

## LETTER

# Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks

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## Abstract

Human-mediated species introductions offer opportunities to investigate when and how non-native species to adapt to novel environments, and whether evolution has the potential to contribute to colonization success. Many long-established introductions harbour high genetic diversity, raising the possibility that multiple introductions of genetic material catalyze adaptation and/or the evolution of invasiveness. Studies of nascent invasions are rare but crucial for understanding whether genetic diversity facilitates population expansion. We explore variation and evolution in founder populations of the invasive shrub *Hypericum canariense*. We find that these introductions have experienced large reductions in genetic diversity, but that increased growth and a latitudinal cline in flowering phenology have nevertheless evolved. These life history changes are consistent with predictions for invasive plants. Our results highlight the potential for even genetically depauperate founding populations to adapt and evolve invasive patterns of spread.

## Keywords

Biological invasions, Canary Island St John's wort, exotic species, founding event, life history evolution, quantitative trait variation.

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## INTRODUCTION

Human-mediated species introductions have resulted in thousands of successful colonization events, but there is still very little concrete information about the factors that dictate whether an introduction will spread and invade (Sakai *et al.* 2001). It has been suggested that adaptation to novel conditions might play an important role in promoting invasions (Sakai *et al.* 2001; Cox 2004), however, all introduced species must go through founding events, and we might expect such events to reduce genetic diversity and limit adaptive evolution (Nei *et al.* 1975; Barrett & Kohn 1991). This contrast between the deleterious implications of founding events and the success of introduced species has been called a paradox in invasion biology (Allendorf & Lundquist 2003; Frankham 2005; Elam *et al.* 2007). Recent reviews have emphasized that large losses of variation are rare among invaders, and that many species may resolve the paradox by somehow maintaining genetic diversity during colonization (Novak & Mack 2005; Wares *et al.* 2005). A number of studies have suggested that repeated

introductions of additional genetic material might be the catalyst of invasion in some cases (Ellstrand & Schierenbeck 2000; Kolbe *et al.* 2004; Lockwood *et al.* 2005; Novak & Mack 2005; Lavergne & Molofsky 2007). Where invasions proceed with very low amounts of genetic variation, their success has been understood to rely not on adaptation but instead on plasticity (e.g. Meimberg *et al.* 2006) or species-specific benefits of high genetic similarity (Tsutsui *et al.* 2000).

A more extensive quantitative review of genetic variation in 80 invading species has revealed that some loss of variation is in fact common to most invasions, and that substantial bottlenecks are not rare among invaders (e.g. about half of species showed losses of allelic richness > 20%; Dlugosch & Parker 2008). Moreover, most of these studies have focused on long-established species, where cases of high molecular genetic diversity may simply reflect the accumulation of repeated introductions during the years of expansion. Individual founding events of those same species may have invaded despite substantial losses of molecular variation, bringing into question the potential for genetic diversity to enhance the spread of those populations.

Studies of such nascent invasions are therefore critical for clarifying the putative association between molecular genetic diversity and the evolution of invasive behaviour. In fact, we might predict that the two are poorly correlated, given that adaptive variation often deviates from expectations based upon neutral genetic variation (e.g. Pfrender *et al.* 2000).

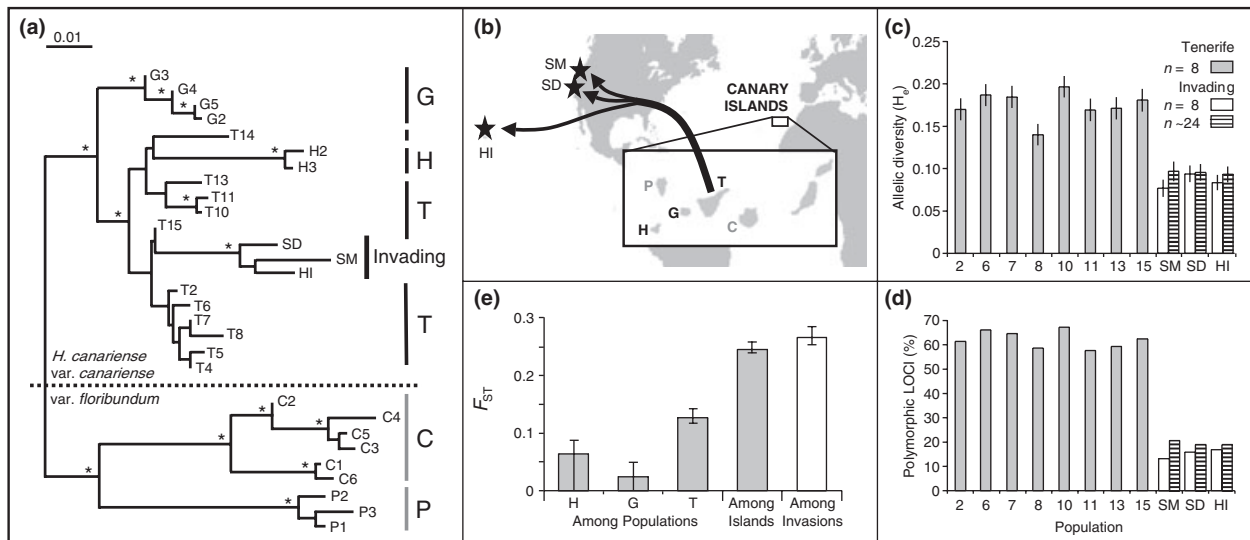
Here we provide an explicit assessment of variation and evolution in isolated introductions of an ornamental shrub. *Hypericum canariense* L. (Hypericaceae) is a perennial plant endemic to the Canary Islands (Robson 1996). Small private plantings (single introductions) of this species have spread aggressively over < 50 years in two isolated sites in California and one location on Maui in the Hawaiian islands, USA. Although still limited in range, this species is considered to have the potential for widespread invasion because of its rapid rate of spread and ability to displace other vegetation (see Appendix S1 for details). We use molecular markers to determine the source of the invading material and to ask whether these successful colonization events show evidence of high molecular genetic variation. We then use common gardens in the introduced range to determine whether adaptation in life history has occurred in these populations. We find that each invasion has experienced a large loss of molecular variation relative to native populations, but that changes in growth and flowering phenology have nevertheless evolved according to predictions for invading plants.

## MATERIALS AND METHODS

### Study species and collections

*Hypericum canariense* is a multistemmed perennial shrub that can reach 3 m in height. It is common across the mesic mid-elevations of the western five Canary Islands (Bramwell & Bramwell 1984; see Fig. 1b). The native range is characterized by a Mediterranean climate type, with mild wet winters that are the plants' primary growing season, and dry summers during which reproduction occurs. In spring, plants begin flowering and typically drop most of their leaves. Flowers are yellow, conspicuous (2–3 cm across) and have many exposed stamens, suggesting generalist insect pollination. A single plant can produce hundreds of flowers, and individual fruits can yield thousands of tiny (< 0.1 mg) seeds. Fruits are dry capsules that persist on the plant, and seeds have no specialized adornments for dispersal. Plants are capable of limited (*c.* 1 m) rhizomatous spread and self-pollination; however, most genetic variation in the native range is harboured within populations, suggesting that outcrossing is common (Dlugosch & Parker 2007).

Collections of leaves and seeds were made during August 2002 and 2003 from 18 native sites described previously (those with 5–25 samples per site in Dlugosch & Parker 2007) and from introductions (23–25 samples per site) to San Mateo County, CA, USA (37°0'41" N,



**Figure 1** Origin and molecular variation of invasive founding populations in *H. c. var. canariense*. (a) Neighbor-joining phenogram of Nei's genetic distances among sites in the native range: La Palma (P), El Hierro (H), La Gomera (G), Tenerife (T), and Gran Canaria (C); and from invasions in San Mateo county (SM), San Diego county (SD) and Maui (HI), USA. Distances are based upon 244 polymorphic AFLP markers, and (\*) indicates bootstrap values > 90% from 500 resampled datasets. (b) Map indicating the putative source of the introductions on the Canary Island of Tenerife. (c) Mean expected allelic diversity ( $H_e$ ) and (d) the percent of polymorphic loci (estimated frequency > 0.05) for each invasion and for populations across Tenerife. Values for increased sample sizes are shown for the invasions ( $n = 23$ –25). Error bars around  $H_e$  show standard errors across loci. (e)  $F_{ST}$  values within and among islands and among invasions; error bars show 95% confidence intervals generated by 1000 permutations of the data.

122°21'25" W; hereafter SM), San Diego, CA, USA (32°42'5" N, 117°14'39" W; hereafter SD) and Kula, Maui, USA (20°43'37" N, 156°18'37" W; hereafter HI; Appendix S1). Replicates at each site were collected  $\geq 5$  m apart along transects roughly parallel to road or trail access. Leaf samples from the invasions were collected from the areas of initial colonization (see Appendix S1) to best reflect the diversity present among the founders at each site (verified through additional sampling, KMD unpublished data), while seeds were collected from across each invasion to include more recent cohorts at the invasion fronts.

### Molecular variation

The small native range of *H. canariense* permits unusually intensive sampling of potential introduction sources. We have previously used DNA sequences of the nuclear ribosomal internal transcribed spacer (ITS) region as well as 244 amplified fragment length polymorphism (AFLP) loci to characterize the phylogeographic structure of the native range (Dlugosch & Parker 2007). ITS sequencing and AFLP fragment analyses of the invading populations were conducted using the same primers and conditions (Dlugosch & Parker 2007). For AFLP data, a neighbour-joining phenogram of Nei's genetic distances among the invading and native populations was constructed using PAUP 4.0 (Swofford 1998). Allele frequencies and genetic distances were estimated using a Bayesian approach implemented in the program AFLP-SURV 1.0 (Vekemans *et al.* 2002), and 500 resampled data sets were used to generate bootstrap values in PHYLIP 3.65 (Felsenstein 1989). Expected heterozygosity and the proportion of polymorphic alleles in each population were calculated in AFLP-SURV using the 189 markers that were polymorphic across the invasions and their source island of Tenerife (see Results). All Tenerife populations included eight individuals per site. For the invasions, a subsample of eight individuals was used for direct comparison of diversity metrics with the Tenerife sites. Diversity metrics for the full sample of 23–25 individuals per invasion were calculated to assess the influence of sampling effort on these values. Genetic differentiation ( $F_{ST}$ ) among populations was estimated using AFLP-SURV, and confidence intervals around  $F_{ST}$  values were generated using 1000 permutations.

### Life history evolution

Growth and flowering traits were compared among the invasions and the three native islands where plants of the same genetic variety are found (El Hierro, La Gomera, and Tenerife, see Results). Three offspring from each of 10

individuals per invading population and per native island were included in a randomized rooftop common garden at the University of California campus in Santa Cruz, CA [180 individuals total, data from native populations previously included in a study of differentiation across the Canary Islands (Dlugosch & Parker 2007)]. Seeds were germinated in the greenhouse, but seedlings were reared outside where they experienced ambient conditions similar to those found in their native range (Mediterranean climate with coastal fog input).

Seeds were germinated during November 2002 by placing 20–30 seeds on the surface of moistened soil (Pro-mix HP; Premier Horticulture Inc., Quakertown, PA, USA) in 5 cm by 5 cm pots. Flats of pots were covered with a clear, ventilated lid and kept in a greenhouse at 21° C 16-h days/13° C 8-h nights for 8 weeks. After 4 weeks, seedlings were thinned as needed to prevent shading among individuals. During week 8, seedlings were transplanted individually to Ray Leach pine cell 'conetainers' (Stuewe & Sons Inc., Corvallis, OR, USA) and fully randomized. Conetainers were watered daily and fertilized weekly with 130 ppm equal parts NPK fertilizer (JR Peters Inc., Allentown, PA, USA). On 15 February (week 13), plants were moved outside to the greenhouse roof for the spring and summer, and were watered during delivery of weekly fertilizer. In June (week 30) plants were potted in 7.6-L pots, re-randomized, and fertilized with applications of slow-release fertilizer (Osmocote; Scotts Miracle-Gro Co., Marysville, OH, USA).

Changes in biomass were monitored using a non-destructive size index developed from observations of naturally occurring *H. canariense* at the San Mateo county invasion {linear regression:  $N = 20$ ,  $r^2_{adj} = 0.96$ ,  $P < 0.0001$ , yielding the relationship: [wet biomass (g) =  $218.5 \times \text{basal area (cm}^2) \times \text{maximum height (cm)}$ ] (Dlugosch & Parker 2007). Exponential growth rates were fit to estimated biomass values from 1 July, 1 October and 22 November 2003. Growth exponents and log-transformed final sizes were compared among the populations using restricted maximum likelihood (REML) estimation of variance components (Lynch & Walsh 1998). The models included locations nested within provenance (native vs. introduced) and a random family effect nested within site. All statistical analyses of common garden data were conducted using JMP 7 (SAS Institute, Cary, NC, USA).

Beginning in July, plants were checked three times per week for their first fully open flower. Flowering date were compared among populations using REML analysis, with family (random effect) nested within location and location nested within provenance (native vs. introduced). Growth rate was included as a covariate in the analysis to test for independent evolution of these two traits.

Maternal effects could influence patterns of population differentiation. Typically, maternal environment is thought to have the greatest influence on traits expressed very early in life, such as germination timing and initial growth rate (Roach & Wulff 1987). Our measurements of growth and flowering were taken from plants several months old; nevertheless, we tested for an influence of seed mass (a common metric of maternal investment, Roach & Wulff 1987) on our data. Individuals were assigned the average mass of seeds from their respective fruits, quantified by weighing samples of 50 seeds per fruit. We found no effect of seed mass as a covariate in any of our models (growth rate:  $P = 0.68$ , size:  $P = 0.65$ , flowering date:  $P = 0.10$ ), although we note that unmeasured maternal effects may still have been present.

Rates of evolution were calculated as Haldanes, the per-generation change in pooled standard deviations of the trait  $[(\text{mean}_1 - \text{mean}_2)/\text{SD}/\text{generation}]$  (Gingerich 1983), and as Darwins, the change in log-transformed means per million years  $[\ln(\text{mean}_1) - \ln(\text{mean}_2)/\text{years} \times 10^6]$  (Haldane 1949). Means and standard deviations were derived from least squares means and total phenotypic variances generated by REML analyses with nested family effects. For growth rate, invasions as group were compared with their source island of Tenerife (see Results). For flowering date, growth rate was used as a covariate in the model, and the HI and SM populations were compared with their midpoint to make the conservative assumption that each has evolved minimally from a common intermediate phenotype (see Results).

The potential for future life history evolution was investigated by comparing variance of growth rate and flowering date among the invasions and their source island of Tenerife. Bartlett's tests were used to test for significant changes in phenotypic variance, and coefficients of variation were calculated using least squares means and both total phenotypic variance and maternal family variance from REML models fit to each population. Maternal family variance was examined to provide an index of genetically based variance in each population.

### Selection on size in the field

We quantified the fitness implications (survival and reproduction) of different growth rates in the invaded range. We planted invading genotypes into the ground under natural levels of competition, predation, and disturbance, and followed them for 2 years. In March 2003, seedlings reared under the same conditions used for the rooftop garden were planted into a field garden at the University of California Santa Cruz Arboretum. This site is  $\approx 40$  km south of the SM invasion and includes similar coastal Mediterranean climate and old field vegetation. The common garden site receives

less fog input than the invading populations, however, and a drip watering system was used to supplement soil moisture in the garden weekly.

Pairs of half-sib seedlings from 16 to 20 families per invasion were randomized and planted 0.9 m apart in a rectangular block. The seedlings in each pair were planted  $\approx 10$  cm apart. In June 2003, vacancies due to mortality were replanted with additional seedlings from the same rearing group (additional individuals were not included in estimates of survival). This design was replicated in four contiguous blocks, using seedlings from the same families. Pairs were thinned to one individual in November of 2003 to prevent crowding among growing plants. From May to November 2004, plants were checked weekly for appearance of the first fully-open flower. The effect of log-transformed size at the beginning of each season on survival and flowering was assessed using a logistic regression with population and family effects, and significance was determined using likelihood ratio tests.

We did not allow field-planted individuals to continue flowering and contaminate the site with seed. A survey of size and flower number in the nearby SM invasion was used to predict field flower production from size after log transformation of both variables.

## RESULTS

### Molecular genetic structure and diversity

We identified a single island in the native range of *H. canariense* as the source of all three introductions. Both ITS and AFLP markers placed invading populations within the *H. canariense* variety *canariense*, found across the islands of El Hierro, La Gomera and Tenerife (Fig. 1a). All individuals of this variety had an identical ITS genotype, distinct from the *H. c.* var. *floribundum* genotype (GenBank accession no. EF034040–72, Dlugosch & Parker 2007). Furthermore, the invading populations formed a single, well-resolved clade within the larger Tenerife clade (Fig. 1a), indicating that they share a common lineage derived from Tenerife and are effectively replicate introductions of the same stock (Fig. 1b).

Levels of heterozygosity and allele polymorphism revealed that the invading populations have experienced a large loss of genetic variation, with only about half of the diversity found within Tenerife populations (Fig. 1c,d). Tripling the sample size within each invasion did little to change diversity estimates, indicating that under-sampling was not the cause of the low values (Fig. 1c,d). Despite their shared lineage and their low genetic diversity, the invading populations displayed strong genetic differentiation from one another (Fig. 1e). Indeed, their degree of differentiation more closely resembled that among the different native

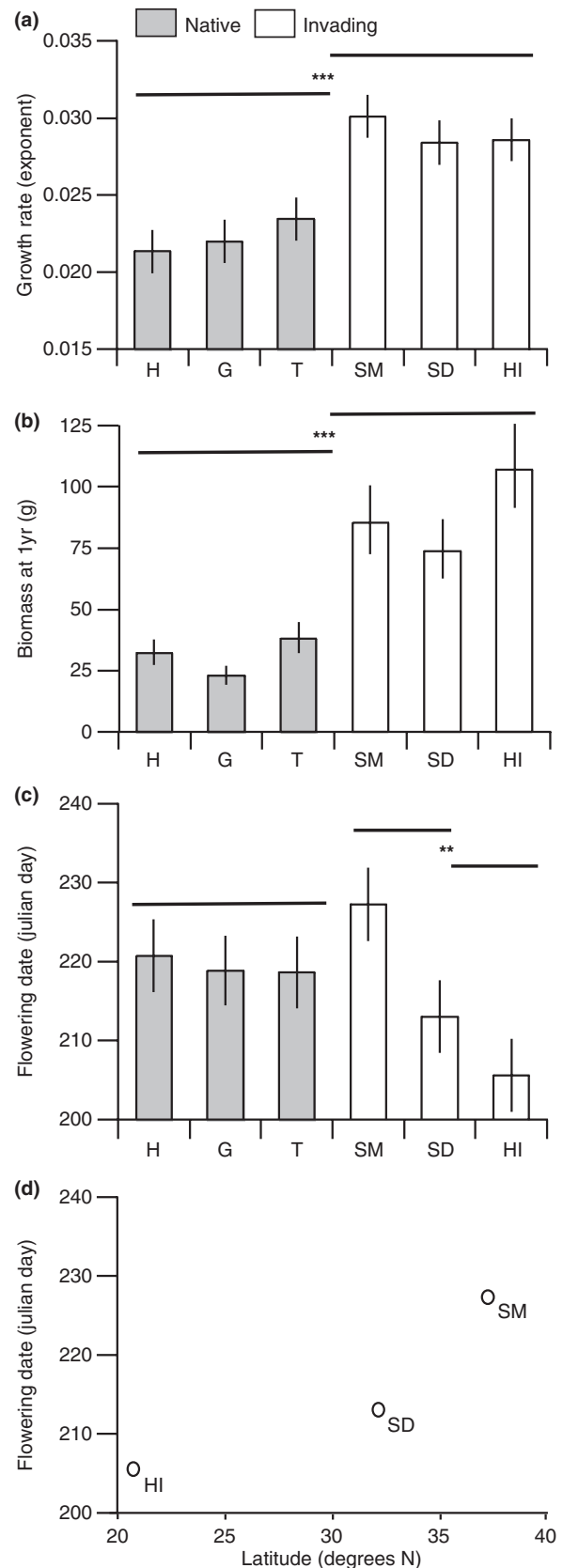
*H. c. var. canariense* islands than among populations within any one of these islands (Fig. 1e).

### Life history evolution

Rapid evolution of growth rate, size at 1 year, and the date of first flowering were apparent in the founding populations. Each trait showed similar mean values across islands in the native range of *H. c. var. canariense* but deviated in the invasions (Fig. 2a–c). Invading genotypes displayed increased growth rates (Fig. 2a, Table 1) that resulted in larger final sizes (Fig. 2b, Table 1), as well as flowering times that were divergent across populations (Fig. 2c, Table 1). The divergence in flowering time was consistent with a latitudinal cline where more southerly populations flower earlier (Fig. 2d), as is typical for spring-flowering plants such as *H. canariense* (White 1995).

Field data indicated that increased growth was associated with several benefits over the 2 years of our study. Survival through the first year was only 63% overall in the field garden, but the probability of surviving was significantly improved by a larger size at planting (logistic regression, likelihood fit:  $\chi^2 = 7.35$ ,  $P = 0.007$ ,  $n = 370$ ; family effects:  $\chi^2_{55} = 71.4$ ,  $P = 0.07$ ). These plants did not reach reproduction in their first year, but reproductive maturity in the second year was much more common for individuals of larger size (logistic regression, likelihood fit:  $\chi^2 = 87.2$ ,  $P < 0.0001$ ,  $n = 151$ ; family effects:  $\chi^2_{53} = 51.9$ ,  $P = 0.52$ ). Moreover, individuals within the nearby SM invasion showed a positive effect of size on the number of flowers produced (linear regression:  $[\ln(n \text{ flowers}) = -10.1 + 1.5 \times \ln(\text{g biomass})]$ ,  $r^2_{\text{adj.}} = 0.49$ ,  $P < 0.0001$ ,  $n = 36$ ).

Verbal histories of the introductions indicate that each is between 25 and 45 years old (Appendix S1). If we assume that populations have been evolving for as much as 50 years and that generation time is at minimum 2 years (time to reproduction under field conditions, resulting in at most 25 generations), conservative rates of evolution can be estimated. The observed increase in growth rate corresponds to



**Figure 2** Growth (a, b) and flowering (c, d) traits in native and invading (founder) populations of *H. c. var. canariense* grown in a common garden. Growth rates (a) are from exponential fits to changes in estimated wet biomass over one year, and size (b) is back-transformed from the natural log of final biomass values. Flowering dates (c) reflect the date of the first fully open flower on each plant, with growth rate as a covariate, and means are plotted against the latitude of each invading population in (d). Values for (a–c) are least squares means from REML models (see Material and methods and Table 1), and error bars show standard errors. Horizontal bars connect locations that were not significantly different. \*\* $P < 0.001$ , \*\*\* $P < 0.0001$ .

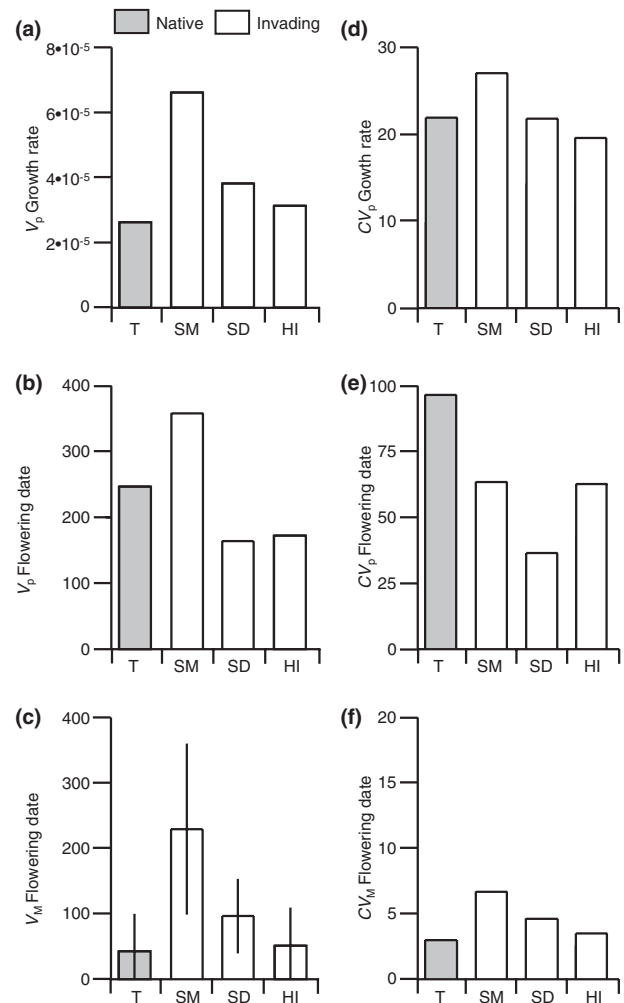
**Table 1** Evolution of *H. canariense* life history traits, from restricted maximum likelihood (REML) analyses

Factor	<i>n</i>	Test or variance
<b>Growth rate</b>		
Native/introduced	2	$F_{(1, 54.01)} = 36.1^{***}$
Location (nested)	6	$F_{(4, 54.01)} = 0.52$
Family (nested)	61	$\chi^2 = 1.56$
Whole model	180	$V_c = 4.76 \cdot 10^{-5}$
<b>Size</b>		
Native/introduced	2	$F_{(1, 54.54)} = 69.5^{***}$
Location (nested)	6	$F_{(4, 54.48)} = 2.13$
Family (nested)	61	$\chi^2 = 0.85$
Whole model	173	$V_c = 0.614$
<b>Flowering date</b>		
Native/introduced	2	$F_{(1, 57.62)} = 1.22$
Location (nested)	6	$F_{(4, 51.49)} = 3.02^*$
Growth rate covariate	–	$F_{(1, 135.7)} = 34.1^{***}$
Family (nested)	61	$\chi^2 = 49.04^{***}$
Whole model	176	$V_c = 268.3$
<b>Flowering date: invasions only</b>		
Latitude	–	$F_{(1, 25.7)} = 16.7^{**}$
Population	3	$F_{(1, 25.0)} = 2.79$
Growth rate covariate	–	$F_{(1, 66.7)} = 25.9^{***}$
Family w/in population	30	$\chi^2 = 14.2^{**}$
Whole model	86	$V_c = 79.5$

Growth rates (exponent) and flowering dates (Julian day) were assessed for genotypes from native and introduced regions using 10–11 families per location (within region) with two to three offspring each. *F*-statistics (ndf, ddf) are given for fixed effects, and  $\chi^2$  statistics (from likelihood ratio tests) are given for random effects (\*\* $P < 0.0001$ , \*\* $P < 0.001$ , \* $P < 0.05$ ).

0.04 Haldanes (per generation rate) or 4286 Darwins (annual rate), and the divergence in flowering time to 0.03 Haldanes or 979 Darwins. These values indicate substantial rates of evolutionary change in the invasions, and ones that are not unusual among studies of contemporary evolution (Reznick *et al.* 1997; Bone & Farres 2001).

Significant family variation for flowering time (Table 1) suggests that variation and opportunities for further evolution of this trait continue to be maintained in the invasions. For growth rate, phenotypic variance and coefficients of variance were greater in the invasions than their source population, while those for flowering date were slightly lower in most cases (Fig. 3). The differences in phenotypic variation do not have strong statistical support (growth rate:  $P = 0.07$ , flowering date  $P = 0.11$ ), implying little change in trait variation among native and invading populations. Our models estimated values of maternal family variance in flowering date that were slightly higher in the invasions, though none of these could be significantly differentiated from zero (Fig. 3).



**Figure 3** Variances (a–c) and coefficients of variation (d–f) for growth rate and flowering date of native and invading populations of *H. c.* var. *canariense*, grown in a common garden. Variances are total phenotypic variance ( $V_p$ ) and maternal family variance ( $V_M$ ) estimated by REML. Error bars for  $V_M$  (c) show standard errors and all values are not significantly different from zero.

## DISCUSSION

Our results demonstrate that, while introduced species can experience large losses of molecular genetic diversity during founding events, these losses do not preclude the rapid evolution of life history among invading lineages. All three active invasions of *H. canariense* showed *c.* 50% declines in molecular genetic variation relative to native populations. This represents a severe decline in diversity relative to most other invaders studied to date (Dlugosch & Parker 2008), and demonstrates that the number of founders must have been very low (Nei *et al.* 1975). These populations are also isolated from gene flow and show strong molecular

differentiation from one another. This pattern runs counter to observations of low among-population variation in some introduced plants (reviewed in Novak & Mack 2005) and suggests that individual founding populations might have opportunities for adaptive phenotypic divergence prior to future spread and homogenization of neutral variation via gene flow.

Indeed, plants from invading populations displayed increased growth and divergent flowering phenology in common gardens. Increased growth was associated with benefits to survival and reproduction early in life, which could increase rates of population expansion (e.g. Hastings 1996). Flowering phenology diverged in accordance with a predicted latitudinal cline, suggesting local adaptation to seasonal variation. Previous observations of parallel clines in life history traits within the native and introduced ranges of plants have demonstrated that introduced species can rapidly evolve in response to familiar abiotic gradients (e.g. Maron *et al.* 2004; Leger & Rice 2007). In *H. canariense*, population divergence developed *de novo* in a species whose native range spans only *c.* two-third of a degree of latitude, indicating a novel use of existing variation. These findings demonstrate that even genetically depauperate introduced species may not require multiple introductions and/or hybridization events in order for evolution to contribute to fitness in the invaded range.

Invaders may evolve either in response to selection in the introduced range or as a result of non-random introduction of particular phenotypes, as in horticultural selection or biased dispersal (e.g. Kliber & Eckert 2005). In *H. canariense*, the divergence of flowering phenology among introductions of the same lineage is strong evidence of a response to selection post-introduction. The driver of increased growth across the invasions is less clear, although the invasion history of these particular populations suggests that very few generations were spent under cultivation (Appendix S1), and we have shown that increased growth is favoured in the field. Nevertheless, without knowledge of the precise genotypes that were introduced, all patterns of evolution within invasive species must be interpreted with caution.

Importantly, the changes that we observed in growth and flowering traits are consistent with predictions for invasive plants. Growth characteristics have featured prominently in studies of introduced species ever since early observations suggested that invading populations can be more vigorous than native ones (Elton 1958; Crawley 1987). A number of experimental studies have supported this pattern and suggested that it represents a shift toward greater competitive and/or reproductive abilities (e.g. Blossey & Notzold 1995; Leger & Rice 2003; Blair & Wolfe 2004; Lavergne & Molofsky 2007). Likewise, evolutionary changes in flowering phenology have often been associated with colonization (Levin 2006), and genetically based latitudinal clines have

been demonstrated for flowering phenology of several invasive plants (Weaver *et al.* 1985; Warwick & Black 1986; Weber & Schmid 1998; Tranel & Wassom 2001; Kollmann & Banuelos 2004). Constraints on the evolution of flowering phenology may play a direct role in setting range limits, and widespread species may rely on local adaptation of this trait, suggesting a critical role for phenology in invasive spread (Griffith & Watson 2006).

Such rapid adaptive evolution may seem improbable where large losses of molecular diversity have occurred, however, life history trait variation is not necessarily expected to decline similarly in response to founding events. Outcrossing species generally harbour most of their variation within populations and may be able to maintain substantial adaptive variation despite large proportional losses during colonization (Hamrick & Godt 1989). This is likely to be true for *H. canariense*, based upon our previous observations of high within population variation in the native range (Dlugosch & Parker 2007). Rapid increases in population size following a founding event should also enhance a population's retention of beneficial mutations and response to selection (Nei *et al.* 1975; Otto & Whitlock 1997). Moreover, during a demographic bottleneck, dramatic allele frequency changes at non-additive loci can sometimes effectively increase heritable variation in quantitative traits (e.g. Turelli & Barton 2006 and references therein). Experimental populations have shown such increases, particularly for life history variation (Neiman & Linksvayer 2006; Willi *et al.* 2006). Thus even severely reduced molecular diversity does not necessarily imply limits on adaptive evolution. Indeed, our estimates of variance within native and invading populations of *H. canariense* suggest that the invasions are not experiencing large losses of adaptive variation and that they may continue to respond to selection.

Adaptive evolution during colonization has become a major focus of invasion biology because it has the potential to initiate invasions in otherwise benign species (Sakai *et al.* 2001; Cox 2004). Studies of nascent invasions in particular offer us insights into the role of evolution in the expansion of founding populations. Young founding populations are the most likely to endure large reductions in molecular genetic diversity, and the historical success of these populations suggests that either trait variation remains sufficient for adaptive evolution (Dlugosch & Parker 2008), or that adaptation is unnecessary in some cases (e.g. Parker *et al.* 2003). Our data support the prediction that rapid evolution can occur even in founding populations that have passed through a bottleneck, and suggest that evolution could have been important to the success of the many invaders that show reduced genetic variation in their introduced ranges. By virtue of studying *H. canariense* early in its colonization history, we cannot be certain that this

particular species will demonstrate widespread invasive behaviour in the future. Nevertheless, our findings caution that small plantings of seemingly benign ornamental species can retain the ability to evolve into more aggressive invaders without the aid of gene flow or hybridization.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Figure S1** *Hypericum canariense* (yellow) dominates other vegetation at the San Mateo county, USA site.

**Table S1** Descriptions of invading *H. canariense* populations in California and Hawaii, USA.

**Appendix S1** Invasion history.

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