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PREGRADO

"VARIATION OF PHENOTYPIC ATTRIBUTES OF THE INVASIVE PLANT  
*Eschscholzia californica* ACROSS THREE BIOGEOGRAPHIC REGIONS"

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Sofía Paz Figueroa Sepúlveda

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Director de Seminario de Título:

Dr. Ramiro Bustamante Araya



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“Variation of phenotypic attributes of the invasive plant *Eschscholzia californica* across three biogeographic regions”

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Ramiro Bustamante Araya

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Comisión revisor y evaluador

Presidente Comisión  
Alejandra González

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Evaluador  
David Veliz

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## RESUMEN

Las invasiones biológicas son una de las principales amenazas para la biodiversidad en todo el mundo; una forma de entender por qué algunas especies son más invasoras que otras, es analizando sus rasgos fenotípicos (o rasgos funcionales) relevantes para el desempeño, pero en un contexto biogeográfico, o sea comparar estos rasgos entre individuos provenientes de rangos nativos y los rangos invadidos. Esta comparación puede ser considerada un experimento biogeográfico y puede servir también para estudiar el potencial evolutivo de las especies enfrentadas a nuevos ambientes. Para este trabajo se compararon dos regiones invadidas (Chile y Nueva Zelanda) con su correspondiente región nativa (California) en una especie de hierba originaria de California, *Eschscholzia californica*. Los rasgos a comparar fueron a) Tamaño de semilla b) Fecundidad c) Presión de propágulo y las comparaciones fueron California vs Chile y California vs Nueva Zelanda, considerando dos poblaciones locales sometidas a diferentes temperaturas ambientales (10°C y 12°C). Los resultados han mostrado diferencias entre las regiones sugiriendo que las plantas producen semillas más grandes en las regiones invadidas, teniendo relación con su origen como planta ornamental lo que podría estar dándole ventajas para invadir, para la región nativa la fecundidad pareciera ser mayor y presión de propágulo no muestras diferencias, sin embargo, las diferencias locales son aparentemente más importantes. Finalmente, el análisis de componentes principales mostró más cercanía entre nueva Zelanda y California que California y Chile.

## ABSTRAC

Biological invasions constitute a biodiversity threat worldwide; One way to understand why some species are more invasive than others are to analyse their phenotypic traits (or functional traits) relevant for fitness ideally between invaded range in relation to native ranges. These comparisons can be considered a biogeographical experiment which can help to elucidate the evolutionary potential of species facing to new environments. in this study, we examined two invaded regions (Chile and New Zealand) and the native range of *Eschscholzia californica*, a perennial grass original to California. We compared traits such as Seed size, Fecundity and Propagule pressure and the comparisons were California vs Chile and California vs New Zealand; at each region, we considered two local populations which differ in the thermal environment: (10°C and 12°C). Our results have shown differences between the regions suggesting that the plants produce bigger seeds in the invaded regions, In opposition to our expectations, at the native range fecundity was higher and for propagule pressure there were no differences. Local differences between populations, seem to be more important to take account to phenotypic variability. Finally, the principal components analysis showed more proximity between New Zealand and California than California and Chile.



## INTRODUCTION

Biological invasions represent one of the major threat to biodiversity worldwide (Alonso & Castro-Díez, 2015; McKinney & Lockwood,1999); to elucidate the causes of invasions as well as their ecological consequences, the invasion have become an important research issue in ecology (Palacio López & Gianoli Molla, 2012; Godfray & Crawley, 1998; Zilletti & Capdevila Argüelles, 2003; Hierro *et al.*, 2005; Carlton,1996).The process of invasion of an unoccupied region by new taxa may be integrated into the following three phases: Introduction, naturalization and colonization, which basically consist of the movement of gametes or propagules, from native to a new range, by anthropogenic vectors (Carlton, 1989) that allows the geographic expansion of the species to novel places that probably they would have never reached on their own (Vitousek *et al.*,1997). In order to succeed, one species has to surmount several demographics barriers from their native range: dispersal barriers (Parendes & Jones, 2000), reproductive and establishment barriers (Jaksic & Morales, 2014). Once these barriers have been overcome, the invasive process proceeds, and species are able to form a viable population which expands across the invaded range, producing reproductive off- spring in areas distant from sites of introduction (Richardson *et al.*, 2000).

One way to understand invasion is to examine phenotypic traits, that confer invasiveness (Radford & Cousens 2000, Lockwood, et al 2009). Evidence indicates that invasiveness can be determined by performance-related traits as well as by life-history traits (Kolar & Lodge 2001; Grotkopp *et al* 2002; Van Kleunen & Richardson 2007), In plants, life history traits are good predictors of invasiveness due their adaptive value (Stearns, 1989); these traits, evolved in the native range, can result adaptive in the

invaded range as well or they may evolve in response to natural selection (Richardson & Pysek, 2006; Catford *et al.*, 2009). Three features can be analysed among regions in order to explain plant invasiveness.

Firstly, seed size; large seeds size improves seedling establishment, they provide more resources to the emerging seedlings (Armstrong & Westoby, 1993; Bonfil, 1998); large seeds increase the probability of survival and recruitment (Moles & Westoby 2004), particularly under conditions of higher stress (Winn, 1988). Plants that produce large seeds tend to produce a lower number of them, following an ecological trade-off (Zamorano & Bustamante,2017); seed size is also related to dispersal ability, where small seeds can spread more rapidly to new habitat than the larger ones (Howe & Smallwood, 1982; Smith & Fretwell,1974; Leishmann *et al.*, 2000).

Secondly, fecundity; the number of seed produced per plants is particularly sensitive to unfavourable conditions (Forbis, 2003). Exotic plants tend to be more fecund in their introduced range than in their native range (Grigulis, 2001; Moroney *et al.*,2013).

Thirdly, propagule pressure; the total number of released propagules or the frequency of propagules introduction, is one of the most important features to assess invasiveness (Eschtruth & Battles, 2009). According to Lockwood *et al.* (2005), propagule pressure explains significantly invasive success.

If we have information about phenotypic attributes of this species in three different biogeographic regions (native and two invaded regions), we have two biogeographic experiment (Hierro *et al.*, 2005); this approach that has been specially successful in invasion ecology (Moroney & Rundel 2013), can help us to examine whether species

faced to similar or different environments have the potential to promote phenotypic differentiation. .

*Eschscholzia californica* (Papaveraceae) (California poppy), is a perennial herbaceous plant, that occurs naturally in western North America from the Columbia River south to California and from the coast of California eastward into the Great Basin. Within this extensive region, it grows in open sites, frequently associated with grasslands (Cook, 1965). *E. Californica* is a successful Invasive plant in the South Island of New Zealand and has an altitudinal distribution from sea level to 700 m and in Chile; it was introduced in the mid-nineteenth century and its current altitudinal distribution occurs from sea level to 2300 m (Leger & Rice, 2003). This plant can affect soil microbial diversity (De Armas-Ricard *et al.*, 2016), and invasive populations of the California poppy are more resistant to herbivores than native populations (Leger & Foratister, 2005). Studies of the reproductive biology of the species in Chile suggest that it is self-incompatible at high altitude and partially self-compatible at low altitude, being able to successfully colonize different environments (Arredondo-Núñez, 2011), pollinator visitation rate is independent of the number of plants, (Anic, *et al.*, 2015), and seeds have negative photoblastism (Castillo *et al.*, 2013). Previous studies have documented niche conservatism between California and Chile (Peña-Gómez *et al.* 2014), a result that is consistent to the general ideas that phenotypic traits are conserved in climatic-analogue biogeographic regions.

## **HYPOTHESIS**

Given that phenotypic attributes can change in function of biotic and abiotic factors, we can hypothesize:

- a) If the invaded range is similar to the native range, then no phenotypic changes are expected; then, we predict no phenotypic differences between and within California and Central Chile.
- b) If the invaded range is different to the native range, then phenotypic changes are expected; we predict phenotypic differences between and within California and New Zealand.

## **GENERAL GOALS**

To examine phenotypic trait variation in *E. californica* plants between California (the native range) and Central Chile and New Zealand (the invaded ranges).

## **SPECIFIC GOALS**

- 1.- To compare phenotypic traits of *E. californica* between native and invaded range with two different local populations in each region.
- 2.- To analyse the existence of differences of phenotypic traits between native and invaded range and between local populations.

## **METHODS**

### **Study regions**

California (37°0'N ;120°0'O) has a Mediterranean climate, but due to the large size of the state, it has variations towards the coasts being subtropical, with an average annual thermal temperature 25 ° C (minimum average of 22 ° C and maximum average of 27°C). Meanwhile, its annual rainfall is approx. 120,3 mm (Major, 1977).

Central Chile (~ 33°0'S ;70°0'O) has a Mediterranean climate, with an average annual temperature 14.4°C (average minimum of 8.3°C and maximum average of 22.5°C). Meanwhile, its annual rainfall is approx. 350 mm. The rains are concentrated in winter, while the summers are dry.

New Zealand, South Island, (~ 43°0'S ;172°0'E) has a temperate climate, with an average annual thermal temperature 11.6 °C (minimum average of 6.4 °C and maximum average of 16.8 °C). Meanwhile, its annual rainfall is approx. 623 mm (Contreras, 2016).

### **Data collection**

We selected two kinds of nested populations per biogeographic region (Local populations), which were equivalent in thermal environments: 10° C (correspond to 3 transect for New Zealand, 1 to California and 2 to Chile) and 12° C (correspond to 6 transect for New Zealand, 2 for California and 2 for Central Chile) properly recorded from Worldclim data base (Hijmans *et al.*, 2005).

For each population we constructed 10 continual 2 x 1 m plots; at each plot, we recorded the number adult per plot (an estimation of plant density); then, we selected three individuals per plot, for each individual, we counted the number of reproductive structures (flowers and pods). We randomly selected three pods, and, in the laboratory, we counted the number of seed per pod.

Seed size estimation was obtained simply dividing the weight of the total seeds by the number of seed per pod. Plant fecundity was estimated multiplying the number of seeds per pod by the number of reproductive structures. Propagule pressure (or seed rain) was estimated simply multiplying plant fecundity by adult density. Field information was recorded in spring-summer but in different years: 2015 Central Chile, and 2016 in New Zealand and California.

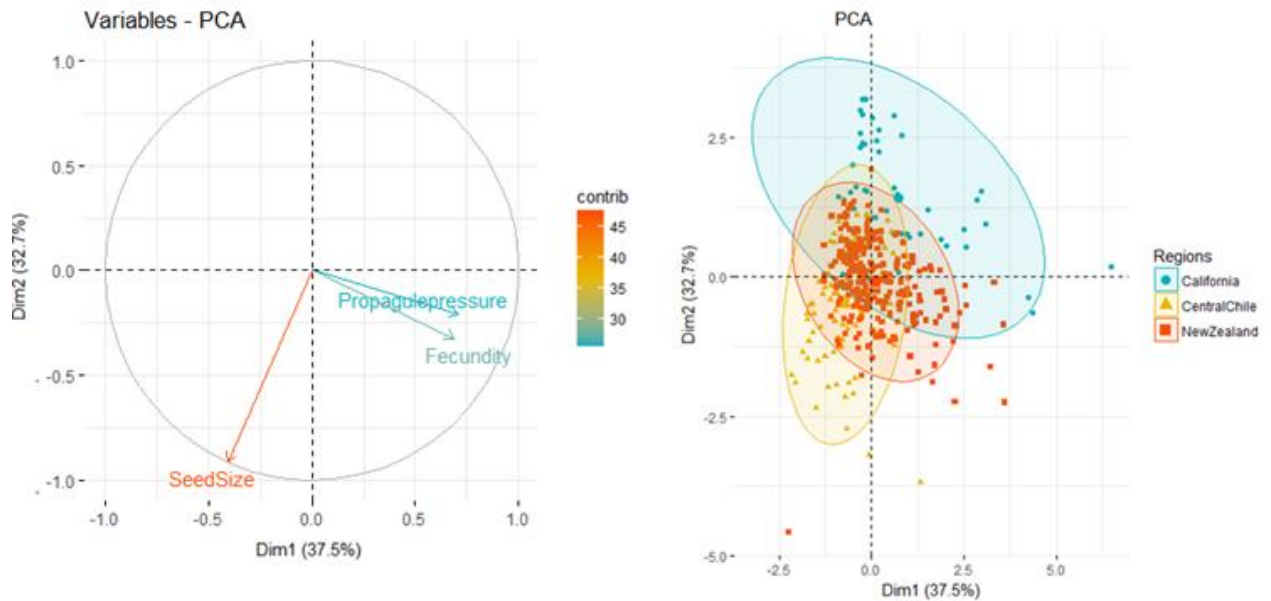
### **Data analysis**

Nested Anova analysis was performed where region and local populations (1 and 2) were the factors and a) Seed size b) Fecundity c) Propagule pressure were dependent variables. Finally, a Tukey HSD test was made to evaluate the existence of significant differences between the pairs of treatments. All the analyses were performed using the R I 386 3.4.2 software (R. Core team, 2017). To complement the Anova, a multivariate analysis was performed (Principal components analysis), and finally the Malahanobis distances between pairs of regions (California – central Chile and California – New Zealand) was calculated.

## RESULTS

### Principal components analysis

To complement the previous results, a Principal components analysis was performed, this showed that the principal component 1 and principal component 2 represent approximately 70% of the variance (figure 4) and the variables important for PC1 are fecundity (loading  $P = 0,64$ ) and propagule pressure (loading  $P=0.66$ ), and for the PC2 is seed size (loading  $P= 0.92$ ). Then Mahalanobis distance was calculated between dispersion points of regions, this showed longer distance between California And Central Chile (Mahalanobis distance =10,5) than California and New Zealand (Mahalanobis distance =9,18).



**Figure 4.** Biplot of Principal components analysis (PCA) of the phenotypic variables of *E. californica* in Central Chile and New Zealand (invaded regions) and California (native region).

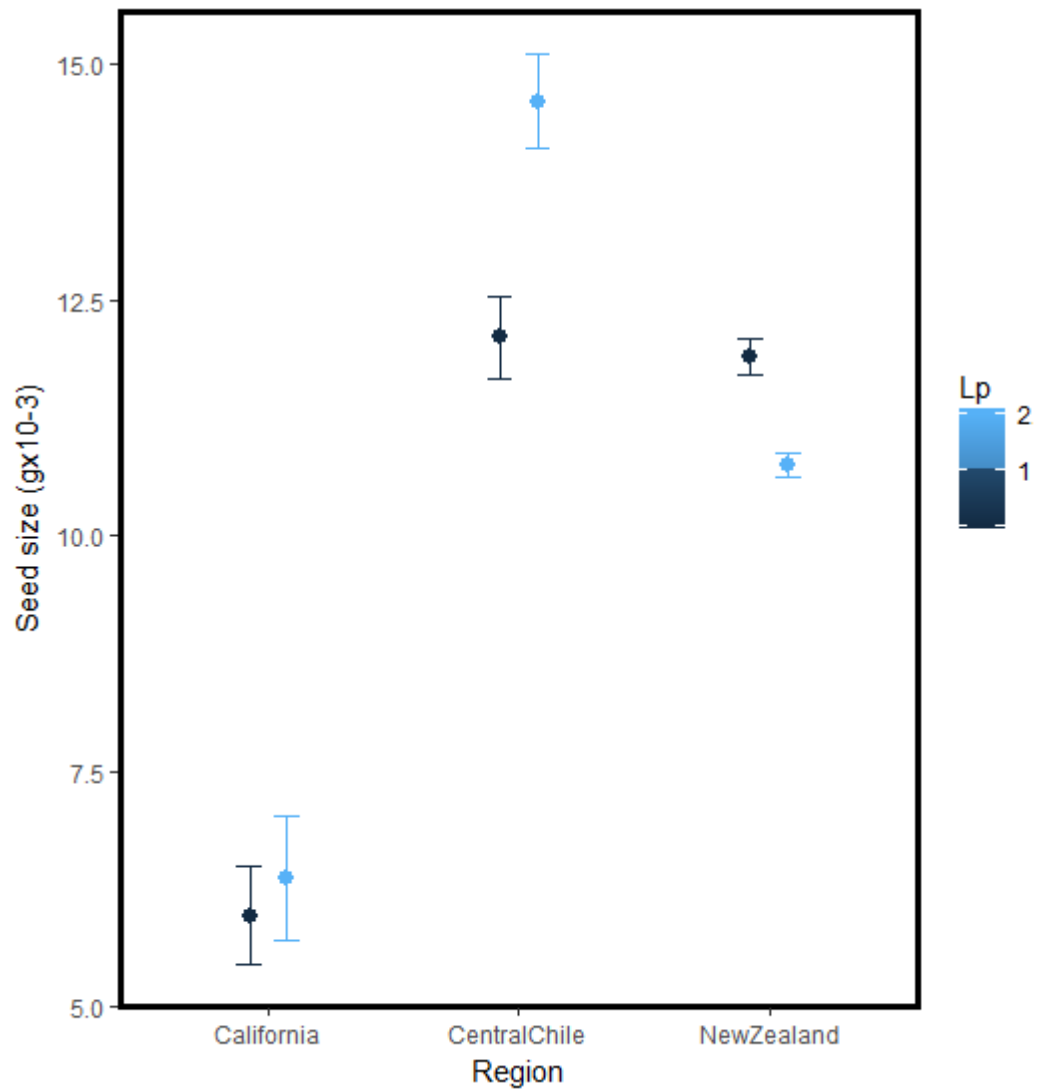
## Seed size

Seed size varied significantly among regions; (Table 1; Figure 1); was significantly higher in Chile and New Zealand (Tukey  $p < 0,001$ ). In New Zealand, seeds are smaller at population 2 than at 1 (Tukey  $p < 0,001$ ); in Chile, seeds are significantly larger at local population 2 (Tukey  $p < 0.001$ ) and in California, there are no differences between local populations (Tukey  $p=0.40$ ).

**Table 1.** Nested ANOVA to evaluate the effects of region and local populations on *E. californica* seed size in two invaded regions: Central Chile and New Zealand and the native region: California.

	<b>Df</b>	<b>F</b>	<b>p</b>
<b>Region</b>	2	221,38	< 0.001***
<b>Local populations (Region)</b>	3	8,81	< 0.001***





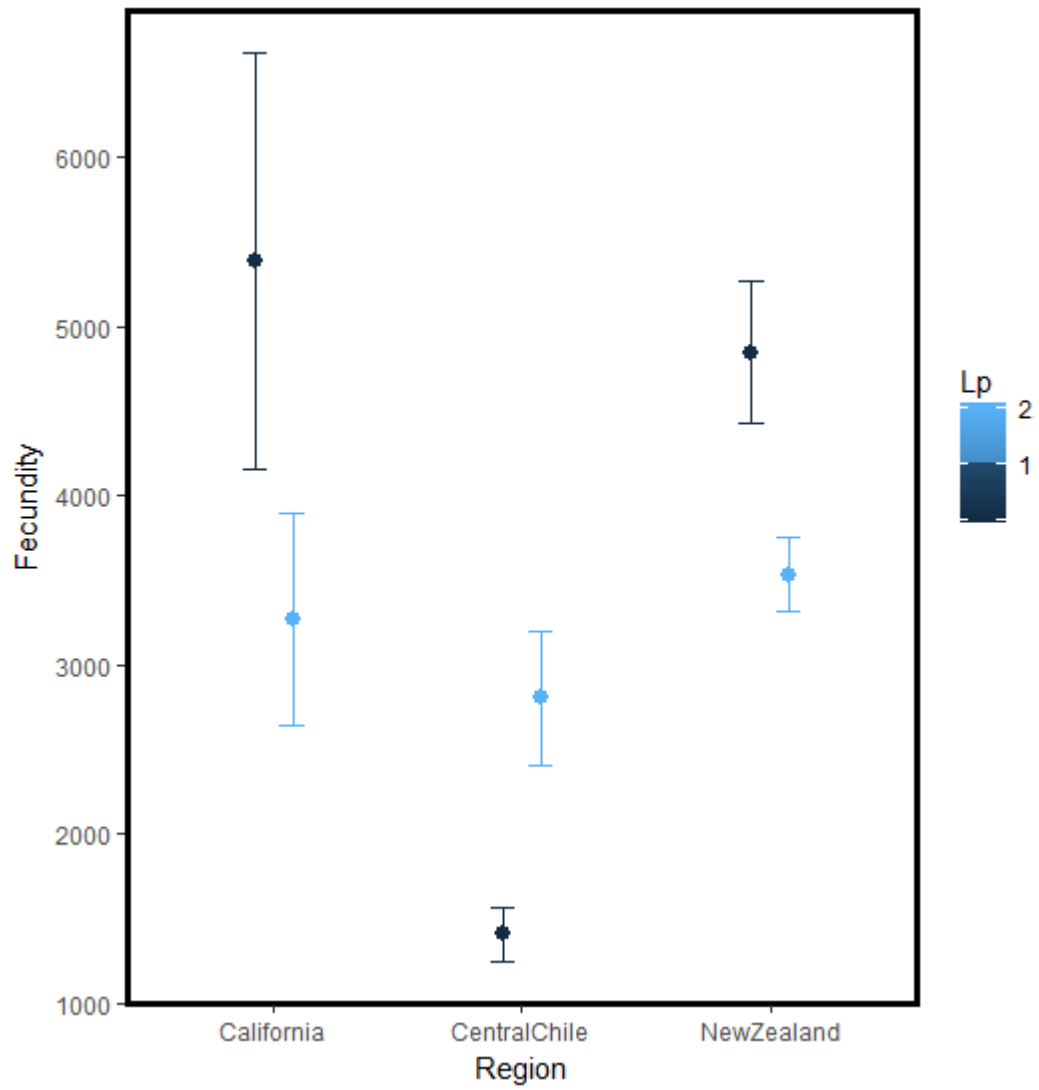
**Figure 2.** Seed size variation of *E. californica* in Central Chile and New Zealand (invaded regions) and California (native region) and at local populations (Lp).

## Fecundity

Fecundity varied between regions and for local populations (Table 2, Figure 2). Between regions California fecundity was significantly higher than Chile (Tukey  $p < 0,001$ ) and there is no difference between California and New Zealand (Tukey  $p = 0,1$ ). Within the regions for California and New Zealand, fecundity was significantly higher at population 1 (Tukey  $p = 0,05$ ), but in Chile it was significantly higher at population 2 (Tukey  $p = 0.03$ ).

**Table 2.** Nested ANOVA to evaluate the effects of region and local populations on *E. californica* fecundity in two invaded regions: Central Chile and New Zealand and the native region: California.

	<b>Df</b>	<b>F</b>	<b>p</b>
<b>Region</b>	2	13,12	< 0.001***
<b>Local population (Region)</b>	3	6,45	< 0.001***



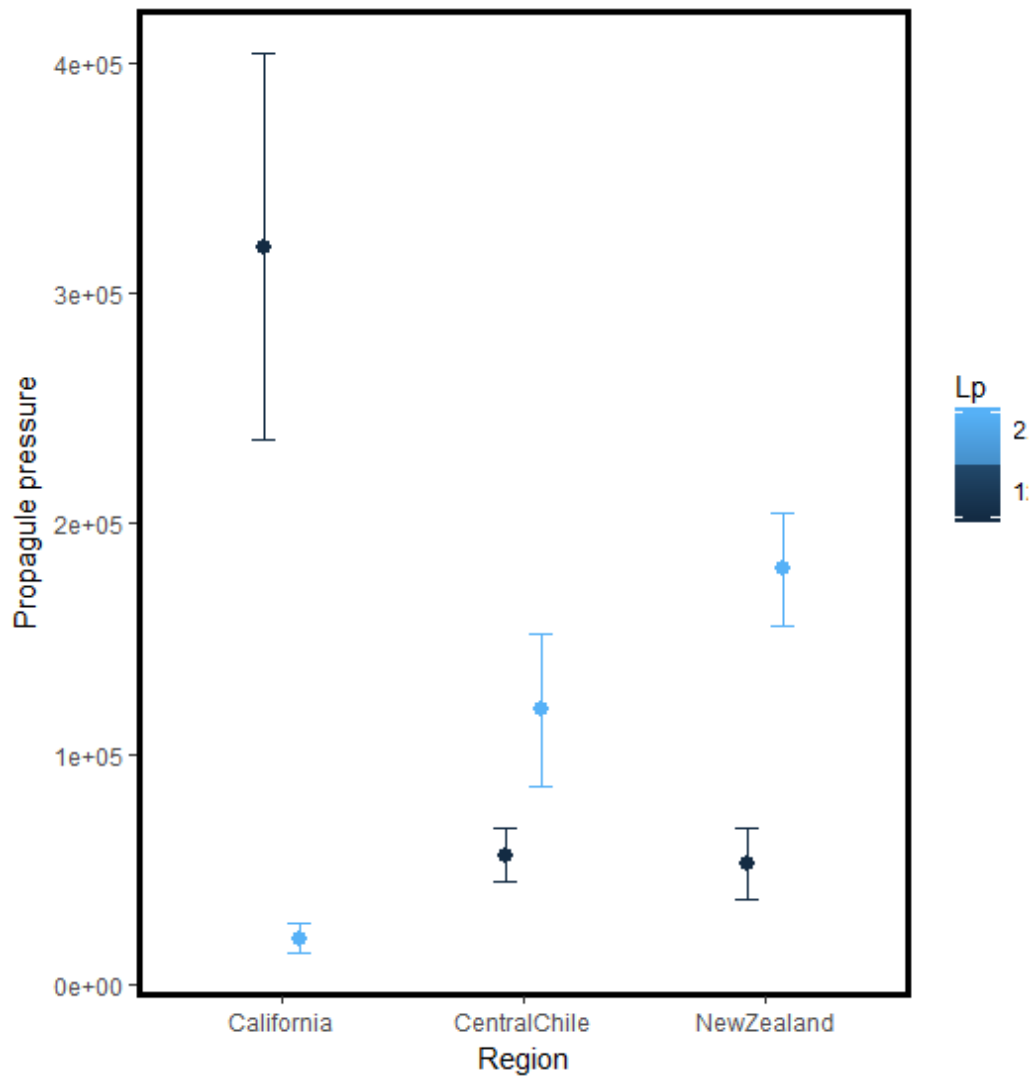
**Figure 3.** Fecundity variation of *E. californica* in Central Chile and New Zealand (invaded regions) and California (native region) and at local populations (Lp).

## Propagule pressure

Propagule pressure varied significantly only between local populations (Table 3, Figure 3); there was no significant difference between California and Central Chile or California and New Zealand ( $p > 0,05$  all the cases). Within the regions in California, propagule pressure at local populations 1 was significantly higher (Tukey  $p < 0,001$ ); in Chile there is no difference (Tukey  $p = 0,99$ ) and for New Zealand was higher at local population 2 (Tukey  $p < 0,001$ ).

**Table 3.** Nested ANOVA to evaluate the effects of region and local populations on *E. californica* propagule pressure in two invaded regions: Central Chile and New Zealand and the native region: California.

	<b>Df</b>	<b>F</b>	<b>p</b>
<b>Region</b>	2	2,74	0,06
<b>Local populations (Region)</b>	3	18,85	< 0.001***



**Figure 4.** Propagule pressure variation of *E. californica* in Central Chile and New Zealand (invaded regions) and California (native region) and at local populations (LP).

## DISCUSSION

The results showed significant effects either between pairs of regions and populations in most of the analyzed phenotypic attributes. Seed size was smaller in California than in the two invaded regions and varied significantly between local populations in all the regions. Fecundity was higher in California than in Chile but similar to New Zealand, within the regions, all showed differences. Propagule pressure was similar in California and the two invaded regions and variation between populations was significantly different only in California and New Zealand. Finally, PCA showed that the three variables are important representing 70% of the variance and larger distance between California and Chile.

The PCA showed a very separated dispersion of California points from the invaded regions, however the ellipses of the regions seem to be overlapped in the principal component 1, that means that there are no differences in fecundity and propagule pressure and they are apparently to be more preserved in the regions, but in the principal component 2 we can see a more separate dispersion, that mean seed size differences the regions and California is the region with the smallest ones, this analysis complement and supports what the ANOVA showed previously and also showed a relation between the invaded regions, where genetic shifts or phenotypic plasticity might driving changes differently than in the native region as Leger & Rice, 2003 showed, so our hypothesis was rejected, showing more similitudes between California and New Zealand instead of Chile, but a more interesting result might be the similitudes between the invaded regions (Mahalanobis distance =6,7), that was not discussed in this study.

One and the most interesting result was for seed size, even when there are differences in local populations, there is an evident increase of seed size in both invaded ranges compared with California; our expectation of similar size between Chile and California was rejected; the most parsimonious explanation for the increase of seed size in invaded region is an introduction bias; i.e. the founding populations for *E. californica* were selected artificially by individuals with large seeds to assure seedling survival for ornamental purposes (Buckley *et al.*, 2003). Given that the advantages of larger seeds in plants, these differences can be the simplest explanation for the high invasiveness of this species (Leishman *et al.*, 2000). Once invasion have occurred, phenotypic differentiation can be analyzed at local scale (Leger & Rice, 2007). For Chile and New Zealand, we found significant seed size differences between local populations; however, these differences were completely opposites: while in New Zealand, seed size was higher at colder populations (higher altitude), in Chile, it was lower at the same conditions. Given that small seeds increase dispersal, and large seeds increase recruitment (Westoby *et al.*, 1996; Leishman *et al.*, 2000), we hypothesize that in Chile, environment is selecting small seeds to increase dispersal ability and the opposite for New Zealand given the different condition in vegetation (Contreras, 2016). This remarkable seed size differentiation either at regional and at local scale is presumably consequence of phenotypic plasticity (Stearns, 1989).

In opposition to seed size, fecundity differ between regions, but not as we expected. California had higher fecundity than Chile and in the figure 2 we can see that the mean for California is higher than New Zealand even when is not significative. This difference can be simply the result of a trade-off between seed size and fecundity i.e. individuals with smaller seeds will have the highest fecundity values (Smith & Fretwell,

1974, Messina & Fox, 2001). In other words, populations at invaded range do not necessarily express a higher fecundity because larger seed will compensate a reduction in Fecundity. Our results are consistent with recent investigations that have documented that exotic species not necessarily are more fecund in invaded range, then our hypothesis was rejected (Parker et al., 2013), nevertheless, local variation is more important for this trait; for Chile fecundity decreased at local population 1 (higher altitudes) and the opposite for New Zealand and for California, at lowers temperatures and local population 1 (higher altitudes) fecundity was higher. For *E. californica* the pattern in invaded regions can be explained by the importance of perturbation because it attains greater fecundity for populations that grown in disturbed environments with reduced competition (Leger & Rice, 2003); on the other hand, at local conditions such as drier environments existing in Los Angeles, fecundity increased in *E. californica* (Leger & Rice, 2007).

Propagule pressure was higher in the native range at local population 1 (Figure 3), but there were no differences among the regions, and there are differences in local populations that apparently are more important that the differences between regions, our hypothesis was rejected. It is important to note that propagule pressure is a neutral hypothesis suggesting that one species will succeed invasion because more propagules are arriving to the invaded range (Lockwood, J. L. *et al.*, 2005; 2009). Our results suggest that in the invaded sites in spite of there are no increases in propagule pressure, invasion was possible due to factors that facilitate invasion in later stages of the life cycle. For local populations, if invaded sites exert a low biotic resistance due to competition with resident species the case of ecosystems of higher altitudes (Antonio *et al.*, 2001), invasion is possible even if few propagules arrive to these sites. When competition becomes



important due to high species diversity (MacArthur, 1972; Billing & Mooney, 1968), in order to succeed, a higher propagule pressure is important to assure establishment.

In spite of we have increased our knowledge of the ecology, biogeography and evolution of *E. californica*, given the climatic, vegetation and topographic analogy between Chile and California, we expected similar ecological responses, due firstly, we have demonstrated climatic niche conservatism (Peña-Gomez *et al.*, 2014), therefore we expected convergence in phenotypic traits. Secondly, the remarkable differences in seed size suggests introduction bias (we just discussed that) or the existence of large phenotypic plasticity as it has been suggested in other investigations (Gallegos, data no published.) or the evolution of larger seed size to deal with a new environment. Particular factors of the invaded ranges, not assessed in this study, can shape these phenotypic changes and deserve further investigations (Sáez, data no published).

## **CONCLUSIONS**

For the populations studied of *E. californica* we can conclude that traits changes, but not in the way we expected. For ecosystems of higher altitudes in central Chile and New Zealand, invasion has been possible in spite of low propagule pressure and no increases in fecundity. Our study indicated that differences in seed size is sufficient to overcome barriers imposed by high altitude ecosystems in the invaded range.

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