.

We tested for this type of genotypic diversity in New England populations of *P. cespitosum*, using a two-phase genotypic screening approach (details in Ref. 66). We collected achenes from ≈30 field parents in each of 14 geographically disjunct populations in the region and raised them to maturity under uniform glasshouse conditions. In the first experimental phase, we grew one plant from each of these 416 inbred genotypes in a resource-rich glasshouse treatment designed to mimic the full-sun, moist habitat into which the species has recently spread in this region[34] and determined lifetime reproductive output. The top-reproducing 5% of genotypes in this favorable treatment were designated as *putatively high performance*; we assembled a control group for comparison by randomly selecting two genotypes per population from the remaining 95% of the fitness distribution. In the second phase, we raised replicates of each high-performance and control genotype in three contrasting glasshouse habitat treatments: the resource-rich, open, moist treatment; a stressful open, dry treatment; and a moist but light-limited simulated understory treatment. To our surprise, the *P. cespitosum* genotypes that had expressed the highest relative fitness in sunny, moist conditions—producing over 5000 achenes per plant in this favorable environment—also produced significantly more offspring on average

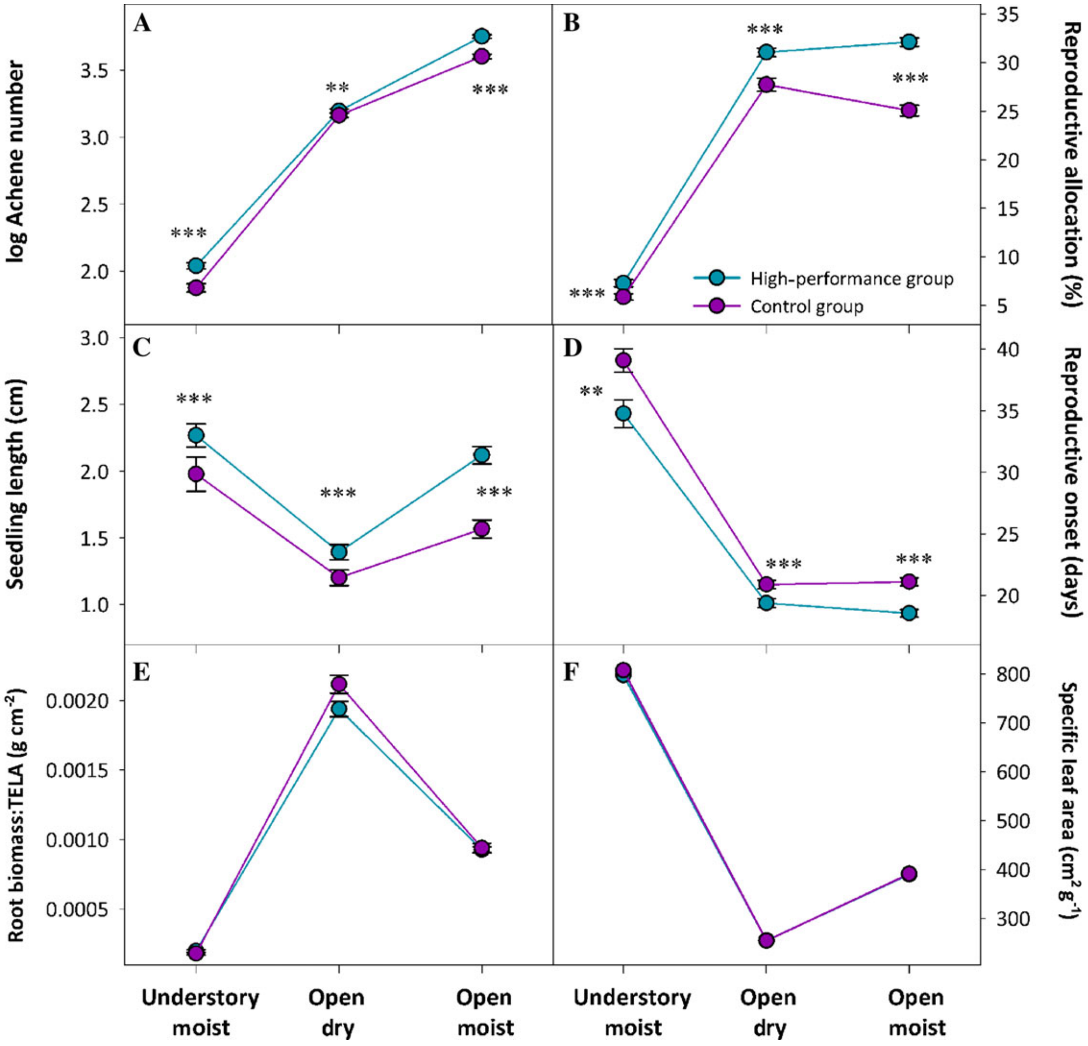

Figure 4. Broadly adaptive high-performance genotypes occur in certain introduced-range populations of *P. cespitosum.* Plots show fitness, life history, and functional trait expression of high-performance versus control genotypes grown in contrasting habitat treatments. Treatment means ± 1 SE are shown for (A) total lifetime reproductive output, (B) proportional biomass allocation to reproduction, (C) seedling height at day 10, (D) timing of reproductive onset, (E) root biomass per unit plant leaf area (TELA = total estimated leaf area), and (F) specific leaf area. Asterisks indicate significant trait differences between high-performance and control genotypes within habitat treatments (based on ANOVA); differences within and across treatments were nonsignificant for traits shown in E and F. $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$. Data reprinted (by permission) from Ref. 66.

than the random control group in both of the other, differently stressful treatments (Fig. 4A). These were indeed consistently high-performance genotypes across diverse conditions—general-purpose genotypes of the type that Baker had hypothesized might characterize aggressive invaders.

Along with greater reproductive output in both resource-rich and stressful environments, the high-performance group differed on average from the control group for a suite of ontogenetic traits: they germinated faster and at higher rates, elongated more rapidly as seedlings, made an earlier transition to flowering, and allocated proportionally more biomass to reproduction (Fig. 4B–D)—all life-history traits associated with invasiveness.[67–70] (These life-history differences were not simply mediated by enhanced offspring provisioning, as individual achene mass was the same in the two

Figure 5. Phenotypic plasticity expressed by *P. cespitosum* genotypes. Inbred replicates of a single, typical *P. cespitosum* genotype expressed dramatically different phenotypes when grown in contrasting glasshouse environments. When given full sun with dry soil (open/dry treatment; left), plants produced small, thick leaves, increased allocation to root tissue, and had significantly higher water-use efficiency (WUE). Plants grown in simulated shade with moist soil (understory/moist treatment; right) instead produced elongated stems bearing very large leaves of higher specific area (SLA), responses that increase total photosynthetic surface area. Photograph by S. Matesanz.

groups of genotypes.) On the other hand, the high-performance genotypes did not differ from the control plants in norms of reaction for functional traits (nonsignificant effects of group and group-by-treatment interaction[66]). All of the *P. cespitosum* genotypes, whether high performance or control, expressed similar, functionally appropriate plastic responses to contrasting glasshouse habitats, substantially increasing root tissue allocation per unit leaf area in the open, dry treatment, for instance, and producing large, thin leaves in shade to maximize light capture (Figs. 4E–F and 5).

In a separate experiment, we tested the competitive success of the generalist, high performance *P. cespitosum* genotypes relative to control genotypes randomly sampled from the introduced-range populations. We grew competitive arrays in 1-L clay pots, each consisting of a single high-performance or control target plant (representing one of 26 genotypes) in a competitive background of six plants drawn from three different high-performance or control genotypes. We replicated all competitive combinations of high-performance and control genotypes in full sun and simulated shade glasshouse treatments, both amply watered.[71] Although the two groups of genotypes did not differ competitively in the shade treatment, high-performance genotypes were superior in full-sun conditions in terms of both competitive *response* (the ability to grow and reproduce in spite of competition from neighbors), and competitive *effect* (the ability to reduce the growth and reproduction of neighboring individuals[72,73]). In the open treatment, high-performance target plants maintained significantly greater lifetime reproductive output and total biomass when grown against either type of competitive background than did control plants, and suppressed growth and reproduction of both types of target plant more strongly than control plants

(C. Corliss and S. E. Sultan, in review). Of the four possible competitive combinations grown in full sun (a high-performance target versus a high-performance competitive background, high-performance target versus control background, control target versus high-performance background, and control target versus control background), the highest reproducing target plants were high-performance genotypes competing with a background of control plants. This specific outcome suggests that high-performance genotypes could outcompete other introduced-range *P. cespitosum* genotypes in open, moist field sites. A competitive advantage in resource-rich conditions would magnify the greater reproductive output found in high-performance plants grown individually (previous section), further promoting the selective increase of these broadly adaptive genotypes in sunny populations.

Plasticity and adaptive breadth at the population level

On the basis of a very broad sample of current genotypes from populations in the species' introduced New England range, these experiments revealed two important insights regarding the genotypic basis of invasiveness and ecological spread in *P. cespitosum*. First, diverse genotypes share generally similar, broad repertoires of functional plasticity in response to contrasting light and moisture conditions. This suggests that it is likely individual developmental and physiological plasticity, rather than genotypic diversity for specialized adaptations to sun, shade, and drought stress, that underlies the species' ability to colonize diverse light and moisture habitats. Second, there is genotypic variation for life-history traits: certain genotypes express accelerated germination and development, along with greater reproductive allocation. This ontogenetic syndrome results in greater reproductive output in both favorable and stressful conditions, as well as greater competitive success in full sun.

Further norm of reaction studies showed that the above pattern of genotypic diversity in New England *P. cespitosum*—plasticity-based ecological breadth rather than adaptive specialization, combined with consistent across-environment fitness differences—was mirrored at the population level. To evaluate adaptive population diversity, we compared nine well-established, geographically disjunct *P. cespitosum* populations representing the species' range of habitats in northeastern North America: from open meadows and clearings with either moist or dry soil, to patchily shaded moist or mesic roadsides, to forest trails in heavy shade with mesic to moist soil (details in Ref. 74). Patterns of plasticity for functional, fitness, and life-history traits were determined for 13–19 genotypes from each population (inbred under uniform conditions) in response to two contrasting glasshouse habitats, full sun with dry soil (open/dry treatment) and simulated shade with moist soil (understory/moist treatment), to determine population mean norms of reaction.[25] Despite their very different local conditions, the nine populations shared generally similar, functionally appropriate patterns of plasticity: replicates of each genotype increased root allocation per unit leaf tissue, photosynthetic rate, and water-use efficiency in the open/dry conditions, and elongated seedling internodes made much broader, thinner leaves, and reduced root tissue allocation in the understory/moist treatment (Figs. 5 and 6A–D). Every genotype in all nine populations survived and reproduced successfully in both of these very different glasshouse environments, producing very high lifetime reproductive output in the open treatment.[74]

Although there were (subtle) among-population differences in the means and slopes of these plastic responses, the differences among populations were not consistent with local adaptation to particular habitats. We assessed local adaptation by testing for a match between populations' performances in the alternative glasshouse treatments, and either light or moisture conditions at their sites of origin. If populations were locally adapted to light availability, their reproductive output in the open/dry treatment would be expected to correlate positively with light availability at their sites of origin, while reproductive output in the understory/shade treatment would be expected to correlate negatively with home-site light levels. Similarly, with local adaptation to soil moisture levels, reproductive output in understory/moist conditions would be predicted to correlate positively with soil moisture at the populations' sites of origin, and output in open/dry conditions to correlate negatively. Yet all four of these predicted local-adaptation correlations were nonsignificant (P values of 0.32–0.99; Fig. 7A–D). At the population level, as was true for genotypes, we

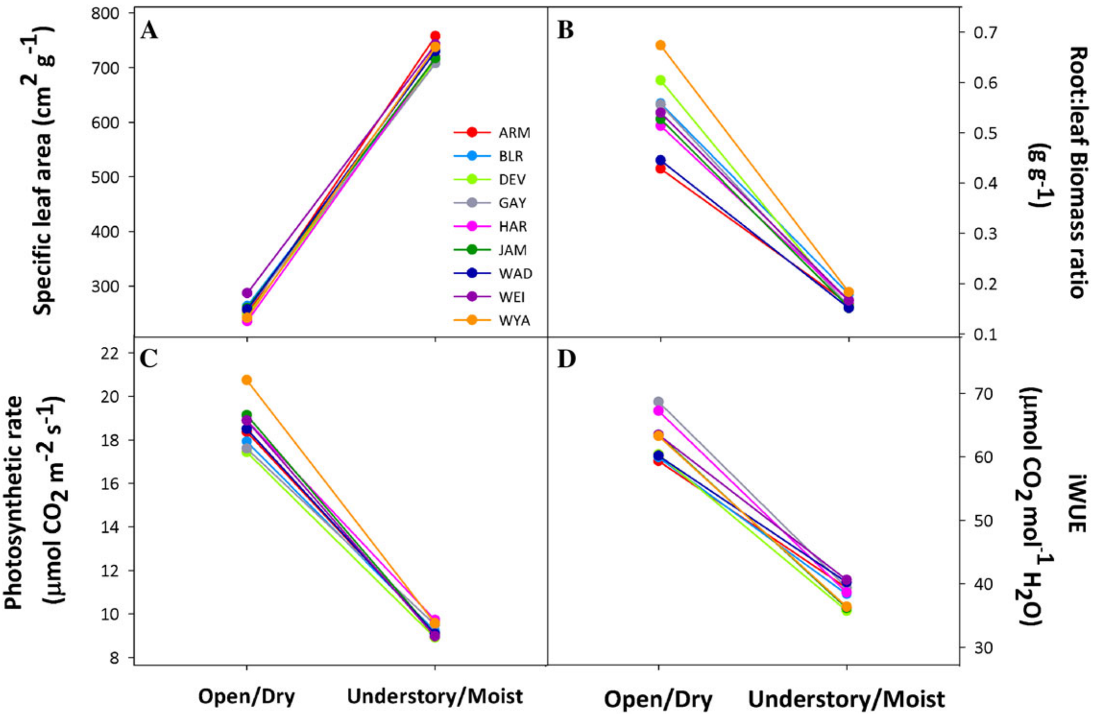

Figure 6. Population mean norms of reaction for morphological, allocational, and physiological plasticity in response to contrasting habitat treatments. Trait means in contrasting glasshouse environments are shown for each of nine northeastern North American *P. cespitosum* populations, based on replicated genotypic norms of reaction for 13–19 genotypes per population. Traits shown include (A) specific leaf area, (B) root:leaf biomass ratio, (C) instantaneous photosynthetic rate, and (D) water use efficiency. Differences among populations within treatments were nonsignificant for all traits, based on mixed-model nested ANOVA. Figure modified from Ref. 74.

found no evidence of functional trade-offs associated with ecological specialization. This is consistent with the view that ecological breadth in northeastern North American *P. cespitosum* is afforded by individual developmental and physiological plasticity.

Yet despite the absence of environment-specific adaptive differences, populations did differ on average in reproductive output across environments. As noted above, the nature of differences at the population level mirrored those among genotypes: the populations with higher reproductive fitness in the full-sun, dry treatment also had higher fitness in the shaded, moist treatment (Fig. 7E). These consistent among-population differences in reproductive output largely reflected differing frequencies of the high-performance genotypes described above. In our previous large-scale screening, genotypes identified as high-performance (according to our criterion of top-5% reproductive output in favorable conditions) were found in only eight of the 14 New England populations sampled, and constituted from 3% to 21% of those populations.[66] Phenotypic selection analyses in the nine-population comparison confirmed that populations with higher average fitness consisted of genotypes with faster seedling growth, earlier reproductive onset, and higher proportional allocation to reproduction—the same life-history traits found to characterize high-performance genotypes.

These large-scale norm of reaction studies have revealed a particular structure to adaptive variation in the introduced range of *P. cespitosum*. All genotypes, in all populations, appear to share broad repertoires of functionally adaptive phenotypic plasticity and can survive and reproduce in both favorable and stressful light and moisture conditions. In addition, in certain populations genotypes are found that express an accelerated life history associated with consistently high reproductive

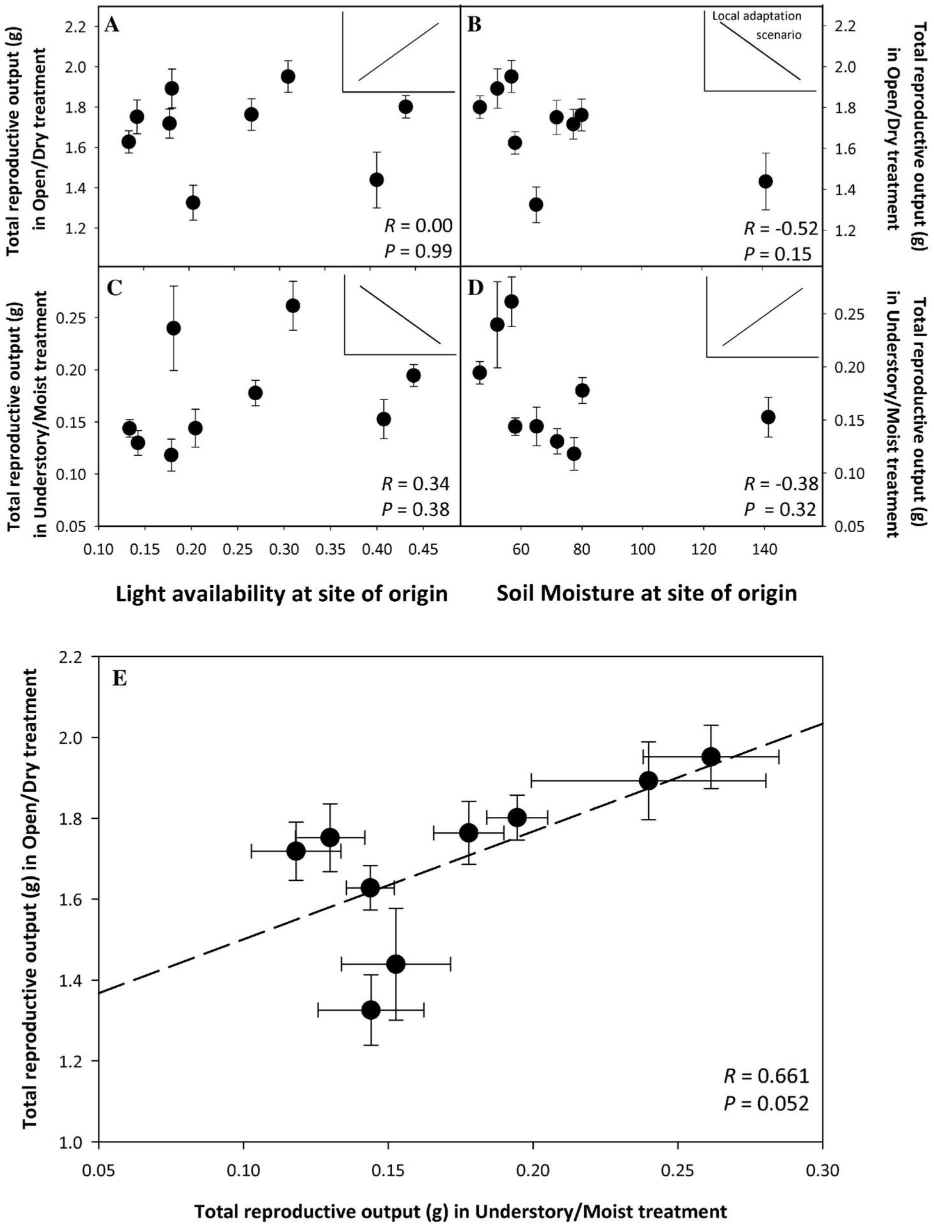

Figure 7. Performance differences among introduced-range *P. cespitosum* populations in relation to contrasting environments. The relative performance of nine populations in contrasting glasshouse light and moisture environments did not match predictions for local adaptation; instead, certain populations performed best across diverse conditions. Reproductive output of each population (means for 13–19 pooled genotypes ± SE) is plotted for each glasshouse treatment, in relation to light availability (global site factor (A, C), and soil moisture (% of soil field capacity (B, D) at each population's site of origin. Inset in each panel shows predicted pattern of local adaptation (i.e., higher reproductive output in the open/dry treatment of populations from sites with higher light availability and lower soil moisture, and higher reproductive output in the understory/moist treatment of populations from sites with lower light availability and higher soil moisture). Correlations of population reproductive output and home-site environment were all nonsignificant (regression coefficients *R* and probability levels are shown for each plot). Instead of a pattern of adaptive differentiation, performance of populations in the open/dry treatment was positively correlated with their performance in the understory/moist treatment (E; mean total reproductive output (± SE) is shown for each population in both glasshouse treatments). Five out of the nine populations ranked in the same position in both treatments. Modified from Ref. 74.

output in both resource-rich and stressful conditions. By combining greater propagule pressure with ecological breadth, these genotypes, and consequently the populations that contain them, can be expected to contribute most actively to the species' ongoing spread across diverse sites in northeastern North America (see Refs. 40 and 41). Moreover, the presence of these particularly high-performing, competitively successful genotypes provides fuel for the evolution of greater invasiveness in those populations and eventually, through their disproportionate spread, in the region.

Evolutionary potential in *P. cespitosum* populations

To more fully understand how *P. cespitosum* populations might differently contribute to the species' evolutionary trajectory in its introduced range, we assessed quantitative-genetic evolutionary potential by examining norm of reaction diversity *within* populations. Such diversity has been extensively studied as *genotype by environment interaction* or *G × E variation* (see Refs. 61, 65, and 75–83). G × E variation for traits that influence fitness constitutes the raw material for selective evolution of plasticity patterns. For each of six New England populations, we characterized norms of reaction of 16–19 genotypes in response to the contrasting open/dry and understory/moist glasshouse habitats.[84] (The total of 165 genotypes included some, but not all, of the high-performance genotypes identified in the broader 14-population sample.)

Consistent with the findings discussed above, genotypes in all populations shared similar patterns of plasticity for functional traits such as leaf structure and photosynthetic rate. However, reaction norm diversity for fitness and life-history traits, and consequently evolutionary potential for these aspects of plant performance, varied considerably among the six populations. Two of the populations included genotypes that differed consistently in these traits, similar to the high-performance genotypes found in several populations. Genotypes in these populations ranked either higher or lower than others in both understory/moist and open/dry conditions and showed a positive genetic correlation between early reproductive onset and high reproductive allocation.[84] This pattern of norm of reaction diversity allows consistently high-performing genotypes to selectively increase, leading to the evolution of especially invasive populations that generate high propagule pressure in diverse environments. In two other populations, there was significant norm of reaction diversity for fitness and life-history traits, but in these populations, some genotypes that achieved high fitness in one environment had relatively low fitness in the contrasting environment (*crossover interaction*). This pattern of decoupled, environment-specific fitness variance makes possible the evolution of altered norms of reaction or, depending on environmental variability, can buffer selection and allow diverse genotypes to persist.[75,78] Interestingly, the last two populations in the study revealed very low levels of quantitative genetic variation (i.e., both genotype and G × E were nonsignificant sources of variation according to analysis of variance (ANOVA).[84] As a result of evolutionary factors such as founder effects, inbreeding, and drift, combined with limited gene flow, some plant populations may lack the genetic variation that could otherwise fuel further selective change (e.g., Refs. 9, 15, 16, and 85–87).

This relatively modest sample of six *P. cespitosum* populations revealed considerable variation in quantitative genetic potential for future adaptive evolution in the species' introduced range. As a result of such differences in evolutionary potential, populations may contribute differentially to the invasion process. In particular, increased invasiveness may evolve in introduced-range populations that contain general-purpose, high-performing genotypes; those populations may then become the key sources for a species' further, increasingly aggressive spread in the new range. This points to an interesting possible difference between invasive taxa and their noninvasive congeners (see also Refs. 88–90). As Baker[1] noted, in many cases only one of a group of similar congeneric species is an aggressively colonizing, widespread weed. Within the monophyletic *Persicaria* section of the genus *Polygonum*, for instance, three introduced Eurasian annual species closely related to *P. cespitosum* are naturalized in northeastern North America but not invasive, although two of these species also exhibit substantial adaptive plasticity and have been present for many more generations in the region (references in Ref. 36). Previous data indicate that fitness norm of reaction diversity in New England populations of these species typically consists of crossover interaction (S.E. Sultan, D.L. Bell, and

A.M. Wilczek, unpublished data); the type of consistently high-output genotypes that can strongly promote invasive spread may not have evolved in these other introduced taxa—or at least not yet.

Dynamics of the *P. cespitosum* invasion: quantitative-genetic and microsatellite insights

Note that, in *P. cespitosum,* high-performing genotypes evidently do not represent a genetically distinct entity. The experimentally identified high-performance group was as genetically diverse as the control genotypes that were randomly sampled from across populations: both groups included substantial quantitative genetic variation, as well as similar amounts of variation for neutral microsatellite markers.[66,91] Thus, there is no evidence that a few specific "super-genotypes" have spread across the introduced range, as has occurred in certain well-studied plant invasions (e.g., single super-genotype of the invasive grass *Pennisetum setaceum;*[92] aggressive lineages of *Phragmites australis*[93,94]). Instead, *P. cespitosum* genotypes with accelerated life histories and consistently high reproductive output may have evolved independently in a number of different introduced-range populations. If such generalist genotypes can arise from diverse origins, the among-population variation we identified in their occurrence and frequency could reflect founder effects, outcrossing levels, population size and age, gene flow, and other evolutionary factors.[12,15,87]

Alternatively, high-performance genotypes of *P. cespitosum* may have evolved in the species' native Asian range and been transported to North America. Preliminary data do not support this alternative. Although four Asian populations were included in the initial, broad sample, not a single genotype from these Japanese and Korean populations reproduced at the top-5% level in resource-rich glasshouse conditions (see Appendix E in Ref. 66). While the lack of high-performance Asian genotypes may simply reflect a limited sample, it is also possible that increasingly generalist genotypes with accelerated life histories are evolving uniquely in the species' introduced range. If this is indeed the case, it could reflect several aspects of the species' circumstances in North America. Novel genetic admixtures can arise when multiple introductions bring into contact genotypes from distant parts of a species' home range.[14,95–99] Levels of environmental variability that favor evolution of generalist norms of reaction may be higher in the disturbed New England habitats into which the species is spreading.[62,100] In the absence of coevolved herbivores or pathogens, selection pressures for defensive traits may be relaxed in ways that permit norms of reaction for accelerated life histories with high reproductive output to evolve.[101,102] The phenological trade-off between relatively rapid early development and delayed reproductive onset may be advantageous in New England's moderate conditions, but less so in colder or montane areas in the native range. Expanded studies of Asian populations of *P. cespitosum* are currently underway to clarify whether ecologically generalist, high-performing genotypes occur only in North America or are also found in native-range populations, and whether plants in the native range undergo more severe herbivory.

A different type of insight to the species' genetic diversity and possible invasion history in northeastern North America was provided by a multi-population survey of neutral molecular variation.[91] In this collaborative study, we examined nine polymorphic microsatellite markers in a sample of 35 individuals from each of 16 New England populations (total $N = 516$). As expected for a largely self-fertilizing species, observed heterozygosity was low at all nine loci. Yet substantial genetic variation was present both within and among populations (Fig. 8). Within populations, we found an average of 10 alleles per polymorphic locus (range 3–23), with up to five private alleles occurring in most populations. Among-population variation was quite high (i.e., pairwise F_{ST} values were >0.5 in over 60% of comparisons). High among-population divergence is consistent with the species' limited dispersal and with drift resulting from modest population sizes and high inbreeding due to self-fertilization (see also Refs. 15 and 96).

A more surprising finding was that the distribution of molecular-genetic clusters among populations showed neither a geographic nor an ecological pattern. Geographically closer populations were no more genetically similar than geographically distant ones (Fig. 8), and there was no association between genetic similarity and habitat similarity along either light or moisture axes.[91] This result is concordant with the lack of local adaptation found in the quantitative-genetic studies of population diversity

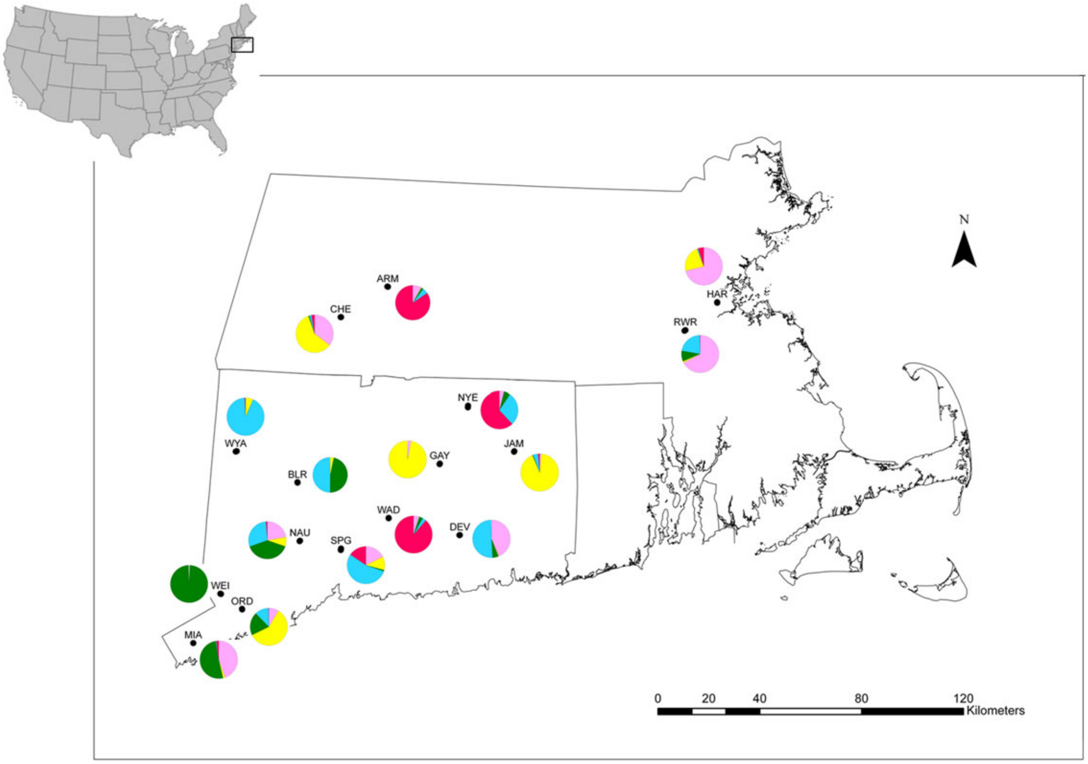

Figure 8. Spatial distribution of DNA microsatellite variation in 16 New England *P. cespitosum* populations. Microsatellite analyses revealed substantial genetic variation within as well as among populations in the introduced range, but there was no relation between geographic distance and degree of genetic similarity. Pie charts for each population show average assignment coefficients (posterior likelihood) estimated by Bayesian clustering (using Structure 2.3) of nine polymorphic microsatellite markers, on the basis of 22–45 individuals per population (total $N = 516$). Different colors show independent genetic clusters. Figure modified from Ref. 91.

discussed above (Refs. 74 and 84; in highly selfing species such as *P. cespitosum*, the entire genome is inherited, so variation in neutral markers can be expected to correspond generally with variation in quantitative traits). With respect to the species' recent spread to more open sites, the microsatellite data are consistent with a history of multiple independent colonization events, rather than the spread of a certain population or genetically distinct ecotype into these sites.

In general, the species' population structure in New England suggests random colonization and establishment of genotypes in different locations and habitats, with among-population variation driven by chance factors such as founder effects and drift. Such an idiosyncratic invasion process could be driven in part by repeated introduction events and subsequent human-mediated dispersal into disturbed sites such as roadsides, parks, forests, and meadows. The high levels of genetic variation within introduced-range populations show that the species did not undergo a genetic bottleneck in reaching this new region, as is often predicted for species introductions.[15] Indeed, four Asian populations of *P. cespitosum* had lower within-population allelic richness than the New England populations (see Appendix S4 in Ref. 91). A pattern of increased rather than reduced molecular-genetic diversity in introduced-range populations has been found in several invasive plants and animals.[95,98,103–107] Our microsatellite data suggest a history of multiple introductions of *P. cespitosum* to northeastern North America; the occurrence of different genetic clusters within populations in this introduced range further indicates that individual populations may have had several different sources. Consequently, the species maintains considerable genetic variability in its introduced range, leading to the possibility of new genetic admixtures and selective change in future.

Conclusions

Our studies of *P. cespitosum* have focused on patterns of individual plasticity—i.e., genotypic norms of reaction—to investigate (1) an introduced plant's recent transition to aggressive spread and (2) the evolutionary potential for increased invasiveness within and among its introduced-range populations. Field data and microsatellite analyses provided environmental and molecular-genetic contexts, respectively. Our specific findings point to some intriguing implications and key questions for understanding species invasions more generally.

Comparative field environmental measurements across a 15-year interval confirmed that *P. cespitosum* had spread into a broader range of habitats within northeastern North America (New England). An introduced species may undergo ecological range expansion, even within an existing geographical range; this critical dimension of a species' invasive spread is seldom examined.

Resurrection experiments comparing genotypes sampled from the same environmentally patchy *P. cespitosum* field populations in 1994 and again in 2005 revealed that more broadly adaptive norms of reaction had evolved during this period. This change in individual plasticity accompanied the species' enlarged ecological distribution and transition to invasiveness. Evidently, altered plasticity patterns can evolve quite rapidly, even in the absence of strong directional selection. Could the evolution of greater adaptive plasticity be a common event during the lag phase between a species' introduction to a new range and its invasive spread? This particular type of evolutionary change is especially likely if an introduced species colonizes variable habitats that selectively favor generalist, adaptively plastic genotypes. Norm of reaction resurrection experiments conducted on introduced-range populations can directly test this possibility.

Although all *P. cespitosum* genotypes expressed functional plasticity, several introduced-range populations included Bakeresque general-purpose genotypes that consistently reproduced more than others across diverse conditions including drought, sun, and shade. These high-performance individuals (of diverse genetic origin) exhibited a suite of life-history traits associated with invasiveness: rapid germination and growth, early reproductive onset, high reproductive allocation, and competitive success in high-resource conditions. Clearly, in some populations and taxa, it is possible for evolution to produce genotypes that are "masters of all." Perhaps it is those systems in which a transition to invasiveness is particularly likely, as such genotypes can be expected to powerfully promote a species' spread across diverse sites via consistently high propagule pressure. An important future question is whether the novel admixtures that may occur in an introduced range following multiple introductions from diverse native-range sites are particularly potent sources of such high-performance genotypes.

The presence of high-performance genotypes created an unexpected pattern of diversity within certain introduced-range populations of *P. cespitosum*—consistently higher- and lower-performing genotypes. In these populations, selection can be expected to result in increased invasiveness, as broadly adaptive, high-fitness individuals increasingly predominate over time. Populations that include a higher-versus-lower pattern of genetic diversity may therefore be especially likely to undergo an evolutionary transition to invasiveness, possibly during a lag phase. By contrast, populations or entire taxa characterized by the more common diversity pattern of crossover G × E interaction among genotypes (i.e., higher relative success in certain environments than others) may be less likely to evolve in this way. Evolutionary potential for invasiveness, like other aspects of genetic diversity, may differ substantially among populations of an introduced species; norm of reaction data for key life-history traits can provide direct insight to this issue.

Mirroring these patterns of genotypic diversity, *P. cespitosum* populations in the introduced range did not show local adaptive diversification. Instead, certain populations exhibited consistently higher reproductive fitness in all experimental habitats, reflecting a greater proportion of high-performance individuals. In general, populations that include high-performance genotypes are likely to be the main sources of a species' immediate invasive spread; as such genotypes increase selectively within those populations, the latter may also serve as evolutionary foci for greater invasiveness that will then spread across the introduced range. It may be that an introduced species becomes invasive owing to the evolutionary changes that occur in a subset of populations that subsequently spread most effectively. These insights highlight the importance of population-level data for understanding invasion dynamics, including types and patterns of genotypic diversity within and among introduced-range populations.

In an "eco-devo" approach, plasticity is not an alternative to evolutionary change, but constitutes the genotypic diversity on which selection acts, and that itself evolves.[108] Even in an annual plant characterized by individual adaptive plasticity, certain genotypes may arise, in certain introduced-range populations, that play critical roles in the transition to invasiveness. Further eco-devo studies identifying such "ideal weeds" may lead to a greater understanding of the individual and population-level factors that contribute to invasiveness and of the broader interplay of adaptive plasticity and selective evolution.

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Conflict of interest

The authors declare no conflicts of interest.

References

1. Baker, H.G. 1965. "Characteristics and modes of origin of weeds." In *The Genetics of Colonizing Species.* H.G. Baker & G.L. Stebbins, Eds.: 147–172. New York: Academic Press.
2. Barrett, S.C.H. 2015. Foundations of invasion genetics: the Baker and Stebbins legacy. *Mol. Ecol.* **24:** 1927–1941.
3. Richardson, D.M. 2001. "Plant invasions." In *Encyclopedia of Biodiversity.* Vol. 4. S.A. Levin, Ed.: 677–688. San Diego, CA: Academic Press.
4. Mack, R.N. *et al.* 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10:** 689–710.
5. Pimentel, D., R. Zuniga & D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* **52:** 273–288.
6. MacIsaac, H.J., R.A. Tedla & A. Ricciardi. 2011. "Patterns and rate of growth of studies in invasion ecology." In *Fifty Years of Invasion Ecology. The Legacy of Charles Elton.* D.M. Richardson, Ed.: 51–60. Chichester, UK: Wiley-Blackwell.
7. Levine, J.M. *et al.* 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. Biol. Sci.* **270:** 775–781.
8. Mooney, H.A. & E.E. Cleland. 2001. The evolutionary impact of invasive species. *Proc. Natl. Acad. Sci. U. S. A* **98:** 5446–5451.
9. Parker, I.M., J. Rodriguez & M.E. Loik. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus. Conserv. Biol.* **17:** 59–72.
10. Sakai, A.K. *et al.* 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32:** 305–332.
11. Wares, J.P., A.R. Hughes & R.K. Grosberg. 2005. "Mechanisms that drive evolutionary change: insights from species introductions and invasions." In *Species Invasions, Insights into Ecology, Evolution and Biogeography.* D.F. Sax, J.J. Stachowicz & S.D. Gaines, Eds.: 229–257. Sunderland, MA: Sinauer.
12. Lee, C.E. 2002. Evolutionary genetics of invasive species. *Trends Ecol. Evol.* **17:** 386–391.
13. Huey, R.B., G.W. Gilchrist & A.P. Hendry. 2005. "Using invasive species to study evolution. Case studies with Drosophila and salmon." In *Species Invasions: Insights into Ecology, Evolution, and Biogeography.* D.F. Sax, J.J. Stachowicz & S.D. Gaines, Eds.: 139–164. Sunderland, MA: Sinauer Associates.
14. Whitney, K.D. & C.A. Gabler. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity Distrib.* **14:** 569–580.
15. Dlugosch, K.M. & I.M. Parker. 2008. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Mol. Ecol.* **17:** 431–449.
16. Prentis, P.J. *et al.* 2008. Adaptive evolution in invasive species. *Trends Plant Sci.* **13:** 288–294.
17. Dormontt, E.E., A.J. Lowe & P.J. Prentis. 2011. "Is rapid adaptive evolution important in successful invasions?" In *Fifty Years of Invasion Ecology: The Legacy of Charles Elton.* D.M. Richardson, Ed.: 175–194. Wiley-Blackwell.
18. Parker, J.D. *et al.* 2013. Do invasive species perform better in their new ranges? *Ecology* **94:** 985–994.
19. Crooks, J.A. & M.E. Soulé. 1999. "Lag times in population explosions of invasive species: causes and implications." In *Invasive Species and Biodiversity Management.* O.T.

Sandlund, P.J. Schei & A. Viken, Eds. The Netherlands: Kluwer Academic Publisher.

20. Baker, H.G. 1974. The evolution of weeds. *Annu. Rev. Ecol. Syst.* **5:** 1–24.
21. Sultan, S.E. 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* **5:** 537–542.
22. Sultan, S.E. 2003. Phenotypic plasticity in plants: a case study in ecological development. *Evol. Dev.* **5:** 25–33.
23. Richards, C.L. *et al.* 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol. Lett.* **9:** 981–993.
24. Sultan, S.E. 2004. Promising directions in plant phenotypic plasticity. *Perspect. Plant Ecol. Evol. Syst.* **6:** 227–233.
25. Sultan, S.E. & S.C. Stearns. 2005. "Environmentally contingent variation: phenotypic plasticity and norms of reaction." In *Variation: A Central Concept in Biology*. B. Hall & B. Hallgrimsson, Eds.: 303–332. Boston, MA: Elsevier Academic Press.
26. Kim, S.T. & M.J. Donoghue. 2008. Molecular phylogeny of Persicaria (Persicarieae, Polygonaceae). *Syst. Bot.* **33:** 77–86.
27. Franks, S.J. *et al.* 2008. The resurrection initiative: storing ancestral genotypes to capture evolution in action. *Bioscience* **58:** 870–873.
28. Blake, S.F. 1932. *Polygonum caespitosum* var. longisetum in the United States. *Rhodora* **34:** 146–147.
29. Paterson, A.K. 2000. Range expansion of *Polygonum caespitosu*m var. longisetum in the United States. *Bartonia* **60:** 57–69.
30. Anjen, L. *et al.* 2003. "Polygonaceae." In *Flora of China.* Vol. 5 (Ulmaceae through Basellaceae). Beijing: Science Press, and St. Louis: Missouri Botanical Garden Press.
31. Gleason, H.A. & A. Cronquist. 1991. *Manual of Vascular Plants of NE United States and adjacent Canada.* New York: New York Botanical Gardens.
32. Mitchell, R.S. & J.K. Dean. 1978. "Polygonaceae of New York State." In *Contributions to a Flora of New York State I.* Albany: Bulletin 431 University of the State of New York, New York State Museum.
33. Stanford, E.E. 1925. The inflorescence and flower-form in *Polygonum*, subgenus Persicaria. *Rhodora* **27:** 41–47.
34. Matesanz, S., T. Horgan-Kobelski & S.E. Sultan. 2015. Evidence for rapid ecological range expansion in a newly invasive plant. *AoB Plants* **7:** plv038.
35. Mehrhoff, L.J. *et al.* 2003. *IPANE. Invasive Plant Atlas of New England.* Storrs, CT: Department of Ecology & Evolutionary Biology, University of Connecticut. http://www.invasive.org/weedcd/html/ipane.htm.
36. Sultan, S.E. *et al.* 1998. Contrasting ecological breadth of co-occurring annual *Polygonum* species. *J. Ecol.* **86:** 363–383.
37. Hastings, A. *et al.* 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.* **8:** 91–101.
38. With, K.A. 2002. The landscape ecology of invasive spread. *Conserv. Biol.* **16:** 1192–1200.
39. Theoharides, K.A. & J.S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* **176:** 256–273.
40. Lockwood, J.L., P. Cassey & T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* **20:** 223–228.
41. Simberloff, D.S. 2009. The role of propagule pressure in biological invasions. *Annu. Rev. Ecol. Evol. Syst.* **40:** 81–102.
42. Franks, S.J., S. Sim & A.E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci. U. S. A.* **104:** 1278–1282.
43. Bustos-Segura, C., J. Fornoni & J. Núñez-Farfán. 2014. Evolutionary changes in plant tolerance against herbivory through a resurrection experiment. *J. Evol. Biol.* **27:** 488–496.
44. Sultan, S.E. *et al.* 2013. A resurrection study reveals rapid adaptive evolution within populations of an invasive plant. *Evol. Appl.* **6:** 266–278.
45. Carroll, S.P. *et al.* 2007. Evolution on ecological time-scales. *Funct. Ecol.* **21:** 387–393.
46. Stockwell, C.A., A.P. Hendry & M.T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* **18:** 94–101.
47. Ghalambor, C.K. *et al.* 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21:** 394–407.
48. Ellner, S.P., M.A. Geber & N.G. Hairston. 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol. Lett.* **14:** 603–614.
49. Maron, J.L. *et al.* 2004. Rapid evolution of an invasive plant. *Ecol. Monogr.* **74:** 261–280.
50. Dlugosch, K.M. & I.M. Parker. 2008. Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecol. Lett.* **11:** 701–709.
51. Burger, J.C. & N.C. Ellstrand. 2014. Rapid evolutionary divergence of an invasive weed from its crop ancestor and evidence for local diversification. *J. Syst. Evol.* **52:** 750–764.
52. Colautti, R.I. & S.C.H. Barrett. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* **342:** 364–366.
53. Vandepitte, K. *et al.* 2014. Rapid genetic adaptation precedes the spread of an exotic plant species. *Mol. Ecol.* **23:** 2157–2164.
54. Grossman, J.D. & K.J. Rice. 2014. Contemporary evolution of an invasive grass in response to elevated atmospheric CO_2 at a Mojave Desert FACE site. *Ecol. Lett.* **17:** 710–716.
55. Colautti, R.I. & J.A. Lau. 2015. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* **24:** 1999–2017.
56. Rollins, L.A., M.F. Richardson & R. Shine. 2015. A genetic perspective on rapid evolution in cane toads (*Rhinella marina*). *Mol. Ecol.* **24:** 2264–2276.
57. Bone, E. & A. Farres. 2001. "Trends and rates of microevolution in plants." In *Microevolution Rate, Pattern, Process.* Vol. 8. A.P. Hendry & M.T. Kinnison, Eds.: 165–182. The Netherlands: Springer.
58. Hendry, A.P. & M.T. Kinnison. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53:** 1637–1653.

59. Hendry, A.P., T.J. Farrugia & M.T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* **17:** 20–29.
60. Kawecki, T.J., N.H. Barton & J.D. Fry. 1997. Mutational collapse of fitness in marginal habitats and the evolution of ecological specialisation. *J. Evol. Biol.* **10:** 407–429.
61. Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24:** 35–68.
62. Sultan, S.E. & H.G. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. *Am. Nat.* **160:** 271–283.
63. Moran, N.A. 1992. The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139:** 971–989.
64. Lande, R. 2015. Evolution of phenotypic plasticity in colonizing species. *Mol. Ecol.* **24:** 2038–2045.
65. Zenni, R.D. *et al.* 2014. Adaptive evolution and phenotypic plasticity during naturalization and spread of invasive species: implications for tree invasion biology. *Biol. Invasions* **16:** 635–644.
66. Matesanz, S. & S.E. Sultan. 2013. High performance genotypes in an introduced plant: insights to future invasiveness. *Ecology* **94:** 2464–2474.
67. Van Kleunen, M. *et al.* 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol. Lett.* **13:** 947–958.
68. Hayes, K.R. & S.C. Barry. 2007. Are there any consistent predictors of invasion success? *Biol. Invasions* **10:** 483–506.
69. Pyšek, P. & D.M. Richardson. 2007. "Traits associated with invasiveness in alien plants: where do we stand?" In *Biological Invasions. Ecological Studies.* Vol. 193. W. Nentwig, Ed.: 97–126. Berlin, Heidelberg**:** Springer-Verlag.
70. van Kleunen, M., W. Dawson & N. Maurel. 2015. Characteristics of successful alien plants. *Mol. Ecol.* **24:** 1954–1968.
71. Corliss, C.T. 2014. Evolutionary potential for increased invasiveness: genetic variation for competitive ability in the invasive plant *Polygonum cespitosum*. Masters Thesis. Wesleyan University.
72. Goldberg, D.E. & K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J. Ecol.* **79:** 1013–1030.
73. Wang, P. *et al.* 2010. Are competitive effect and response two sides of the same coin, or fundamentally different? *Funct. Ecol.* **24:** 196–207.
74. Matesanz, S., T. Horgan-Kobelski & S.E. Sultan. 2012. Phenotypic plasticity and population differentiation in an ongoing species invasion. *PLoS One* **7:** e44955.
75. Via, S. & R. Lande. 1985. Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution* **39:** 502–522.
76. Des Marais, D.L., K.M. Hernandez & T.E. Juenger. 2013. Genotype-by-environment interaction and plasticity: exploring genomic responses of plants to the abiotic environment. *Annu. Rev. Ecol. Evol. Syst.* **44:** 5–29.
77. Gomulkiewicz, R. & M. Kirkpatrick. 1992. Quantitative genetics and the evolution of reaction norms. *Evolution* **46:** 390–411.
78. Gillespie, J.H. & M. Turelli. 1989. Genotype–environment interactions and the maintenance of polygenic variation. *Genetics* **121:** 129–138.
79. Scheiner, S.M. & R.D. Holt. 2012. The genetics of phenotypic plasticity. X. Variation versus uncertainty. *Ecol. Evol.* **2:** 751–767.
80. Barton, N.H. & M. Turelli. 1989. Evolutionary quantitative genetics – how little do we know. *Annu. Rev. Genet.* **23:** 337–370.
81. Falconer, D.S. & T.F.C. Mackay. 1996. *Introduction to Quantitative Genetics.* Essex, England.
82. Kingsolver, J.G. *et al.* 2007. Relating environmental variation to selection on reaction norms: an experimental test. *Am. Nat.* **169:** 163–174.
83. Kruuk, L.E.B., J. Slate & A.J. Wilson. 2008. New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annu. Rev. Ecol. Evol. Syst.* **39:** 525–548.
84. Matesanz, S., T. Horgan-Kobelski & S.E. Sultan. 2014. Contrasting levels of evolutionary potential in populations of the invasive plant *Polygonum cespitosum. Biol. Invasions* **16:** 455–468.
85. Al-Hiyaly, S.A. *et al.* 1993. The effect of zinc contamination from electricity pylons – genetic constraints on selection for zinc tolerance. *Heredity* **70:** 667-667.
86. Al-Hiyaly, S.A., T. McNeily & A.D. Bradshaw. 1988. The effects of zinc contamination from electricity pylons – evolution in a replicated situation. *New Phytol.* **110:** 571–580.
87. Byers, D.L. 2005. Evolution in heterogeneous environments and the potential of maintenance of genetic variation in traits of adaptive significance. *Genetica* **123:** 107–124.
88. van Kleunen, M. *et al.* 2011. Preadapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *J. Biogeogr.* **38:** 1294–1304.
89. van Kleunen, M., E. Weber & M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* **13:** 235–245.
90. Mack, R.N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biol. Conserv.* **78:** 107–121.
91. Matesanz, S. *et al.* 2014. Genetic diversity and population structure in *Polygonum cespitosum*: insights to an ongoing plant invasion. *PLoS One* **9:** e93217.
92. Le Roux, J.J. *et al.* 2007. Super-genotype: global monoclonality defies the odds of nature. *PLoS One* **2:** e590.
93. Mozdzer, T.J. & J.C. Zieman. 2010. Ecophysiological differences between genetic lineages facilitate the invasion of non-native *Phragmites australis* in North American Atlantic coast wetlands. *J. Ecol.* **98:** 451–458.
94. Saltonstall, K. 2003. Genetic variation among north American Populations of *Phragmites australis*: implications for management. *Estuaries* **26:** 444–451.
95. Facon, B. *et al.* 2008. High genetic variance in life-history strategies within invasive populations by way of multiple introductions. *Curr. Biol.* **18:** 363–367.
96. Novak, S.J. & R.N. Mack. 2005. "Genetic bottlenecks in alien plant species." In *Species Invasions, Insights into Ecology, Evolution and Biogeography*. D.F. Sax, J.J. Stachowicz & S.D. Gaines, Eds.: 201–228. Sunderland, MA**:** Sinauer.

97. Ellstrand, N.C. & K.A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc. Natl. Acad. Sci. U. S. A.* **97:** 7043–7050.
98. Lavergne, S. & J. Molofsky. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. U. S. A.* **104:** 3883–3888.
99. Wolfe, L.M., A.C. Blair & B.M. Penna. 2007. Does intraspecific hybridization contribute to the evolution of invasiveness? An experimental test. *Biol. Invasions* **9:** 515–521.
100. Matesanz, S., E. Gianoli & F. Valladares. 2010. Global change and the evolution of phenotypic plasticity in plants. *Ann. N. Y. Acad. Sci.* **1206:** 35–55.
101. Colautti, R.I. *et al.* 2004. Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.* **7:** 721–733.
102. Liu, H. & P. Stiling. 2006. Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions* **8:** 1535–1545.
103. Kolbe, J.J. *et al.* 2004. Genetic variation increases during biological invasion by a Cuban lizard. *Nature* **431:** 177–181.
104. Novak, S.J. & R.N. Mack. 1993. Genetic variation in *Bromus tectorum* (Poaceae): comparison between native and introduced populations. *Heredity* **71:** 167–176.
105. Pawlak, A.R. *et al.* 2015. Invasion of *Bromus tectorum* (L.) into California and the American Southwest: rapid, multidirectional and genetically diverse. *Biol. Invasions* **17:** 287–306.
106. Molins, M.P. *et al.* 2014. Biogeographic variation in genetic variability, apomixis expression and ploidy of St. Johns wort (*Hypericum perforatum*) across its native and introduced range. *Ann. Bot.* **113:** 417–427.
107. Veale, A.J. *et al.* 2015. An invasive non-native mammal population conserves genetic diversity lost from its native range. *Mol. Ecol.* **24:** 2156–2163.
108. Sultan, S.E. 2015. Organism and Environment: Ecological Development, Niche Construction and Adaptation. London: Oxford University Press.