

Assessing the speed and predictability of local adaptation in invasive California poppies (*Eschscholzia californica*)

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Keywords:

Chile;
clines;
invasive species;
local adaptation;
rapid evolution.

Abstract

Insight into the speed and predictability of local adaptation can be gained by studying organisms, such as invasive species, that have recently expanded their geographical ranges. Common garden studies were designed to address these issues with the California poppy, *Eschscholzia californica*, collected from a wide range of environments in both its native (California) and invasive (Chile) ranges. We found similar patterns of plant trait variation along similar abiotic gradients in plants collected from both areas. Multivariate analysis demonstrated that coastal plants from both areas tended to be shorter, smaller plants with smaller seeds and flowers that germinate and flower later than plants collected from inland locations. In addition, size and fecundity traits in both native and invasive poppies were correlated with average rainfall totals; the plants that grew the largest and were the most fecund during the first year of growth originated from the driest areas. This parallel variation suggests that these traits are adaptive and that these patterns have evolved in Chile during the 110–150 years since introduction.

Introduction

As a result of the intentional and accidental movement of organisms around the world by humans, we are surrounded by plants and animals that have very recently expanded their geographical ranges. Although this expansion has been disruptive to natural communities, it is valuable for answering two questions. First, how rapidly can species become adapted to novel biotic and abiotic conditions? Species colonizing new environments have shown some of the most rapid rates of evolution yet observed, and the time since introduction for many of these organisms is known, often < 200 years (Bone & Farres, 2001; Reznick & Ghalambor, 2001). Secondly, is local adaptation predictable? When presented with similar conditions, will organisms consistently produce the same adaptive solutions to the same selective pressures? This question has been investigated in studies of parallel evolution in which independent lineages have

colonized similar environments and converged upon predictable ecotypes or morphologies over thousands of years or more (e.g. fishes in post-glacial lakes; Schluter, 1998, 2000). Only recently have we begun to use invasive species as a means to address the predictability of evolution over shorter periods of time (Huey *et al.*, 2000; Gilchrist *et al.*, 2001; Maron *et al.*, 2004).

The invasion of the California poppy, *Eschscholzia californica* Cham., in Chile is well suited for testing both the speed and predictability of local adaptation. Chile and California exhibit a remarkable similarity of geography and climate, and comparisons between plant and animal communities in the two areas have been historically useful for investigations into convergent evolution (e.g. Mooney, 1977). Previous results suggested that the invasive *E. californica* in Chile has evolved a superior colonizing ability since introduction in the 1850s, because it attains greater size and fecundity than do native populations when grown in disturbed environments with reduced competition (Leger & Rice, 2003). Here we address whether or not selection has also acted to favour locally adapted forms within the introduced range, looking particularly for evidence of adaptation to local climatic conditions. Although we cannot calculate a rate of

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evolution for the California poppy in Chile (e.g. Hendry & Kinnison, 1999) because we have no knowledge of what traits characterized the founding populations, nor when particular populations were established, we do know that if plants from Chile have evolved locally adapted traits, these adaptations have arisen in the last 150 years.

Common garden experiments can be used to demonstrate that plants are locally adapted. If variation in phenological or morphological traits is expressed when plants are grown in a common environment, and if this variation is correlated with the environment where plants were collected, this is evidence that natural selection has contributed to the observed pattern (Endler, 1986). When multiple populations or multiple species show similar patterns of trait variation associated with geography or climate, this is considered very strong evidence that the traits in question are adaptive (Endler, 1986). Among invasive plants, genetically based clinal variation has been observed in plants collected from Chile (Del Pozo *et al.*, 2002), western North America (Knowles, 1943; Rice & Mack, 1991; Neuffer & Hurka, 1999), eastern North America (Reinartz, 1984; Lacey, 1988), and Europe (Weber & Schmid, 1998). Despite the variety in collecting locales and organisms in these studies, certain traits consistently vary along similar gradients: for example, flowering time shows clinal variation in every one of the previous studies, with plants from warmer and/or drier regions flowering sooner than plants from wetter and/or cooler regions. This provides strong evidence that the timing of reproductive events is adaptive, and that this trait is under selection in invasive species. However, these studies did not include comparisons between the plants from the native and introduced ranges, and thus are not a good test of parallel adaptation. One exception is Maron *et al.* (2004) who used collections from both native and invasive populations of St John's wort (*Hypericum perforatum* L.), and found latitudinal clines in size and fecundity of both native and invasive populations when grown in common gardens, and greater plant size and fecundity when plants were grown in areas with climates most similar to where they were collected.

These studies have addressed questions of whether or not invasive species have evolved in response to abiotic conditions, but we may also ask what effect the biotic community has in mitigating the expression of genetic variation. Although some non-native species are capable of invading intact ecosystems, the vast majority invade areas that have experienced some type of human or natural disturbance (Harper, 1965; Crawley, 1987; Rejmanek, 1989; Davis *et al.*, 2000). Because heavily disturbed sites, such as roadsides, can have lower vegetation cover than intact areas, we tested whether disturbed environments without competitors and environments with resident competitors would differentially affect the expression of clinal variation of plant traits. One prediction is that differences between genotypes might be

weakest, and possibly not apparent, when plants are grown in a noncompetitive environment because plants in a resource-rich environment might be able to compensate for any maladaptation. Alternately, growing with competitors may constrain the growth of all genotypes, so much so that genetic differences between plants can only be expressed in open environments.

In this study, we looked for evidence of local adaptation in invasive plants by growing plants collected from similar environmental gradients in California and Chile in common gardens in California. Using this approach we address the following questions. First, do traits of *E. californica* from California and Chile show evidence of similar clinal variation along environmental gradients? Secondly, does the expression of clinal variation in plant traits depend on the conditions in which plants are grown? We addressed the first question by testing for a relationship between variation in plant size, fecundity, phenology, seed size, and flower characteristics with environmental variables associated with the geographical locations from which seeds were collected. This relationship between plant traits and environment was investigated first by comparing coastal and inland phenotypes (*E. californica* in its native range has distinctive coastal and inland forms; Munz, 1963), and second in a broader context encompassing the latitudinal gradients in rainfall and temperature in both countries. In order to address the second question involving the consistent expression of traits in different growing environments, the plants were grown in common gardens in two different locations and under two different conditions (either alone or with competition from other plants).

Materials and methods

Study system

This study focuses on the invasion of *E. californica* into the Mediterranean-climate region of Chile. Native to the west coast of North America, *E. californica* was reportedly introduced into Chile during the California gold rush in the 1850s, when travel and trade between the two areas increased (Gilliss, 1855). *Eschscholzia californica* was introduced into botanic gardens in the mid and late 19th century, and further introductions may have been made through horticulture or as a contaminant of alfalfa seed from California (Hillman & Henry, 1928; Frias *et al.*, 1975; Arroyo *et al.*, 2000). The plant began to spread outward from these initial introductions in the 1890s, and today grows in disturbed areas along a 750 km region of central Chile (Arroyo *et al.*, 2000).

The study areas within both countries have Mediterranean-type climates, with the majority of rainfall occurring during the winter months, followed by dry summers. Both areas also have a coastal and an inland mountain range running parallel to each other from north to south, surrounding a large central valley. In

both Chile and California, rainfall generally increases as distance from the equator increases, and average minimum temperatures increase and maximum temperatures

decrease (in conjunction with a decrease in elevation) towards the coast (di Castri & Hajek, 1976; Miller *et al.*, 1977) (see Fig. 1). Climatic conditions are somewhat

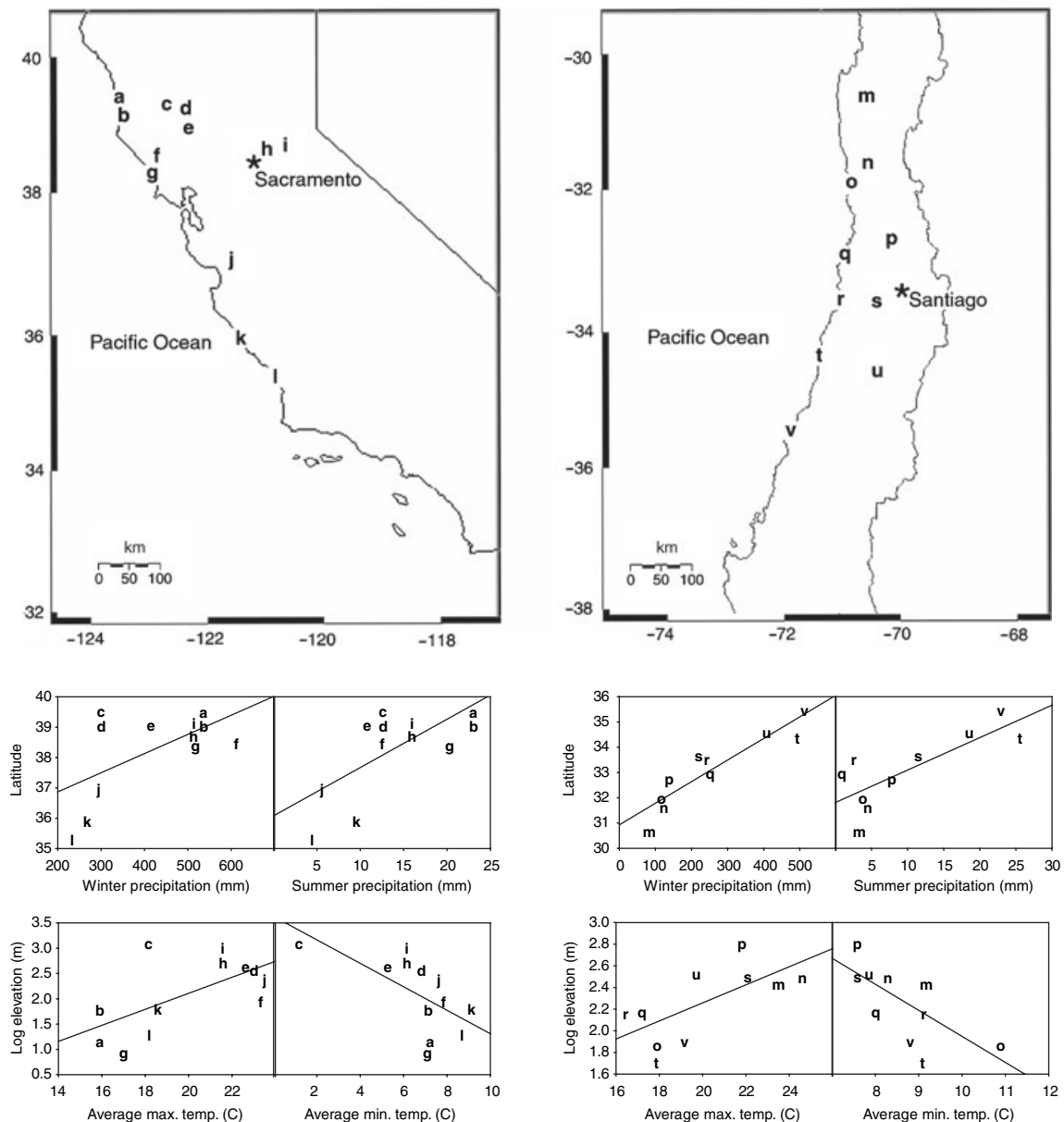


Fig. 1 Collection locations in California and Chile, and climate information. All populations used in all experiments, except: 'd' and 'h' used in container experiment only; 'c' and 'f' used in field experiment only. Population 'd' was grown from a bulk collection of seeds from plants grown from wild collected seeds. ANCOVA was performed to test if the sampling locations reflect the expected climatic gradients, and to determine if the gradients were similar in both countries. ANCOVA results are presented with the response variable listed first, followed by model effects. Degrees of freedom for all effects are 1, 18. Winter precipitation: country ($F = 10.33$, $P = 0.0048$), latitude ($F = 27.46$, $P = 0.0001$), and country \times latitude ($F = 1.89$, $P = 0.1865$). Summer precipitation: country ($F = 0.63$, $P = 0.4371$), latitude ($F = 22.43$, $P = 0.0002$), and country \times latitude ($F = 1.05$, $P = 0.3181$). Maximum temperature: country ($F = 0.28$, $P = 0.6023$), elevation ($F = 10.8643$, $P = 0.0040$), and country \times elevation ($F = 1.37$, $P = 0.2575$). Minimum temperature: country ($F = 17.43$, $P = 0.0006$), elevation ($F = 7.76$, $P = 0.0122$), and country \times elevation ($F = 0.0198$, $P = 0.8896$). All climate information for California is from the Western Regional Climate Center (<http://www.wrcc.com>). Precipitation data in Chile is from the Global Historical Climatology Network (GHCN 1), except for population 'v' which is from Weatherbase (<http://www.weatherbase.com>). Temperature data for Chile is from di Castri & Hajek (1976), except for populations 'u' and 'v', which are from GHCN 1, and population 't', which were calculated as averages between values for populations 'r' and 'v'.

shifted latitudinally: because of differences in storm patterns, the Mediterranean-type climate area of Chile is located about four degrees higher than that of California (Miller *et al.*, 1977).

There is considerable variation in traits among populations of *E. californica* in California. At one point, the genus was split into 112 different species (Greene, 1905), but today only 10 species are recognized, and much of the previously noted variation is now included within *E. californica* (Hickman, 1993). Three currently recognized variants of *E. californica* are: (i) perennial plants from coastal environments that are usually short in stature with prostrate growth and yellow flowers; (ii) perennial plants from nondesert, inland areas that generally grow taller and have orange flowers, sometimes called *E. californica* var. *crocea* (Benth.); and (iii) an annual form that occurs in desert regions, sometimes called *E. californica* var. *peninsularis* (Greene) (Munz, 1963). These varietal differences are assumed to be genetic because the differences persist when plants are grown from seed in a common environment, where both F1 and F2 coastal and inland plants have phenotypes that are readily distinguishable from one another (E.A. Leger, pers. obs.). All *E. californica* plants used in these experiments were entirely self-incompatible (E.A. Leger, unpublished).

Experimental design

We collected seeds from plants growing across a similar range of environmental conditions in both Chile and California, and sampled plants from both coastal and inland environments (Fig. 1). Abiotic conditions at the sampling locations reflected the expected temperature and precipitation gradients in both areas, and these gradients were very similar in Chile and California (analyses presented in the caption of Fig. 1). Climatic information was gathered from the weather station close to each population (for sources of climate information see caption of Fig. 1). Variables used were average winter precipitation (the total of average precipitation over three months of winter), summer precipitation (total average precipitation over three months of summer), and the average annual maximum and minimum temperatures (shown in Fig. 1). Precipitation and temperature data for California locations were from, on average, 53.7 years of observations; in Chile, precipitation and temperature data were from an average of 30.1 and 22.5 years of observations respectively. On average, plants from California were collected from areas that experienced slightly more winter precipitation and lower minimum temperatures than collection sites in Chile. There were no differences in summer precipitation or yearly maximum temperatures between collection sites on the two continents.

Seeds were collected from 20–25 individuals from each of 12 native populations in California and 10 invasive populations in Chile. As all populations in Chile appear

to be perennial (Frias *et al.*, 1975; E.A. Leger, pers. obs.), annual populations from California were not included in this study. Seeds from each individual plant were kept separate, and all seeds were stored at room temperature until planting. Collected seeds were from naturally pollinated flowers, and are likely a mixture of half and full siblings.

Seeds were planted in common gardens in two locations in California, one in the ground and one in a container experiment. In both common gardens, plants from five coastal populations and five inland populations from both California and Chile (20 populations total) were grown either with or without competition from other plants. The container experiment was established in 3-gallon tree containers placed at an outdoor location in Davis, Yolo County, California (38°32'31"N, 121°45'48"W), planted in April 1999 (detailed in Leger & Rice, 2003). Plants were watered as necessary (transitioning from weekly to daily watering as the growing season progressed) to keep soil in the pots moist. To create a competition treatment, four *E. californica* individuals of horticultural origin were planted within a container. Seeds from 19–20 separate individuals from each of 20 populations were planted both with and without competition, for a total of 786 pots. We recorded days to germination, days from germination to flowering, width of the widest petal of the first flower produced, number of stamens in the first flower produced, final plant height, total number of flowers produced, dry mass of shoots and roots, average mass of an individual seed (averaged from seeds collected from five ripe seed capsules per plant), and the average number of seeds produced per capsule (averaged from five capsules).

The field experiment was established in Montara, San Mateo County, California (37°32'36"N, 122°30'42"W), and seeds were sown directly into the ground in November 2001 (detailed in Leger & Rice, 2003). Supplemental water was not needed in this common garden (cool temperatures and fog drip prevent water stress at the site, despite California's rainless summers). Competition was provided by the background vegetation, which was primarily invasive annual forbs and grasses. In the field garden, seeds from eight separate individuals from each of 20 populations were planted with and without competition, for a total of 320 plants. Eighteen of the populations were the same as those used in the container experiment; two populations from California were substituted in the field experiment when seed supplies of two original populations were exhausted (see Fig. 1 legend). Because of logistical constraints, we measured a smaller set of traits on these plants: days to germination, days from germination to flowering, plant height, mass of shoots, total number of flowers produced, and the average mass of an individual seed (averaged from 3–5 ripe seed capsules per plant) over one growing season.

Statistical analyses

We used principal component analysis, ANCOVA, and MANOVA to evaluate the relationship between plant traits and their environment of origin. To avoid treating individual plants as independent samples, and to focus on the differences among populations, we created mean population values for each trait. In the container experiment, the average number of plants (\pm SE) surviving per population (out of a possible 20) with competition was 14.5 (\pm 0.55, range 10–19) and 16.0 (\pm 0.78, range 11–20) without competition. Average survival (out of a possible 8) with competition in the field experiment was 5.4 (\pm 0.42, range 2–8) and 5.6 (\pm 0.45, range 2–8) without competition.

Because many of the plant traits we measured were correlated with each other, principal components (hereafter 'trait PCs') were created, based on population mean values, to produce a reduced set of orthogonal response variables. Trait PCs were created separately for each of the two common garden experiments (designated 'trait PC_c' for the container experiment and 'trait PC_f' for the field experiment) and only trait PCs with an eigenvalue > 1 were retained for further analysis. Principal components were also created from four variables (average summer and winter precipitation, and average annual maximum and minimum temperatures) that describe the abiotic environment of each site (hereafter 'environment PCs').

Latitudinal gradients

To test for a relationship between trait PCs and environment PCs, we performed ANCOVA with trait PCs as the dependent variables and the following independent factors: country of origin, competition treatment, population (random factor) nested within country, and the two environment PCs included in the model as covariates ('population' is included in the model because each population is represented twice in the analysis, once in each competition treatment). The model also included the following interactions: each environment PC by country, each environment PC by competition, and each three-way environment PC by country by competition interaction. The final model was run without the three-way interactions, which were never significant. Trait PC_c 1, 2 and 3 were response variables in the container experiment, and trait PC_f 1 and 2 were response variables in the field experiment. A significant environment PC factor indicates a relationship between traits and the environment where plants were collected. A nonsignificant interaction between an environment PC and country or between an environment PC and competition can indicate that populations from both countries are responding similarly to their environment, and that this response does not vary with the competition treatment. Because a nonsignificant interaction term can also result

from a lack of power to detect significant differences in responses, we present power calculations for our whole model and follow-up nonsignificant country by environment PC interactions with ANCOVAs separately for each country in cases where an environment PC is significantly related to a trait PC. We present Spearman's rank correlations between individual traits and environmental variables to allow for the inspection of the behaviour of particular traits.

Coastal and inland comparisons

We looked for evidence of parallel adaptation to coastal and inland environments in two different ways. First, to visually test for principal component groupings between coastal and inland plants, we created biplots by graphing trait PC 1 vs. trait PC 2, overlaying vectors corresponding to each plant trait on the graph. Secondly, MANOVA was used to determine if there were differences in coastal and inland plants from both countries, using the following model: country, region, competition (fixed effects), population (random effect nested within region and country), and all two- and three-way interactions between fixed effects, with all plant traits measured as response variables. We were interested in two results from this MANOVA. First, significant region effects would indicate that coastal and inland forms observed in nature have a genetic basis, whereas region by country interactions would test the degree of similarity of adaptations to coastal and inland environments in plants from California and Chile. Secondly, a significant competition treatment by region and/or a competition treatment by region by country interaction effect would indicate that different competitive environments affect the expression of locally adapted traits. ANOVAs were conducted with the same model on individual traits following MANOVA. All analyses were conducted using JMP 5.0.1a (SAS Institute, 2002), and significance was measured at the $P < 0.05$ level.

Results

Principal components

In the container experiment, trait PC_c 1 was most strongly associated with measures of plant fecundity (number of flowers and average number of seeds made per flower) and plant size (height, root and shoot mass) (Table 1). Trait PC_c 2 was positively associated with stamen number, flower size, and seed size, and trait PC_c 3 was positively associated with seed size and time to germination. In the field experiment, trait PC_f 1 was positively associated with final plant size, plant height, and total number of flowers produced, and negatively associated with time to flowering and germination. Trait PC_f 2 was strongly associated with seed size.

The first environment PC was mostly associated with a positive relationship between summer and winter

	Container experiment			Field experiment	
	PC _c 1	PC _c 2	PC _c 3	PC _f 1	PC _f 2
Number of flowers	0.4267	-0.0542	-0.0776	0.5106	-0.1416
Height	0.3906	0.0497	0.1782	0.3407	0.2161
Shoot weight	0.3828	-0.3357	-0.1002	0.5217	-0.1607
Root weight	0.3673	-0.3613	0.0867	-	-
Seeds per flower	0.3581	-0.0801	0.1604	-	-
Petal width	0.2023	0.4500	-0.1208	-	-
Stamen number	0.1331	0.5498	-0.4254	-	-
Seed size	0.0623	0.4275	0.6626	-0.0062	0.8967
Days to germination	-0.2762	-0.1045	0.4755	-0.3970	-0.3112
Days to flowering	-0.3421	-0.2159	-0.2420	-0.4397	0.0807
Eigenvalue	4.5020	1.5587	1.0752	3.2158	1.0553
% variation explained (cumulative %)	45.02	15.59 (60.61)	10.75 (71.36)	53.597	17.588 (71.185)

Values are eigenvectors for each PC. Plant traits not measured in the field experiment are indicated with '-'.

Table 2 Contributions of climatic information from the collection location of each population to environment principal components (environment PCs).

Weather variables	PC1	PC2
Winter precipitation	0.6405	-0.0681
Summer precipitation	0.6405	0.0503
Annual max temp.	-0.3193	-0.6745
Annual min temp.	-0.2785	0.7330
Eigenvalue	2.0555	1.0898
% variation explained (cumulative %)	51.4	27.2 (78.6)

Values are eigenvectors for each PC.

precipitation, and environment PC 2 indicates that locations with lower maximum temperatures also experience higher minimum temperatures (milder climates) (Table 2).

Latitudinal gradients

In the container experiment, there was a significant negative effect of environment PC 1 ('precipitation') on trait PC_c 1 ('size and fecundity'), and there was no significant interaction between environment PC 1 and country of origin (Table 3a). When ANCOVAs were run separately for each country, there was a significant effect of environment PC1 on trait PC_c for both Californian ($F_{1,7} = 10.67$, $P = 0.0138$) and Chilean ($F_{1,7} = 5.86$, $P = 0.0461$) populations. Plants from both California and Chile that grew the largest and were the most fecund during the first year of growth originated from areas with the lowest levels of summer and winter precipitation [Fig. 2A(a,b)]. Environment PC 2 ('temperature') significantly affected trait PC_c 2 ('flower and seed size'); plants with smaller flowers and seeds originated from areas with more moderate temperatures [Table 2a, Fig. 2A(c,d)]. There was no significant interaction between country

Table 1 Contributions of morphological and phenological traits to trait principal components (trait PCs) in two different common gardens.

and environment PC 2 (Table 2a), however, when this relationship was analysed separately for each country, the relationship between trait PC_c 2 and environment PC 2 was only significant for Californian populations (Californian, $F_{1,7} = 11.74$, $P = 0.0110$; Chilean $F_{1,7} = 3.56$, $P = 0.1012$). There was a significant interaction between environment PC 2 and country with respect to trait PC_c 3 ('seed size and time to germination'): there is a negative relationship between trait PC_c 3 and environment PC 2 in plants from California ($F_{1,7} = 14.87$, $P = 0.0062$), but this is not seen in plants from Chile ($F_{1,7} = 0.0103$, $P = 0.9227$) [Table 3a, Fig. 2A(e,f)]. No other relationships between trait and environment PCs in the container experiment were significant. In the field experiment, environment PC 1 ('precipitation') significantly affected trait PC_f 1 ('size and fecundity'), again with larger, more fecund plants originating from areas with the lowest precipitation, and there was no interaction between country and environment PC 1 [Table 3b, Fig. 2B(a,b)]. As in the container experiment, there was a significant relationship between trait PC_f and environment PC 1 when ANCOVAs were run separately for each country (Californian, $F_{1,7} = 10.04$, $P = 0.0157$; Chilean $F_{1,7} = 5.67$, $P = 0.0488$). No other relationships between trait and environment PCs in the field experiment were significant.

As expected, competition significantly reduced the size and fecundity of plants (trait PC_c 1 and trait PC_f 1) in both the inland and field experiments, but the country by competition interaction was never significant (Table 3a,b). In the field experiment, seed size (trait PC_c 2) was reduced by competition (Table 3a,b). Flower size, seed size, and time to germination (trait PC_c 2 and trait PC_c 3) in the container experiment were not affected by competition. However, the correlations between these trait PCs and environment PCs in both common gardens were not affected by the competitive environment: the treatment by environment

Table 3 Results of ANCOVA analyses comparing the relationship between trait PCs and environment PCs in the container experiment (A) and the field experiment (B).

(a) Source _{d.f.}	Trait PC _c 1 'size and fecundity'			Trait PC _c 2 'flower and seed size'			Trait PC _c 3 'seed size and germination'		
	<i>F</i>	<i>P</i>	β	<i>F</i>	<i>P</i>	β	<i>F</i>	<i>P</i>	β
Country _{1,18}	0.03	0.8652	0.09	0.05	0.8334	0.06	7.33	0.0144	0.46
Population (country) _{18,12}	5.92	0.0016	0.99	2.53	0.9956	0.78	0.77	0.7023	0.26
Competition _{1,12}	45.28	< 0.0001	1.0	2.45	0.1434	0.30	0.08	0.7873	0.06
Country × competition _{1,12}	2.25	0.1596	0.42	0.39	0.5449	0.09	0.01	0.9406	0.05
Environment PC 1 _{1,12}	13.40	0.0033	0.93	1.06	0.3216	0.16	3.77	0.0761	0.43
Environment PC 2 _{1,12}	1.92	0.1914	0.24	12.79	0.0038	0.91	4.30	0.0601	0.48
Environment PC 1 × country _{1,12}	1.46	0.2499	0.24	0.65	0.4364	0.11	1.45	0.2511	0.20
Environment PC 2 × country _{1,12}	0.28	0.6080	0.07	2.47	0.1424	0.30	5.42	0.0382	0.57
Environment PC 1 × competition _{1,12}	0.11	0.7447	0.06	1.02	0.3308	0.15	0.31	0.5877	0.08
Environment PC 1 × competition _{1,12}	0.01	0.9802	0.05	0.72	0.4127	0.12	2.30	0.5510	0.29

(b)	Trait PC _c 1 'size and fecundity'			Trait PC _c 2 'seed size'		
	<i>F</i>	<i>P</i>	β	<i>F</i>	<i>P</i>	β
Country _{1,12}	0.11	0.7436	0.07	0.01	0.9958	0.05
Population (country) _{18,12}	1.34	0.3070	0.45	17.28	< 0.0001	1
Competition _{1,12}	53.21	< 0.0001	1	24.44	0.0003	0.99
Country × competition _{1,12}	0.85	0.3748	0.14	0.62	0.4456	0.11
Environment PC 1 _{1,12}	13.95	0.0028	0.93	1.08	0.3187	0.16
Environment PC 2 _{1,12}	0.30	0.5954	0.08	3.15	0.1015	0.37
Environment PC 1 × country _{1,12}	1.78	0.2072	0.23	0.79	0.3905	0.13
Environment PC 2 × country _{1,12}	0.38	0.5487	0.08	0.35	0.5665	0.08
Environment PC 1 × competition _{1,12}	0.03	0.8679	0.05	3.66	0.0800	0.42
Environment PC 2 × competition _{1,12}	2.37	0.1496	0.29	0.12	0.7402	0.06

Degrees of freedom (d.f.) are presented as subscripts, with numerator and denominator d.f. separated by commas, and β is the power to detect a significant effect given an alpha value of 0.05. Environment PC1 represents latitude and rainfall, environment PC2 represents temperature and elevation. Bold values are significant at the $P < 0.05$ level.

PCs and the treatment by environment PCs by country interactions were never significant.

Correlation coefficients for individual traits in both gardens are given in Appendix S1 (see Supplementary material). Some traits had parallel relationships (significant correlations and very similar slopes) with environmental variables, but others did not, with correlations being considerably stronger in one area, either California or Chile.

Coastal vs. inland ecotypes

There were differences between plants collected from coastal and inland locations in both California and Chile (MANOVA, container experiment $F_{10,7} = 25.81$, $P < 0.0001$; field experiment $F_{10,7} = 178.40$, $P < 0.0001$), but these differences were not composed of entirely the same traits in both areas (MANOVA, region by country interaction, container experiment $F_{10,7} = 4.60$, $P = 0.0274$; field experiment $F_{10,7} = 178.38$, $P < 0.0001$). Coastal and inland plants were different from each other regardless of competition treatment (i.e. no significant treatment by region or three-way interactions, all $P > 0.30$). Results are presented first for the container

experiment, and F and P values from ANOVAs are shown (d.f. for all ANOVA model effects presented are 1, 16). Coastal plants from both areas made fewer flowers ($F = 37.60$, $P < 0.0001$) that were smaller ($F = 13.13$, $P = 0.0023$) and possessed fewer stamens ($F = 20.63$, $P = 0.0003$), and coastal seeds took longer to germinate ($F = 9.91$, $P = 0.0062$) than seeds from inland areas (Fig. 3a–d). Plants from the coast took longer to flower ($F = 73.74$, $P < 0.0001$), made smaller seeds ($F = 36.74$, $P < 0.0001$), were shorter ($F = 63.27$, $P < 0.0001$), and made fewer seeds per flower ($F = 31.11$, $P < 0.0001$) (Fig. 3e–h). Although coastal plants from both California and Chile exhibited a similar response, the result was significantly stronger in plants from California (significant country by region interactions: flowering time $F = 16.47$, $P = 0.0009$; seed size $F = 13.78$, $P = 0.0019$; height $F = 26.92$, $P < 0.0001$; seeds per flower $F = 14.66$, $P = 0.0015$, Fig. 3e–h). Finally, there were no consistent differences in either shoot ($F = 0.30$, $P = 0.5921$) or root size ($F = 0.86$, $P = 0.3668$) between coastal and inland plants (Fig. 3i,j). In the field experiment (data not shown), coastal plants from both Chile and California were significantly shorter than inland plants ($F = 15.35$; $P = 0.0012$). Coastal plants

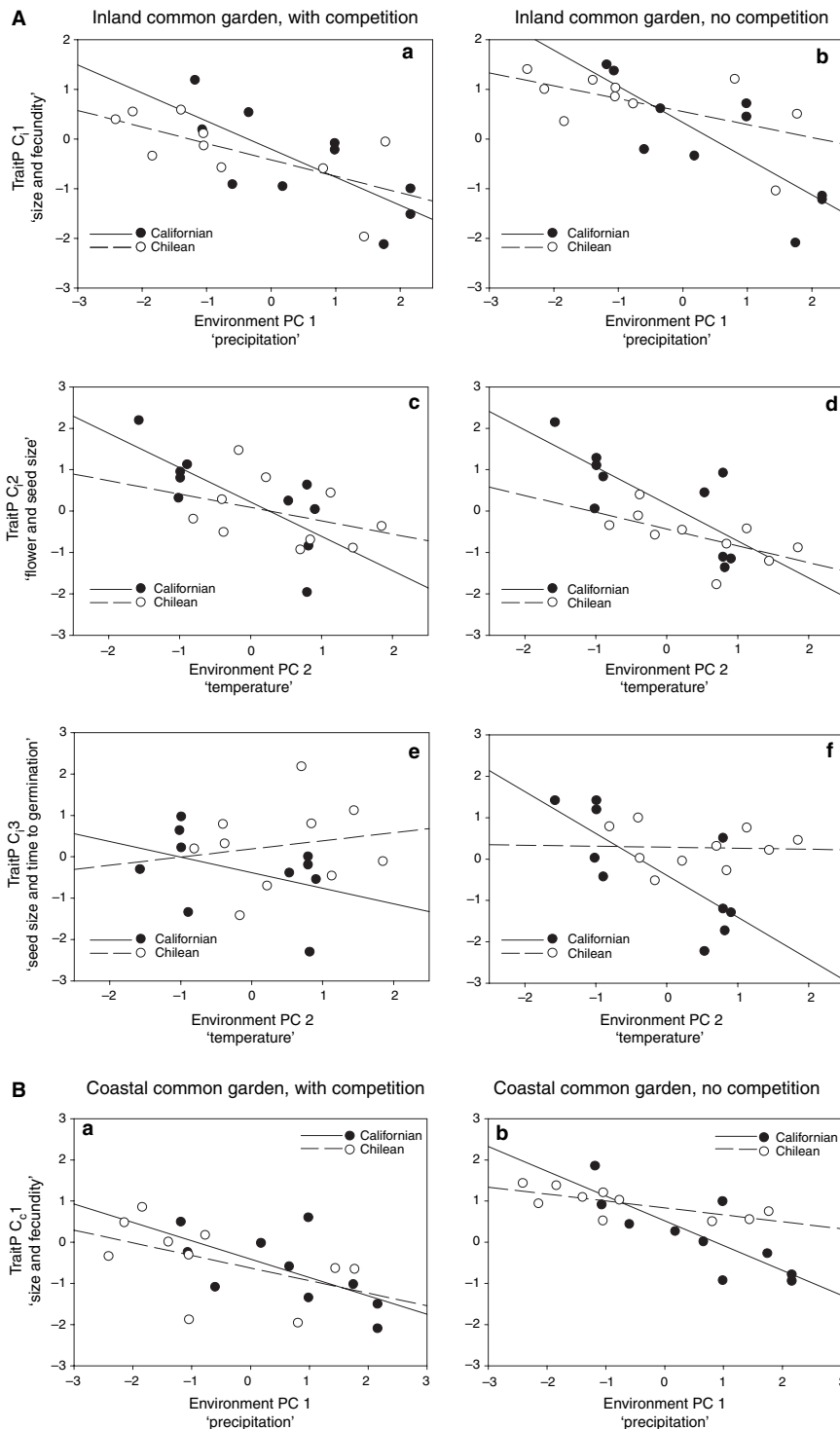


Fig. 2 Relationships between environmental principal components (PCs) (covariates) and plant trait PCs (response variables) in the container experiment (A) and the field experiment (B). Results are shown for plants growing with and without competition. There is a significant relationship between environment PCs and plant trait PCs, and no significant environment PC interaction with either country or treatment, for all figures except figure B, panels e and f, where there is a significant country \times PC 2 interaction (ANVOCA, Table 2).

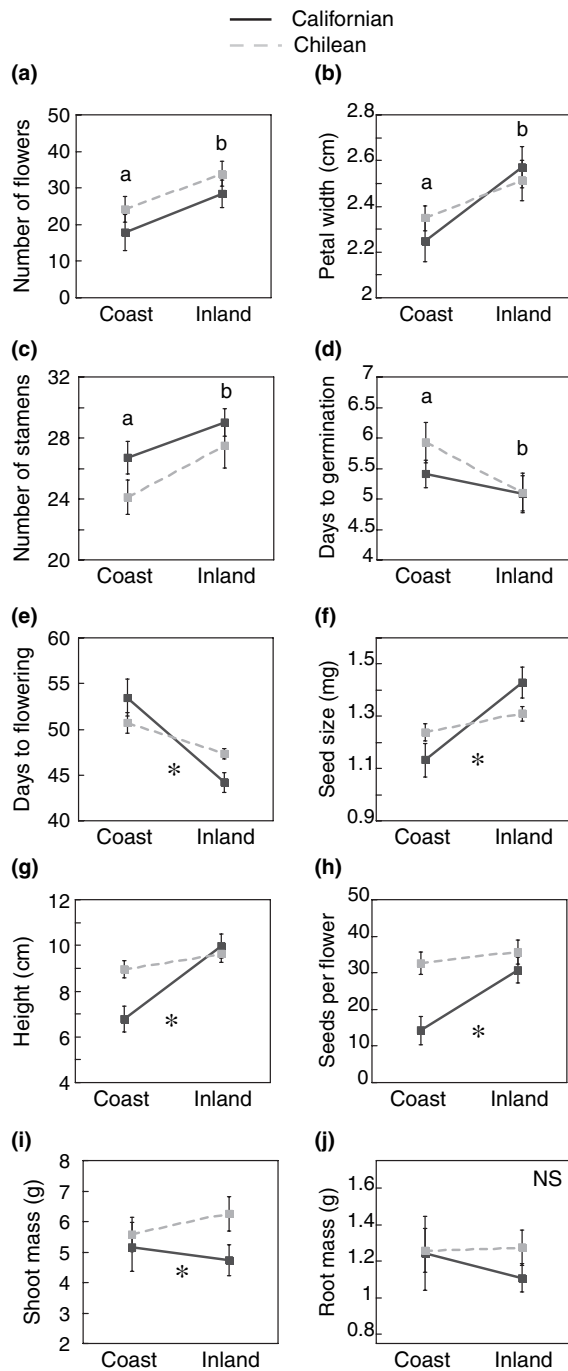


Fig. 3 Traits of coastal and inland populations grown in the container experiment. Values are least square mean values and standard errors, and analyses are ANOVAs performed separately for each trait. Lower case 'a' and 'b' above responses indicate significant differences between regions and no significant region by country interaction (a-f), '*' indicates a significant country by region interaction (e-i), and 'NS' indicates no significant difference between regions for either country (j). In all country by region interactions (e-i), differences between regions were significant for plants from California, but not those from Chile.

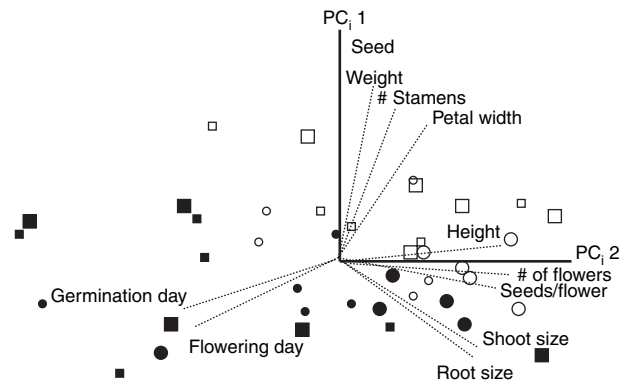


Fig. 4 Biplot of trait PC 1 vs. trait PC 2 in the container experiment. Vectors indicate the strength (proximity to each axis) of the relationship between traits and principal components. Each point represents mean values for a population, and each population is represented twice (grown both with and without competition). Black symbols are coastal populations, white symbols are inland populations. Californian populations are circles and Chilean populations are squares, large symbols are population mean values grown without competition, and small symbols are populations grown with competition.

also made smaller seeds ($F = 660.76$; $P < 0.0001$) and took longer to germinate ($F = 8.37$; $P = 0.0106$), although this was much more obvious in seeds from California (significant country \times region interaction, $F = 692.82$; $P < 0.0001$ and $F = 6.06$; $P = 0.0251$ respectively). Coastal and inland plants did not differ in number of flowers ($F = 3.59$; $P = 0.0762$), shoot size ($F = 3.89$; $P = 0.0662$), or days to flowering ($F = 6.57$; $P = 0.4615$), nor were there significant region by country interactions for these traits.

Multivariate bi-plots of the results also provided support for a coastal/inland syndrome that was consistent in both Chile and California. In the container experiment, coastal plants from both Chile and California grouped together in the lower left quadrant of the bi-plot (Fig. 4). Coastal plants flowered and germinated later (most evident in the populations from California) and produced smaller seeds and smaller flowers with fewer stamens. Coastal plants also tended to be shorter and produce less biomass and fewer seeds, a result most prominent in Chilean coastal plants when they were grown with competition. A distinct grouping along trait PC_f 2 was not as clear for populations grown in the field experiment (bi-plot not shown) primarily because the responses of the inland populations are more variable, but plants of coastal origin were shorter and made smaller seeds than plants collected from inland locations (grouping across PC_f 1).

Discussion

Because invasive species have known dates of introduction, they are ideal candidates for answering questions

about the speed of evolution in natural systems. Evidence of local adaptation in the form of geographical clines has been shown in invasive species (Knowles, 1943; Reinartz, 1984; Lacey, 1988; Rice & Mack, 1991; Weber & Schmid, 1998; Neuffer & Hurka, 1999; Del Pozo *et al.*, 2002; Sexton *et al.*, 2002; Lee *et al.* 2003; Phillips *et al.*, 2006). However, there are very few direct comparisons between native and exotic populations of the same species (Huey *et al.*, 2000; Gilchrist *et al.*, 2001; Maron *et al.*, 2004). Our comparison of a species that has been introduced from California to Chile is particularly useful because the extreme similarities of climate and geography between the two areas has made this system the focus of classic studies on convergent evolution (Mooney, 1977). Additionally, our results are unique in that we looked at the response of many different types of traits (plant size, fecundity, flower, seed and phenological traits) to similar climatic regimes. This allows us to also address not only the speed of evolution, but ask whether similar selection gradients can cause some traits to evolve in similar ways, whereas other traits may diverge.

Evidence of local adaptation

There are two lines of evidence that *E. californica* in both Chile and California has adapted in parallel ways to local environments. First, size and fecundity gradients in both native and invasive *E. californica* were associated with parallel precipitation gradients, a result that was consistent in both common garden experiments. Secondly, in both common gardens there were parallels in trait divergence between plants collected from coastal and inland environments on both continents. This expression of a coastal and inland syndrome was robust across competitive environments. The competitive environment affected certain plant traits (e.g. reducing size and fecundity in both the field and container experiments, and reducing seed size in the field experiment), but plants showed variation between coastal and inland environments and along temperature and precipitation gradients regardless of the competitive environment.

When there were parallels in variation between plants from Chile and California, the pattern was almost invariably weaker in plants from Chile. Slopes of correlation lines between plant traits and environmental variables of Chilean populations were always shallower than those of Californian populations (Fig. 2), and coastal/inland differences were generally more pronounced in Californian populations (Fig. 3). Although flower and seed traits were correlated with gradients of temperature in the overall model in the container experiment (Table 2), this pattern was only significant in Californian populations when analyses were conducted separately for each country. This pattern, with weaker relationships between ecological traits and environmental variables in the introduced range, may be attributable to time since introduction. Selection has

been acting on *E. californica* for a relatively short time in Chile, and populations may not have reached evolutionary equilibrium. A similar pattern was found in populations of *Drosophila subobscura*: slopes of regressions between latitude and chromosome inversion frequencies in introduced populations in North and South America (introduced range) were generally in the same direction as those in Europe (native range) (Ayala *et al.*, 1989; Balanya *et al.*, 2003). Similar to our results, the relationship between latitude and inversions was always less steep in the introduced populations of *D. subobscura*. Alternately, weaker selection or lack of genetic variability in the introduced range could also be responsible for these patterns.

Similarity and divergence in response to selection

It is of interest to consider situations where similar selection agents cause convergence in some traits and divergence in others (e.g. Langerhans & DeWitt, 2004). Our results show a general concurrence of trait variation along clines in plants from Chile and California, but these adaptations have not occurred in precisely the same way in the two areas. An examination of traits of coastal and inland plants illustrates that while some traits vary in similar ways (particularly number of flowers, petal size and number of stamens, Fig. 3a–c), other traits do not. This is especially true for plant height and the number of seeds per flower, which are strongly divergent in coastal/inland plants in California but not so in plants from Chile (Fig. 3g,h). In a second example, principal components indicate a general relationship between plant size and fecundity and precipitation gradients in California and Chile, but plants from California show clinal variation most strongly in traits related to fecundity in the container experiment and shoot weight in the field experiment, whereas in Chile, these clines are most strongly related to height in both common gardens (Table S1a,b in Appendix S1). Finally, a comparison of correlation matrices indicates that individual correlations between plant traits and climatic measures (Table S1a,b) differ in both strength and direction between countries. These divergent patterns could result from differences in selection pressure in California and Chile, or they could be a consequence of the introduction history and particular genotypes introduced into Chile, a case of historical contingency (*sensu* Gould, 1989).

Plants also expressed clinal variation in different ways in the two common gardens. The pattern of clinal variation in plant size and fecundity was seen in both the field and container experiment, but the evidence for a coastal syndrome is seen most strongly in the container experiment. Because of the differences in the design of the two experiments, one cannot conclude that the observed differences between the common gardens result from environmental differences between the sites. The container experiment was conducted in more controlled

conditions, and the sample mean values were likely closer to the true population mean values because of the larger sample size per population, so it is perhaps not surprising that patterns are most easily detected in the container experiment. There is, however, a valuable conclusion to be drawn from the results of the two experiments. Evidence for local adaptation (specifically, the correlation between plant size and precipitation) is robust, and was expressed not only under different competitive regimes but also under a range of environments that included realistic field conditions.

Maternal vs. genetically based traits

Although the differences in traits observed in these plants are likely heritable, it is also possible that they are affected by environmental conditions experienced by the parental plants. These parental effects are known to affect plant traits, and they often affect traits that are expressed early in the plant's life, such as germination timing and early plant size (reviews in Roach & Wulff, 1987; Mousseau & Fox, 1998). Because this study measured many traits that were expressed at different stages of plant development, it seems unlikely that parental effects would be responsible for all the clinal variation seen in this experiment. Although there are other mechanisms through which parental environment can affect offspring, seed size is a parental effect most commonly thought to influence offspring phenotypes. Linear regressions indicated no significant relationship between initial seed size and any of the traits measured in these common gardens, except for the size of the seeds produced in the container experiment (E.A. Leger, unpublished). However, both the initial and the final seed size (after growing for one season in the container experiment) were strongly correlated with the minimum temperature of the environment where the plant was collected (Appendix S1, and Leger, unpublished data). Thus, seed size appears to be at least partially under genetic control. The parental environment may be affecting some traits in this study, but seed size is not obviously the mechanism for this effect.

Evidence of natural selection in the introduced range

We have presented evidence of parallel clines in plants collected from California and Chile that suggest that the clines in the Chilean populations have evolved since introduction. In Table 4, we present four processes that may lead to clines in phenotypic traits of recently introduced species, three of which involve a change in gene frequency over time. The first possibility is that pre-adapted genotypes were introduced directly into appropriate environments (e.g. propagules from higher latitudes in native range introduced directly into higher latitudes in introduced range). Depending on the particular system, this may or may not be a reasonable explanation for clinal variation. Genetic data can rule out

Table 4 Processes that can lead to geographic clines in phenotypic traits of invasive species.

Mechanism	Change in gene frequency over time?	Selection for local adaptation?	Selection acts on phenotypes formed by
Coincidental introductions	No	No	–
Differential establishment	Yes	Yes	Pre-adapted genotypes
Recombination	Yes	Yes	Novel gene combinations
Mutation	Yes	Yes	Novel genes

this possibility by demonstrating that native and introduced species with similar phenotypes are not each other's closest relatives (e.g. Maron *et al.*, 2004). Alternately, records of the phenotypes of founding populations can indicate that clines in introduced species have evolved post-introduction (e.g. Huey *et al.*, 2000; Gilchrist *et al.*, 2001). Historic records of the spread of invasive species can also make this explanation inadequate, particularly if population spread has been in the form of a wave following a few geographically limited initial introductions (e.g. Tower, 1906; Skellam, 1951; Johnston & Sealander, 1964). Finally when the introduced and native ranges are very small, it may be possible that coincidental introductions have occurred, but this explanation loses credulity with increasing area of occupation in the introduced range.

The remaining three possibilities in Table 4 all involve selection as the force responsible for creating patterns of clinal variation. They vary in the degree of novelty of the gene combinations upon which selection acts to produce locally adapted phenotypes. The most novel genotypes would be formed through new mutations in introduced plants. This seems unlikely to be a principal mechanism of adaptation, because the time since introduction of most invasive species is quite short relative to the rate of beneficial mutations in natural populations (Dobzhansky, 1970).

An introduction of a diverse number of genotypes, followed by strong selection for pre-adapted genotypes (i.e. genotypes from a very similar abiotic or biotic environment), could produce clinal variation through the differential establishment of plants with locally adaptive traits. This process is sometimes referred to as 'sorting,' (Sakai *et al.*, 2001; Müller-Schärer & Steinger, 2004) and can take place at two scales. There may be introductions of multiple genotypes across a wide geographical range, followed by selection for pre-adapted genotypes in each location. Alternately, multiple genotypes could be introduced into a smaller geographical range, but only pre-adapted genotypes would spread from this source into appropriate environments. Differential establishment, at any scale, depends upon either strong selection during the establishment and pre-reproductive

stages (before extensive recombination between different genotypes occurs) or following limited crossing between different genotypes (most likely for clonal or highly selfing species, e.g. Neuffer & Hurka, 1999).

If multiple genotypes of an outcrossing species are introduced and establish themselves in a given location, it is likely that there will be crossing between previously isolated populations, and recombination will form new genotypes in the introduced range. As above, introductions and recombination could take place primarily in one location, or multiple genotypes could be introduced across a wide range of environments. There can be a range of novelty among the new genotypes that establish after recombination. At one extreme, strong selection against hybrid genotypes could keep co-adapted gene combinations together, resulting in the establishment of pre-adapted genotypes, even among highly outcrossing species. At the other extreme, entirely new gene combinations that produce locally adapted phenotypes could evolve; some authors have suggested that recombination of genes between previously isolated populations could be an impetus for rapid evolution in invasive species (Ellstrand & Schierenbeck, 2000; Sakai *et al.*, 2001; Lee, 2002).

These processes are neither discrete nor mutually exclusive, but rather represent a continuum of possibilities resulting from gene exchange between previously isolated populations, followed by selection for locally adapted phenotypes. No one mechanism needs to be responsible for all local adaptation in a new range. The important point is that evolution via natural selection is the force responsible for creating a pattern of clinal variation in recently introduced invasive species, for all of the processes described above (new mutations, differential establishment, and recombination), except coincidental introductions.

Circumstances of the formation of clinal variation in *E. californica* introduced in Chile are most consistent with one of these three mechanisms involving selection. The anecdotal reports of spread in Chile (outward spread from a few sites after a brief lag period) are inconsistent with coincidental introductions, as is the geographical extent of the clines seen here (latitudinal gradients over 500 km, as well as between coastal/inland populations). In addition, the fact that plants from Chile express traits differently than Californian plants when grown without competition, do not show the same relationship between seed size and temperature, and differ in other details of their clinal variation (discussed above), are further evidence that these are not the exact same genotypes that have been translocated intact from California. It is most reasonable to assume that selection, rather than coincidental introductions, is responsible for the observed clinal patterns. Regardless of which of the evolutionary mechanisms is involved, clinal variation exists among populations of *E. californica* in Chile. Our common garden results indicate that this clinal structure was developed

by natural selection after poppies were introduced in 1850 and after they began to extend their range in Chile (Frias *et al.*, 1975; Arroyo *et al.*, 2000).

Conclusions

Eschscholzia californica has adjusted rapidly to its role as a non-native plant in Chile. Not only has it become more adept at colonizing disturbed environments (Leger & Rice, 2003), but it has also evolved what appear to be locally adapted genotypes over the course of 150 years. The evidence for local adaptation is robust, as similar clinal patterns are seen when plants are grown in different common gardens. The adaptations of the invasive poppies are broadly convergent with those seen in the native range, but invasive *E. californica* demonstrates that evolution can be flexible, with plants evolving minor differences in traits while retaining the same general syndromes along similar gradients.

Acknowledgments

We thank M. Forister, C. Leger, P. Leger, M. Cornell and the Rice lab for field assistance. The manuscript was improved by suggestions from S. Carroll, E. Espeland, M. Forister, R. Karban, J. Kingsolver and J. McKay, and J. Randall. M. Goedde and N. Willits provided statistical advice. Financial support was provided by the Jastro-Shields Research Scholarship award at the University of California, Davis, the UC Davis Botanical Society, and the National Science Foundation Biological Invasions IGERT program, NSF-DGE#0114432.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Correlation between plant traits and environmental variables in poppies collected from California and Chile in the container experiment and the field experiment.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1420-9101.2006.01291.x>

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Received 7 August 2006; revised 27 October 2006; accepted 8 November 2006