# Potential for higher invasiveness of the alien *Oxalis pes-caprae* on islands than on the mainland

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## Abstract

The higher vulnerability of islands to invasions compared to mainland areas has been partially attributed to a simplification of island communities, with lower levels of natural enemies and competitors on niches for invaders to establish and proliferate. However, differences in invader life-history traits between populations have received less attention. We conducted a broad geographical analysis (i.e. 1050 km wide transect) of plant traits comparing insular and mainland populations to test the hypothesis that alien plants from insular populations have the potential for higher invasiveness than their alien mainland counterparts. For this purpose plants of the annual geophyte *Oxalis pes-caprae* were grown from bulbs collected in the Balearic islands and the Spanish mainland under common greenhouse conditions. There were no significant differences in bulb emergence and plant survival between descendants from insular and mainland populations. However, *Oxalis* descendants from insular populations produced 20% more bulbs without reducing allocation to bulb size, above-ground biomass or flowering than descendants from mainland populations. Based on the lack of sexual reproduction in *Oxalis* and the dependence of invasion on bulb production, our study suggests that the higher occurrence of *Oxalis* in the Balearic islands than in the Spanish mainland can partially be explained by genetically based higher propagation potential of insular populations compared to mainland populations.

## Introduction

Invasion by alien species is one of the most conspicuous human-driven ecological changes with negative effects on biodiversity conservation (Lövei 1997). Invasion depends on propagule pressure, invasibility (the susceptibility of a community to be invaded) and invasiveness (the intrinsic ability of species to invade, Williamson 1996; Lonsdale 1999).

Clearly, some regions, communities or habitats are more invaded than others (Lonsdale 1999; Stohlgren 1999). For example, islands harbor more alien plants than adjacent mainland areas and they are considered to be highly susceptible to invasion (Elton 1958; Lonsdale 1999). This higher vulnerability to invasion of island versus mainland areas has been partially explained by the island simplification of communities with low levels of competitors and natural enemies to

which the invader can adapt (Mueller-Dombois 1995).

There is increasing evidence that alien plants can show fast adaptation in life-history traits to the new biotic and abiotic environmental variation in their new range (Weber and Schmid 1998; Eunmi 2002; Maron et al. 2004). One selection pressure driving rapid evolution of alien plants that has received a fair amount of attention is stated by The Evolution of Increased Competitive Ability (EICA) hypothesis. EICA postulates that introduced plants that are no longer under selection by specialist herbivores may be able to reallocate resources previously spent on herbivore defense to traits that increase competitive ability (Blossey and Nötzold 1995). This hypothesis predicts that under identical growing conditions, plants taken from an area were they have long been introduced without the presence of natural enemies may be larger and more fecund than conspecifics in the native range. This hypothesis could also explain differences in invasion success between populations within the introduced range differing in the presence of natural enemies, as for example between invaded islands and mainland areas. Here we compare plant size and fitness between invading populations of islands and mainland.

Among the plant traits that confer high fitness and therefore higher potential invasiveness are those associated with rapid dispersal. For plants, these traits are mainly short generation time, long fruiting period, seed dispersal by wind or by animals and clonal propagation (Crawley 1986; Rejmánek 1995). Thompson et al. (1995) found that aliens are more likely than natives to be clonal everywhere and that clonal growth becomes more important as the invaded habitat becomes more isolated and less influenced by man. Therefore, the amount of resources that plants allocate to vegetative reproduction or clonal growth can be considered a component of invasiveness that can affect population growth and the species area of distribution.

We compared life-history traits related to invasiveness in *Oxalis pes-caprae* (*Oxalis* hereafter) from Mediterranean insular and mainland populations, to test the hypothesis that populations from the introduced insular region have a genetically-based greater potential invasiveness than introduced populations in the neighboring mainland region. In an extensive survey conducted in Spain we have found *Oxalis* to be much more abundant at the regional scale in the Balearic Islands than in nearby Spanish mainland regions (Gimeno, Vilà and Hulme unpublished data). We mainly focus on vegetative reproduction because bulb production is the main trait in *Oxalis* determining spreading. To the best of our knowledge, this is the broadest geographical species traits analysis between island and mainland populations.

## Methods

### Study species

The South-African herb *Oxalis pes-caprae* occurs mostly in temperate and sub-tropical areas of Europe, Africa, Australia, Eastern Asia, South America and Western North America (Baker 1965), and was introduced to the Mediterranean basin at the beginning of the nineteenth century. *Oxalis* is widely distributed around Mediterranean islands and coastal regions (Stefanake-Nikeforake 1981).

*Oxalis* is heterostylous; sexual reproduction has not been observed in the introduced range. It is a geophyte with vegetative reproduction by means of underground bulbs. In autumn bulbs sprout and form an aboveground shoot and a fleshy contractile root from which new bulbs will be formed (Pütz 1994). In winter plants display rapid aboveground growth while the parent bulb is exhausted and new bulbs are formed, maturing in spring and remaining dormant in summer. Plants senesce in April–May (Galil 1968).

### Bulb collection

From late June to August 2001 we collected bulbs in the three Balearic Islands: Eivissa, Mallorca, and Menorca and in two mainland regions: Andalucía and València. Sampling sites have a Mediterranean climate with a moderate mean annual temperature and the highest temperatures during the summer drier season. Sampling sites were distributed along a 1015 km coastal transect and spanned the broad latitudinal and longitudinal distribution of the species within Spain (Table 1).

*Table 1.* Locality names and geographical coordinates of the study sites in Balearic Islands: Mallorca (MA), Menorca (ME) and Eivissa (IB) and the mainland regions in Spain: Andalucía (A) and València (VA).

| Code | Locality | Habitat | Latitude | Longitude |
|---|---|---|---|---|
| MA 1 | Randa | Agrarian | 39° 31′ N | 2° 54′ E |
| MA 2 | UIB | Agrarian | 39° 38′ N | 2° 40′ E |
| MA 3 | Sóller | Agrarian | 39° 46′ N | 2° 43′ E |
| MA 4 | Esporles | Agrarian | 39° 41′ N | 2° 35′ E |
| MA 5 | Capdepera | Ruderal | 39° 42′ N | 3° 27′ E |
| MA 6 | Artà | Agrarian | 39° 41′ N | 3° 21′ E |
| MA 7 | St. Margarida | Ruderal | 39° 42′ N | 3° 06′ E |
| MA 8 | Inca | Agrarian | 39° 43′ N | 2° 55′ E |
| MA 9 | Costitx | Agrarian | 39° 38′ N | 2° 57′ E |
| MA 10 | Palma de Mallorca | Agrarian | 39° 35′ N | 2° 39′ E |
| ME 1 | Ferreries | Ruderal | 39° 59′ N | 4° 01′ E |
| ME 2 | St. Climent | Agrarian | 39°52 N | 4° 14′ E |
| ME 3 | Cavalleria | Ruderal | 40° 06′ N | 4° 08′ E |
| ME 4 | Ciutadella | Agrarian | 40° 01′ N | 3.50′ E |
| ME 5 | Bco.Algendar | Agrarian | 39° 58′ N | 4° 01′ E |
| ME 6 | St Joan dels Horts | Agrarian | 40° 01′ N | 4° 09′ E |
| ME 7 | Alaior | Ruderal | 39° 56′ N | 4° 09′ E |
| ME 8 | Son Morell | Ruderal | 40° 02′ N | 3° 52′ E |
| ME 9 | Son Parc | Ruderal | 40° 02′ N | 4° 10′ E |
| ME 10 | Biniancolla | Agrarian | 39° 48′ N | 4° 17′ E |
| IB 1 | Can Galvos | Agrarian | 38° 58′ N | 1° 26′ E |
| IB 2 | S'Argentera | Ruderal | 38° 55′ N | 1° 15′ E |
| IB 3 | Es Gorch | Ruderal | 39° 05′ N | 1° 28′ E |
| IB 4 | Can Pep Maians | Ruderal | 39° 02′ N | 1° 22′ E |
| IB 5 | Can Toni Joan | Agrarian | 39° 04′ N | 1° 19′ E |
| IB 6 | Batafi | Agrarian | 39° 01′ N | 1° 31′ E |
| IB 7 | St. Miquel de Balansat | Ruderal | 39° 05′ N | 1° 29′ E |
| IB 8 | St. Llorenç | Ruderal | 38° 54′ N | 1° 22′ E |
| IB 9 | En Salleres | Ruderal | 39° 58′ N | 1° 25′ E |
| IB 10 | Can Senyora | Ruderal | 38° 54′ N | 1° 26′ E |
| A 1 | Sevilla-Huelva (km 5.3) | Agrarian | 37°20 N | 6° 34′ W |
| A 2 | Sevilla-Huelva (km 11) | Ruderal | 37° 22′ N | 6° 15′ W |
| A 3 | St. Lucar la Mayor | Agrarian | 37° 23′ N | 6° 12′ W |
| A 4 | Jerez | Agrarian | 36° 41′ N | 6° 09′ W |
| A 5 | Véjer | Ruderal | 36° 14′ N | 5° 58′ W |
| A 6 | Cadiz | Ruderal | 36° 32′ N | 6° 18′ W |
| A 7 | Lora del Rio | Ruderal | 37° 39′ N | 5° 34′ W |
| A 8 | Solteras | Agrarian | 37° 25′ N | 6° 04′ W |
| A 9 | Alcolea del Rio | Ruderal | 37° 37′ N | 5° 39′ W |
| A 10 | St. Lucar la Mayor | Ruderal | 37° 24′ N | 6° 12′ W |
| VA 1 | Vila-Real | Agrarian | 39° 59′ N | 0° 06′ W |
| VA 2 | Nules | Agrarian | 39° 51′ N | 0° 09′ W |
| VA 3 | Cullera | Agrarian | 39° 10′ N | 0° 15′ W |
| VA 4 | Almenara | Agrarian | 39° 41′ N | 0° 16′ W |
| VA 5 | El Puig | Agrarian | 39° 35′ N | 0° 19′ W |
| VA 6 | Xàvia | Agrarian | 38° 47′ N | 0° 10′ E |
| VA 7 | Oliva | Agrarian | 38° 58′ N | 0° 06′ W |
| VA 8 | Sueca | Agrarian | 39° 12′ N | 0° 20′ W |
| VA 9 | Concentaina | Agrarian | 38° 45′ N | 0° 26′ W |
| VA 10 | Torrevieja | Agrarian | 37° 59′ N | 0° 40′ W |

From ten populations for each island and mainland region (i.e. 30 island sites and 20 mainland sites) we collected apparently healthy and mature bulbs from several holes (20 × 20 × 20 cm). Invaded sites were separated by more than 5 km to reduce the probability of gene flow between

populations. In the laboratory, we stored bulbs from each population at room temperature in paper envelopes until experimentation.

*Greenhouse experiment*

We determined if differences among populations were genetically based by growing plants in common environmental conditions, in this case a greenhouse, which avoided the confounding effects of factors such as herbivory, pathogens and competition. In October 2001 we randomly selected 10 bulbs from each population and each bulb was planted in a plastic pot (5 l, 11 cm diameter × 13 cm high) containing a 4:2:1 mixture of peat:vermiculite:sand and slow-release fertilizer (N:P:K in proportion 15:10:12 + 2 MnO). Soil acidity was neutralized with 0.7 g $CaCO_3$/l. Pots were watered liberally during the course of the experiment.

Before sowing, each bulb was weighed and later, in March, when plants were in full aboveground development, we counted the number of vegetative and flowering stalks. Because the aboveground biomass senesces during the course of bulb formation, it is not possible to estimate it by destructive means. However, aboveground biomass ($B$) is positively related to the number of vegetative stalks per plant ($N$) ($B = 0.18 + 0.01N$, $r^2 = 0.79$). In June 2002 when plants had senesced we counted the number of bulbs produced per plant and weighed them.

*Statistical analysis*

To evaluate the differences in *Oxalis* plant life-history traits from island and mainland regions we performed an ANCOVA with Type I sum of squares. To account for size-mediated maternal effects, initial bulb size was a covariate. We used the following model: response variable = region of the population + size of the parental bulb + size of the parental bulb*region + population nested within region + error. Population nested within region was a random factor and region was a fixed factor. A significant population within region effect indicates that individuals among populations are differentiated, but this differentiation is not due to the weight of the parental bulb since variation among populations due to parental bulb

size is removed before testing the population with region effect. Response variables were the number of vegetative and flowering stalks and the number and total weight of bulbs produced per plant. Data were transformed if needed to meet the assumptions of parametric analysis. Mean ± standard error are given throughout the paper.

**Results**

Almost all bulbs planted emerged (94% and 93.5% from islands and mainland, respectively) and there were no significant differences between regions ($\chi^2$ test = 0.06, $p = 0.80$). A few plants died before finishing their annual cycle (10.6% for insular populations and 11.1% for mainland populations; no significant difference: $\chi^2$ test = 0.04, $p = 0.84$).

*Oxalis* produced 1–70 bulbs per plant. There were significant differences in bulb production between island and mainland regions ($F_{1, 372} = 5.22$, $p = 0.03$ for number of bulbs and $F_{1, 369} = 5.82$, $p = 0.03$ for total bulb biomass). Island populations produced more bulbs ($26.20 \pm 0.85$) than mainland populations ($22.05 \pm 1.12$). Total bulb mass was also larger in island populations ($3.32 \pm 0.11$ g) than in mainland populations ($2.79 \pm 0.17$ g). The initial size of bulbs had a significant but low negative effect on the number of bulbs produced ($F_{1, 372} = 15.82$, $p < 0.001$, $r^2 = 0.1$). There was a high variability in bulb production among populations; however differences were not significant ($F_{45, 334} = 1.16$, $p = 0.23$ for number of bulbs and $F_{45, 334} = 1.08$, $p = 0.34$ for total bulb biomass, Figure 1).

On average island plants produced $103.27 \pm 3.32$ vegetative stalks and mainland plants produced $98.2 \pm 4.58$ vegetative stalks. Differences between regions were non-significant ($F_{1, 471} = 1.62$, $p = 0.21$, Figure 1). However, there were significant differences in the number of vegetative stalks among populations ($F_{45, 325} = 1.78$, $p = 0.003$, Figure 1). Differences in the number of vegetative stalks among populations were also dependent on differences between the parental bulb sizes. The relationship between the initial bulb weight and number of stalks produced was positive but it did not explain much of the variation ($F_{1, 471} = 15.96$, $p < 0.001$, $r^2 = 0.19$).

Almost all plants flowered (89%). Insular plants produced $9.18 \pm 0.39$ flowering stalks and mainland plants $8.21 \pm 0.5$. As for vegetative stalks,
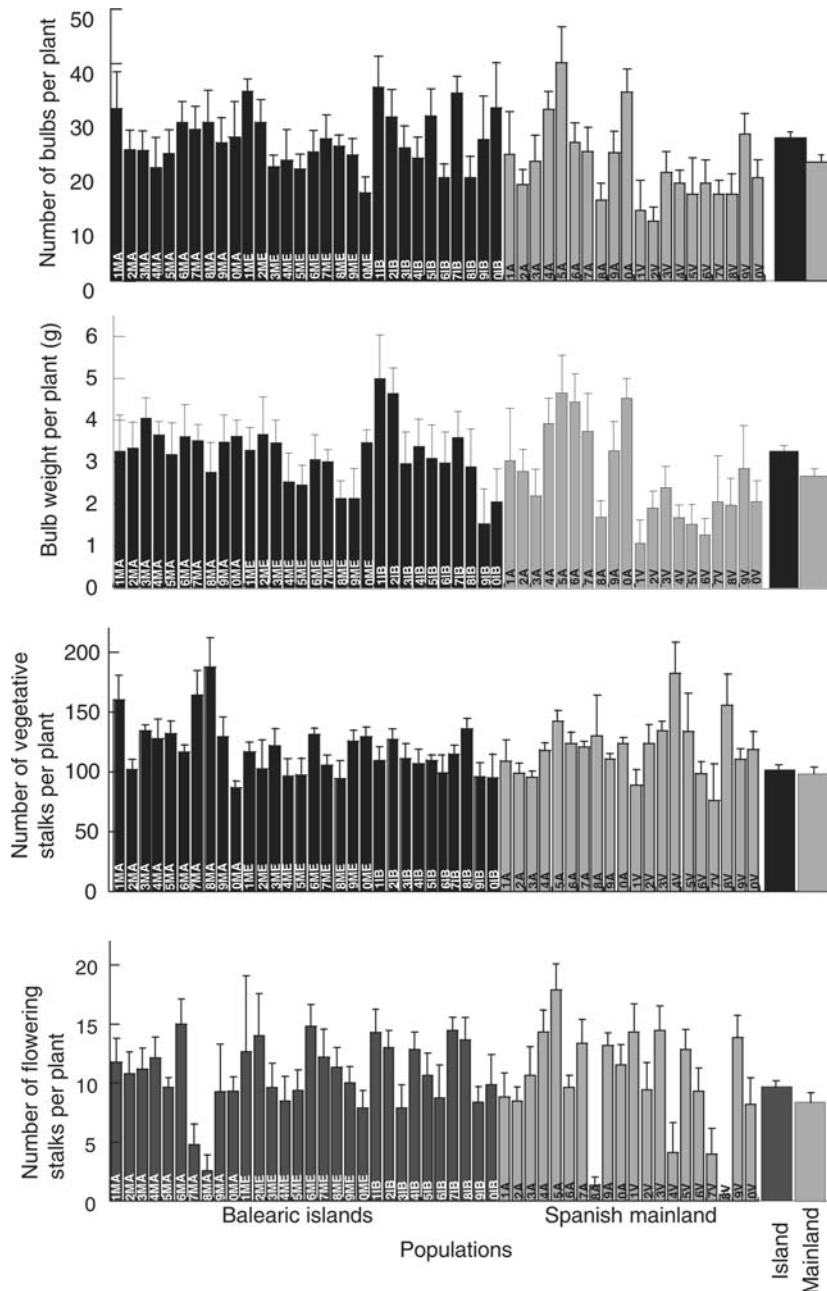
*Figure 1.* Mean (+1 standard error) of the number of bulbs, the total weight of bulbs, the number of vegetative and flowering stalks produced per plant from Balearic island and Spanish mainland *Oxalis pes-caprae* populations. The two columns to the right represent the average value of population means from insular and mainland regions. The total number and weight of bulbs was significantly different between insular and mainland regions. Population codes are the same as in Table 1.

differences between regions were not significant ($F_{1, 471} = 0.97$, $p = 0.34$, Figure 1). However, there were significant differences in the number of flowering stalks among populations ($F_{45, 325} = 28.39$, $p < 0.001$, Figure 1). There was a positive correlation between the number of flowering stalks and the number of bulbs produced per plant ($r^2 = 0.37$, $p < 0.0001$).

## Discussion

*Oxalis* from insular populations produced 20% more bulbs than those from mainland populations, suggesting the existance of genetic differences in bulb production between insular and mainland populations. Because bulb emergence is very high in all regions, our results suggest that island populations have the potential for higher population growth rates than mainland populations.

So far, the higher vulnerability of islands to plant invasions compared to mainland regions has been attributed to extrinsic plant factors related to differences in invasibility (e.g. lower diversity, fewer enemies, more disturbances). In contrast, potential plant differences in life-history traits have received less attention. This is probably due to the notion that both plant and animal taxa have a reduction in dispersal potential in islands favoring fewer but larger propagules than in the mainland. For example, some Asteraceae species found on islands off western Canada have a reduced pappus volume compared to mainland populations (Cody and Overtown 1996). In contrast, because *Oxalis* invasion is dependent on asexual production of bulbs and populations from islands produce more bulbs than mainland populations, our results show that *Oxalis* island populations have a higher dispersal potential than mainland populations. This genetically based higher number of bulbs per plant in island populations was not related to a change in aboveground plant size or a trade-off to flowering allocation. In fact there was a positive correlation between investment in sexual structures and in bulb production. Therefore, some island plants have the potential for higher vegetative propagation than mainland populations without reducing their aboveground biomass vigor and hence their competitive ability. These results are in close agreement with results from an extensive survey in which we found *Oxalis* more widely distributed in the Balearic Islands than in mainland adjacent areas. In the islands, 66% of randomly sampled localities were contained *Oxalis*, compared with 30% on the mainland. Furthermore, in the mainland, invaded habitats are mainly ruderal and disturbed. However, in the islands, *Oxalis* occurs in shrublands, grasslands and coastal habitats (Gimeno, Vilà and Hulme, unpublished data).

The negative correlation between the number of bulbs produced per plant and the size of the parental bulb is in accordance with a direct maternal effect (i.e. environmental induced carry-over). Maternal effects may be due to environmental conditions in which the maternal plant is developing or they may be due to maternal genetic factors by environmental interaction (Roach and Wulff 1987; Mazer and Gorchov 1996).

We can not decipher if the causes of the genetic differences in bulb production between island and mainland populations can be related to genetic differences between the original introduced parental populations or to evolutionary changes after introduction. Both explanations are possible. Despite the variability in life-history traits among populations on islands and the mainland, sexual reproduction of *Oxalis* has not been observed in European. However, this does not preclude high genetic variability among populations (Rottenberg and Parker 2004) suggesting that there have been multiple introductions of genetically differentiated populations. Multiple introductions are more the norm than the exception in naturalized plants (Barrett and Husband 1989; Maron et al. 2004) especially in species deliberately introduced as ornamentals or accidentally introduced as propagules mixed with gardening soil, as is the case for *Oxalis*. In addition, differences could also be due to adaptive responses to fewer natural enemies and less competition on islands compared to the mainland. Field experiments in the presence of natural enemies and manipulation of plant densities, and molecular analysis could address the causes of these genetic differences.

There is evidence for fast evolution in invasive plants, conferring greater growth and size, higher seed output or increased competitive ability (Siemann and Rogers 2001; Leger and Rice 2003). Previous studies have also shown genetic differences in sexual related fitness components between populations within the introduced range (Weber and Schmid 1998; Kollmann and Bañuelos 2004). Here we show for the first time that there is evidence that invaded populations also differ in their vegetative reproduction between insular and mainland introduced regions that can partially explain higher infestation levels on islands compared to mainland regions.

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