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Seed mass, seed number and evolutionary trade-off across geographic distribution: do they explain invasiveness in *Eschscholzia californica*, central Chile?

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Background: Seed mass is a life history trait that is related to invasiveness. Under limiting conditions, a trade-off is observed whereby an increase in seed mass occurs at the expense of seed numbers; if the above trade-off holds across climatic gradients it can provide an opportunity to assess the fitness/invasive potential of exotic plants.

Aims: To examine the variation in the life history traits of *Eschscholzia californica* populations across climatic gradients and to relate these traits to observed invasiveness.

Methods: We examined 19 populations in Chile. For each population we related seed mass, seed number, the slope of trade-off between seed mass and number and plant density with annual precipitation and mean annual temperature.

Results: Seed number and the coefficient of variation in seed mass were positively correlated with climatic variables. Trade-off was detected in 26% of the populations and no relationship was detected with climatic gradient. Plant density was negatively associated with precipitation.

Conclusions: The results suggest that for *E. californica* producing seeds with a variety of sizes is an optimal strategy to face geographic heterogeneity and hence to increase its invasiveness. Increased production of seeds at the cool and wet southern limit of the current range of the species does not contribute to an increase in its invasiveness.

Keywords: *Eschscholzia californica*; invasive plants; seed mass; seed number; trade-off

Introduction

Seed mass is a phenotypic trait that determines offspring and maternal fitness in plants (Venable and Brown 1988; Lalonde and Roitberg 1989; Hutchings 1991). Larger seeds germinate with higher probabilities than smaller ones and increase survival during juvenile stage (Moles and Westoby 2006). Seed mass has a consistent genetic base (Silvertown 1989; Venable 1992; Sadras and Egli 2008), and due to its adaptive value is one of the targets of natural selection (Rees and Venable 2007; Sadras 2007).

Under resource limiting conditions, when there is a restriction on the amount of energy that can be invested in plant reproduction, there will be a trade-off between seed mass and seed number (Grubb 2016; Smith and Fretwell 1974; Leishman 2001; Messina and Fox 2001). The optimal solution to this trade-off may differ depending on the environment in which the plant is found. For instance, in unfavourable environments plants with heavy seeds are likely to be selected; this will lead to a reduction in seed numbers but an increase in offspring fitness. In favourable environments, on the other hand, plants with light seeds are selected owing to their higher dispersal abilities (Sallabanks 1992); this will lead to an increase in seed number and consequently an increase in maternal fitness. This trade-off has been widely examined in ecological studies (Turnbull et al. 1999; Volis et al. 2002; Petru

et al. 2006), but little examined along geographic gradients (but see, Volis et al. 2002; Meng et al. 2014).

Among a variety of phenotypic traits examined to explain invasiveness in exotic plants, seed mass has been one of the most important attributes (Rejmanek and Richardson 1996; Leger and Rice 2003; Van Kleunen et al. 2010). Species with a smaller seed mass appear to be more invasive than species with heavier seeds (Rejmanek and Richardson 1996; Simberloff 2009). This appears to hold at between-species level; however, we are not aware of any studies that have examined the effect of seed mass on plant invasiveness within a single species.

Eschscholzia californica Cham. (Papaveraceae) is an herbaceous plant native to the west coast of the United States (California) and is highly invasive in Mediterranean ecosystems worldwide (Leger and Rice 2007). The species was introduced in central Chile in the late nineteenth century and currently occurs from 30°S to 38.0°S. This extensive geographic distribution concomitantly with the notable precipitation and temperature gradients that occurs in Chile (precipitations increase and temperature decreases with latitude) provide an opportunity to examine the variation in the life history traits of *E. californica* populations across environmental gradients and to relate these traits with plant invasiveness. Assuming that plant density is a proxy of invasiveness, we hypothesised that there would be an inverse relationship between observed plant density and seed mass.

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Materials and methods

The density of *E. californica* individuals was estimated by sampling ten 5 m × 2 m randomly selected plots in each of 19 population, between 30.5°S and 36.9°S (Figure 1). To determine seed numbers and seed mass, we collected an average of 25 individuals per population (ranging from 9 at Hualqui to 30 at Puchuncavi) (Appendix 1) and three to four pods per individual. For each pod we counted the number of seeds and mean seed mass, determined by dividing the total mass by the number of seeds in a pod. Sampling was carried out between October 2009 and February 2010 (late austral spring and summer).

We compared the seed number and seed mass between populations with non-parametric Kruskal–Wallis tests; we also estimated the coefficient of variation (CV) for each trait in each population. As the CV is standardised, it was

possible to conduct comparisons between seed number and seed mass.

Seed mass versus seed number trade-off (sm/sn trade-off) was estimated for each population using the slope of a linear regression analysis. The slope was estimated using the standardised major axis analysis. This procedure optimises the slope in function of the x - and the y -axes, without assuming dependence on y over x , as is the case of mass and seed number (Warton and Weber 2002). We evaluated the significance of the slopes by using bootstrap procedures (Efron and Tibshirani 1994). All statistical tests were conducted using R v 3.2.3 (R Development Core Team 2015).

Current climate data for every sampled site location (Figure 1) was downloaded from WorldClim database (<http://www.worldclim.org/>). We selected mean annual

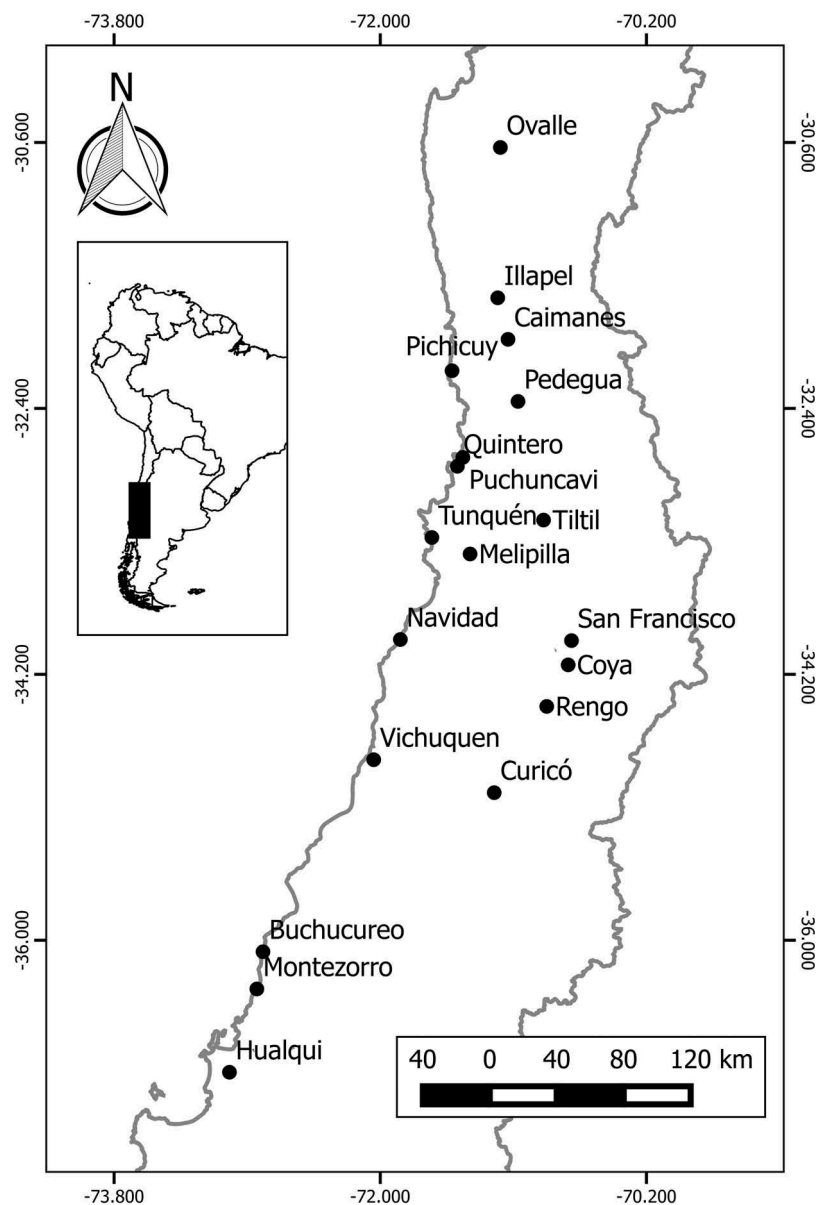


Figure 1. Geographic distribution of sampled populations of *Eschscholzia californica*, central Chile.

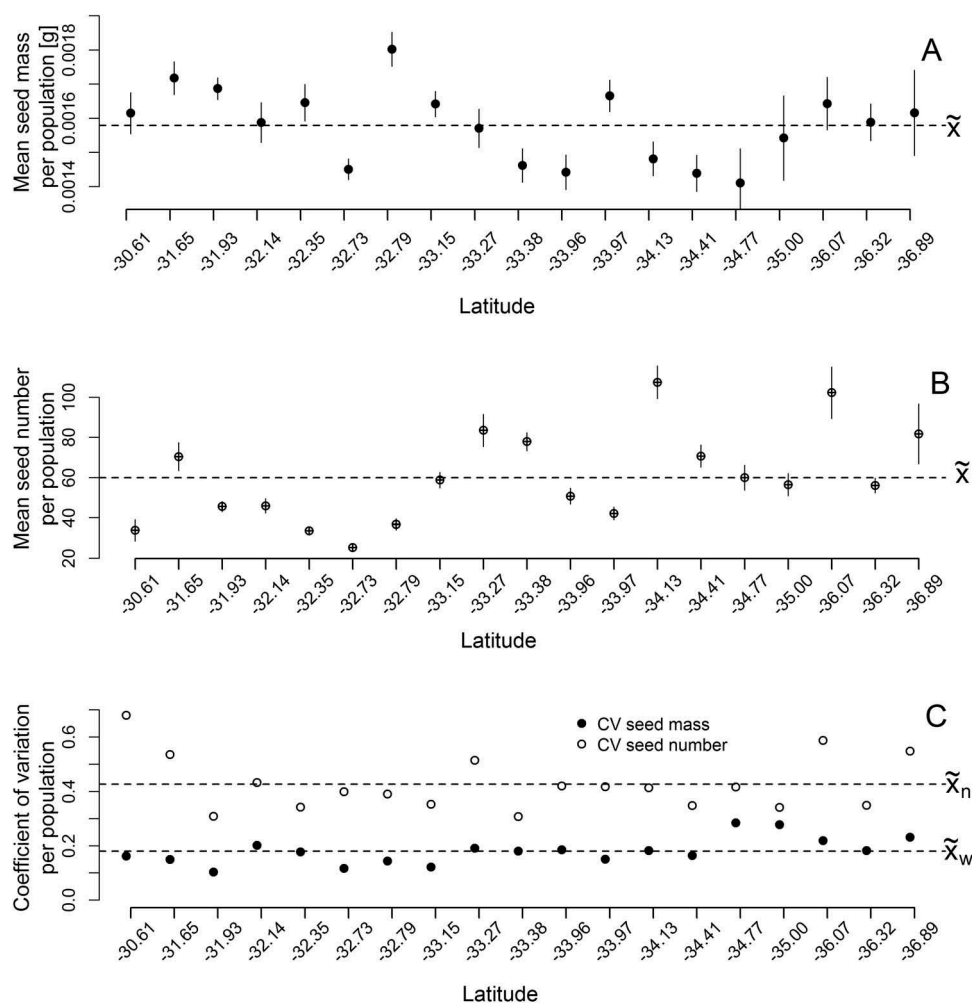


Figure 2. Seed mass (a), seed number (b) and coefficient variation of seed number and coefficient variation of seed mass (c) of *Eschscholzia californica* populations along latitudinal gradient (axis x) (left, northern populations, right, southern populations). The dotted line in the axis y represent mean for each metrics. In A y B, lines on the points represent the SE.

temperature (BIO1) and annual precipitation (BIO12) as the most relevant climatic variables. Although, WorldClim offers a variety of climatic variables, we select these variables for their simplicity to capture the climatic gradient that exist in Chile: they are highly significantly correlated with latitude (Pearson test: $r = -0.94$, $P \ll 0.001$ for annual precipitation; $r = 0.71$, $P \ll 0.001$ for mean annual temperature).

We ran spatial auto-regression models using climatic variables (independent variable) and the life history traits (dependent variables): seed mass, seed numbers, CV of seed mass, CV of seed number; we also included the slope of the sm/sn trade-off. Unlike classic regression analysis, this model weights the numerical differences of pairs of data according to their geographic distance, assuming that geographically close data are more similar than geographically distant ones, correcting a possible genetic relationship between populations and increasing the power of the analysis. For this analysis, we used a software developed for spatial analysis in macroecology (SAM v 4) (Rangel et al. 2010). For the graphical representation of the most significant variables, we used smooth surface analysis (Marra and Wood 2011).

In order to explore the relationship between life history attributes and plant density (as a proxy of invasiveness) we correlated life history attributes and climatic data with plant density through spatial auto-regression models. This analysis was conducted with 13 of the 19 as we were unable to obtain density information for all the populations.

Results

The mean seed mass obtained for all populations was $1.6 \text{ mg} \pm 0.03 \text{ SE}$, ranging from 1.4 mg value at Vichuquen (34.778° S) to value at 1.8 mg at Quintero (32.379° S). The mean number of seeds per pod was $59.9 \pm 5.2 \text{ SE}$, with a range from 25 in Puchuncaví (32.732° S) to 107 in Coya (34.136° S). We detected significant differences for seed number ($\chi^2 = 225.01$; $P < 0.001$) and seed mass ($\chi^2 = 71.69$; $P < 0.001$) among populations (Figure 2(a) and 2(b)). Seed mass varied less than seed number (CV seed mass: $0.18 \pm 0.01 \text{ SE}$; CV seed number: $0.42 \pm 0.02 \text{ SE}$) (Figure 2(c)). A significant negative relationship (trade-off) between seed

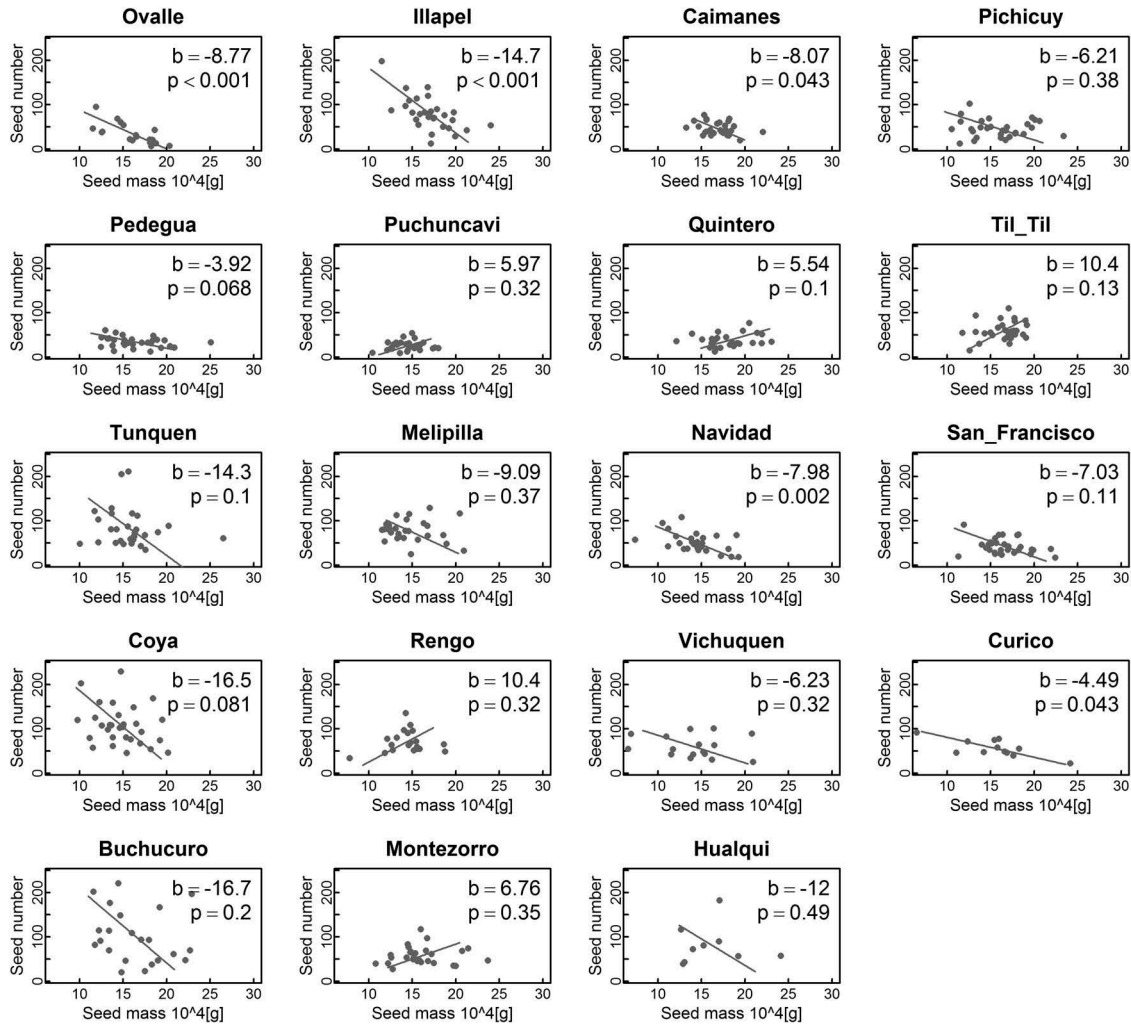


Figure 3. Relationship between seed mass vs. seed number in *Eschscholzia californica* populations, central Chile. Line represents estimated lineal regression conducted with smart wrapper (R program version 3.02). b represent the slope of the relationship, p represent p -values. Populations are displayed from north to south (see Appendix 1).

mass and seed number was detected in 5 of the 19 populations studied (26%) (Figure 3).

Variation in seed mass was associated positively and significantly with the interaction between annual precipitation and mean annual temperature, explaining 51% of the total data variability (Table 1, Figure 4(a)); variation in seed number, in turn, was positively correlated with annual precipitation (24% total variance; Table 1, Figure 4(b)). None of the regression models detected a relationship between climatic variables and seed mass and the slope of the trade-off (Table 1).

Plant density was negatively associated with variation in seed mass ($r^2 = 0.672$; $P = 0.012$) and annual precipitation (Table 1, Figure 5) and showed no relationship with the rest of the plant life history traits.

Discussion

According to life history theory, the trade-off between seed mass and seed number in plants occurs in environments with limiting resources, such as water shortage (Leishman

2001; Messina and Fox 2001). In our study, we confirmed the existence of this trade-off in 5 of 19 populations (Ovalle, Illapel, Caimanes, Navidad, Curicó). This trade-off did not respond to climatic gradients, contrary to our expectations. It is probable that the trade-off is consequence of limiting conditions that occur at local scale, for instance soil chemistry variation, a fact that has been well documented in other studies (Lee and Fenner 1989; Jurado and Westoby 1992). How to explain the 74% of cases where we did not find the trade-off? It is possible that the regression analysis using the totality of individuals can obscure the trade-off (if it exists) because we are including “optimal” and “sub-optimal” individuals in a same analysis. This methodological problem has been largely identified within the literature (Grubb 2016); in field studies, however, it is not possible to discern “a priori” which the optimal individuals are (those that maximise simultaneously seed mass and seed number) within the populations. The only way to do so is to conduct controlled experiments in the laboratory (Grubb 2016).

Table 1. Spatial auto-regression analysis between life history attributes, annual precipitation (P) and annual mean temperature (T) in 19 *Eschscholzia californica* populations distributed along latitudinal gradient, central Chile.

Attributes	Seed weight			CV Seed mass			Seed number			CV Seed number			Slope of the seed mass vs. seed number trade-off			Plant density		
	r^2	p	AIC	r^2	p	AIC	r^2	p	AIC	r^2	p	AIC	r^2	p	AIC	r^2	p	AIC
P	0.203	0.403	-285.905	0.446	0.004	-61.522	0.243	0.046	179.725	0.081	0.763	-23.357	0.073	0.727	146.231	0.539	0.033	39.232
T	0.216	0.968	-286.765	0.127	0.968	-23.115	0.175	0.118	180.38	0.061	0.914	-23.115	0.037	0.968	146.783	0.344	0.146	43.794
$T + P$	0.341	0.203	-286.308	0.56	0.003	-62.07	0.22	0.14	183.077	0.071	0.982	-19.563	0.088	0.415	149.515	0.533	0.124	44.958
$T * P$	0.218	0.256	-286.827	0.516	0.002	-64.013	0.214	0.046	179.846	0.064	0.923	-23.184	0.066	0.769	146.208	0.502	0.043	40.226
$T + P + T * P$	0.43	0.112	-284.695	0.564	0.011	-57.854	0.237	0.25	187.048	0.136	0.51	-16.565	0.134	0.396	152.908	0.542	0.239	52.146

Each analysis was conducted independently. Significant results are in bold. Smallest AIC was selected for best model.

When we analysed each life history trait separately, we found that seed number varied significantly and positively with precipitation, while seed mass did not. The lower variability in seed mass than seed number is consistent with the idea that seed mass has an important component of heritability among plants (Moles et al. 2004, 2005a, 2005b; Moles and Westoby 2006), while seed number is a plastic attribute, highly dependent of environment (Sadras 2007; Sadras and Egli 2008).

An increase in seed numbers with precipitation alone does not necessarily mean that invasive populations will be viable in the future. Evidence shows that the population growth rate of *E. californica* decreases significantly at the humid extreme of the gradient (southern Chile) due to a severe recruitment limitation of seeds to juvenile and juvenile to adult stages (Peña-Gómez and Bustamante 2012). Thus, high fecundity expresses the potential of individuals to maintain viable populations; however, this may be inconsequential if plant survival is low during later life cycle stages (Angert et al. 2009; Peña-Gómez and Bustamante 2012). The species distribution model (SDM) constructed for this species is concordant with these results as they show that it has a very low likelihood of spreading to the south of Chile (Peña-Gómez et al. 2014).

Considering these results, we suggest that the expansion of this species beyond its current southern invasion front is limited due to demographic constraints that occur in areas with low temperature and high precipitation simultaneously (see Stachowicz et al. 2002; Hellmann et al. 2008). Despite lower seed numbers observed at the northern xeric extreme of the gradient, we found increased plant density, thus suggesting the possibility of further expansion beyond the current northern geographic limits if there is not dispersal limitation. This hypothesis is concordant with SDMs which predict an expansion in the north of Chile to approx. 28° latitude (Peña-Gómez et al. 2014). Coastal zones beyond 30° S (Figure 1) are relatively warm and have enough coastal fog during all year around (Rutllant and Fuenzalida 1991; Garreaud et al. 2008), that is, it is possible that potential new migrants of this invasive species may survive and maintain viable populations farther north. In other words, this species has the potential to invade unique coastal desert ecosystem, valuable for their endemism and for their vegetation responses to sudden ephemeral precipitations, producing the “flowering desert” (Armesto et al. 1993; Vidiella et al. 1999).

The significant interaction between precipitation and temperature that appears to be related to seed mass variability suggests that an interesting non-linear synergy affects seed mass. In fact, CV seed mass was highest only at intermediate values of temperature and precipitation at ca. 34° S, the centre of the distribution range of the species (Figure 1). Considering the latitudinal gradient of Chile, an increase in precipitation will result in a decrease in temperature; therefore, at the centre of the geographic distribution of this species, there appears to be a climatic

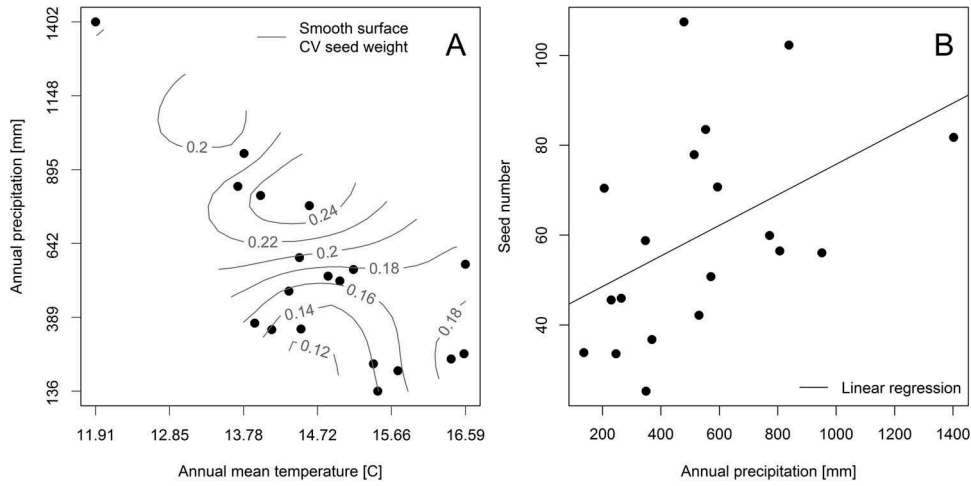


Figure 4. Relationship between environmental variables and the life history traits for *Eschscholzia californica* populations with spatial auto-regression. (a) Smooth surface of the seed mass variation coefficient in relation to annual precipitation (mm) vs. annual mean temperature. Smooth surface explains the 81.2% of variance. (b) Linear regression between seed number and annual precipitation (mm).

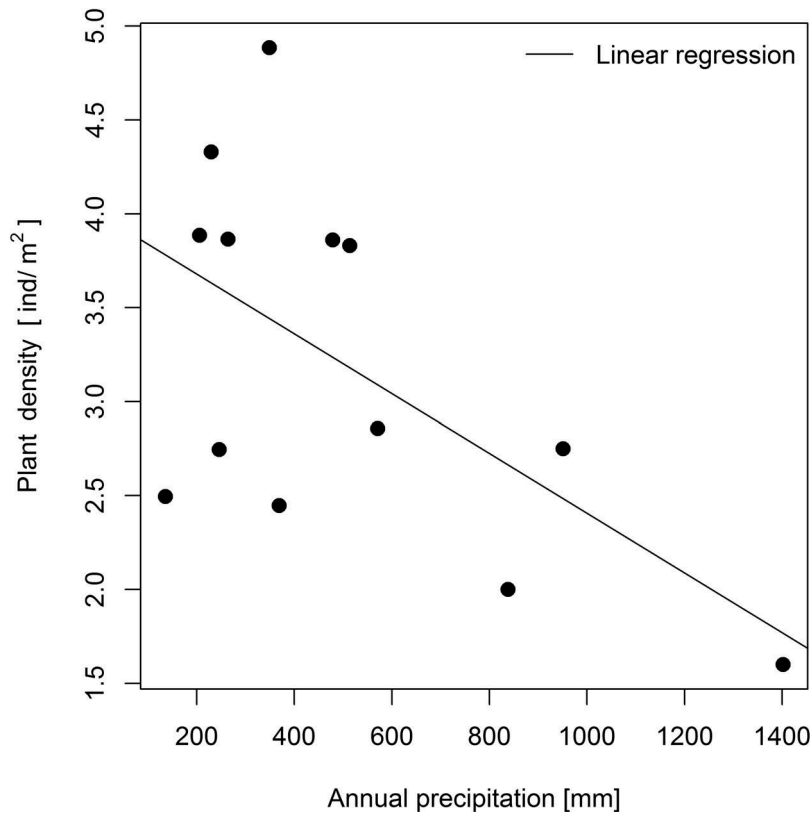


Figure 5. Relationship between plant density and annual precipitation (mm) for *Eschscholzia californica* populations, central Chile.

trade-off which implies a reduction of selective pressures on seed mass, thus allowing the production of a wide range of seed masses amongst individuals (Leishman and Westoby 1994). For an invasive plant, such as *E. californica*, having the ability to switch between maternal fitness (small seeds) and offspring fitness (large seeds) is a significant advantage when faced with highly variable

climatic environments such as those found in central Chile (Rutllant and Fuenzalida 1991).

Conclusions

The trade-off between seed mass and seed number in the case of the geographic distribution of the exotic *E.*

californica does not appear to be related to a climatic gradient. The trade-off detected in some localities suggests that factors not directly related to climate at smaller spatial scales may be shaping their expression. The increase in seed numbers and the increase of seed mass variability suggest plastic responses to the climatic gradient. However, the increase in seed numbers at its southern range limit is not reflected in an increase in invasiveness. In fact, we observed a reduction in plant density to the south. This suggests that invasiveness is reduced at the humid-cold extreme of the distribution range of the species.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

Daniel Zamorano is interested in life history trait variation across populations and how they interact with the environment, at local, landscape and regional scales.

Ramiro O. Bustamante is a full professor. He is interested plant invasions from population ecology and niche-driven range limitation perspectives.

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Appendix 1. Characterisation of population attributes in *Eschscholzia californica* along his distribution range. Longitude and latitude in coordinate GCS WGS84.

Population name	N° collected plants	Longitude	Latitude	Annual precipitation (mm)	Mean annual temperature (°C)	Seed number	Seed mass (g)	CV seed number	CV seed weight	Slope seed weight/seed number trade-off
Ovalle	22	-71.129	-30.614	136	15.48	33.82 ± 5.3	1.61 E-3 ± 6.02 E-5	0.68	0.16	-8.77
Illapel	29	-71.206	-31.652	206	15.74	70.44 ± 7.0	1.72 E-3 ± 4.77 E-5	0.54	0.15	-14.7
Caimanes	31	-71.137	-31.933	230	15.43	45.56 ± 2.6	1.69 E-3 ± 3.19 E-5	0.31	0.10	-8.07
Pichicuy	31	-71.515	-32.145	264	16.58	45.93 ± 3.6	1.59 E-3 ± 5.85 E-5	0.43	0.20	-6.21
Pedegua	31	-71.069	-32.353	246	16.41	33.58 ± 2.1	1.65 E-3 ± 5.35 E-5	0.34	0.18	-3.92
Puchuncavi	32	-71.442	-32.732	349	14.51	25.27 ± 1.8	1.45 E-3 ± 3.03 E-5	0.40	0.12	5.97
Quintero	28	-71.479	-32.792	369	13.93	36.74 ± 2.8	1.80 E-3 ± 4.97 E-5	0.39	0.14	5.54
Til_Til	30	-70.896	-33.156	347	14.14	58.77 ± 3.8	1.64 E-3 ± 3.70 E-5	0.35	0.12	10.39
Tunquen	30	-71.652	-33.274	553	15.18	83.5 ± 8.0	1.57 E-3 ± 5.57 E-5	0.51	0.19	-14.34
Melipilla	30	-71.393	-33.385	514	15.00	77.9 ± 4.4	1.46 E-3 ± 4.89 E-5	0.31	0.18	-9.09
Navidad	29	-71.865	-33.964	571	16.59	50.76 ± 4.0	1.44 E-3 ± 5.05 E-5	0.42	0.19	-7.98
San_Francisco	31	-70.707	-33.972	530	14.85	42.16 ± 3.2	1.67 E-3 ± 4.57 E-5	0.42	0.15	-7.03
Coya	31	-70.730	-34.136	479	14.36	107.46 ± 8.1	1.48 E-3 ± 4.93 E-5	0.41	0.18	-16.45
Rengo	21	-70.875	-34.417	594	14.49	70.71 ± 5.5	1.44 E-3 ± 5.29 E-5	0.35	0.16	10.41
Vichuquen	18	-72.045	-34.778	772	14.62	59.91 ± 6.2	1.41 E-3 ± 1.00 E-4	0.42	0.28	-6.23
Curico	13	-71.230	-35.001	807	14.00	56.46 ± 5.6	1.54 E-3 ± 1.24 E-4	0.34	0.28	-4.49
Buchucuro	24	-72.794	-36.078	838	13.71	102.3 ± 12.8	1.64 E-3 ± 7.67 E-5	0.59	0.22	-16.71
Montezorro	31	-72.835	-36.330	951	13.79	56.06 ± 3.6	1.59 E-3 ± 5.36 E-5	0.35	0.18	6.76
Hualqui	10	-73.020	-36.893	1402	11.91	81.77 ± 14.9	1.62 E-3 ± 1.25 E-4	0.55	0.23	-11.97