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ORIGINAL ARTICLE

Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* L. in the western Mediterranean

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ABSTRACT

Aim We tested the relative vulnerability of islands to *Oxalis pes-caprae* L. invasion compared to mainland regions. *Oxalis pes-caprae* is a South African annual geophyte that reproduces via bulbils, and has spread in many Mediterranean and temperate regions of the world where introduced. Our study is one of the first detailed regional analyses of the occurrence and local abundance of a non-native plant.

Methods We conducted an extensive survey (2000 sampling points) to examine local and coarse-scale patterns in both the occurrence and abundance of *O. pes-caprae* on islands and in neighbouring mainland regions of Spain.

Location We analysed occurrence (number of samples where present) and abundance (percentage cover) on two Balearic Islands (Menorca and Mallorca) and in two mainland administrative provinces of Spain (Murcia and València).

Results *Oxalis pes-caprae* occurrence was consistently higher on islands. Occurrence varied among habitats, being the highest in tree groves and the lowest in forests and shrublands. It was never found in these two habitats on the mainland. Mean *O. pes-caprae* abundance was greatest in tree groves on the mainland, and in field margins and old fields on the islands. However, in general there were not significant differences in local abundances between island and mainland locations.

Main conclusions These findings suggest that local processes (such as the biotic resistance of plant communities) are less important than coarse-scale phenomena (such as environmental driving forces) in explaining differences in the invasion patterns observed between islands and adjacent mainland regions. We suggest that *O. pes-caprae* has occupied a larger proportion of available habitats on islands due to: (1) its strong dependence on domestic animal and human-mediated dispersal which are probably greater on the islands than in mainland areas, and (2) the smaller area encompassed by islands that, over a comparable period of time, enables a greater proportion of available habitats to be colonized (and hence higher occurrence) than equivalent larger mainland areas.

Keywords

Alien species, Balearic Islands, Bermuda butter-cup, dispersal, distribution, disturbance, macroecology, ruderal habitats, Spain

INTRODUCTION

Islands are often highly vulnerable to invasion by non-native species (Loope & Mueller-Dombois, 1989; Atkinson & Cameron, 1993; McDonald & Cooper, 1995; Hulme, 2004). The higher vulnerability of islands relative to comparable mainland areas has been attributed to several insular characteristics: large perimeter : area ratios (Lonsdale,

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1999), the existence of unsaturated communities (Moulton & Pimm, 1986) and the higher susceptibility of insular species to the ecological impacts of invaders (D'Antonio & Dudley, 1995). The relative susceptibility of islands to invasion is often tested through comparison of the ratio of non-native to native species richness on islands versus mainland sites. Yet, although higher proportions of non-native species are frequently found in island communities (Lonsdale, 1999), the trend could be an artefact arising from islands having a smaller native species pool and/or having an increased frequency with which species are introduced (Sol, 2000; Cassey, 2003). An alternative approach is to compare the abundance and distribution of a particular invasive species in comparable mainland and island habitats.

Both the regional distribution and local abundance of an invasive species are major components underpinning their potential impact on the recipient ecosystems (Parker *et al.*, 1999; Pyšek & Hulme, 2005). Thus for a particular non-native species, an analysis of regional distribution and local abundance on islands and comparable mainland areas should be a priority when testing whether islands are more vulnerable to invasion and therefore suffer greater impacts than adjacent mainland areas. A wider regional distribution on islands may reflect coarse-scale differences in island and mainland areas. For example, islands often have a more benign environment (e.g. lower elevation, milder temperatures), a lower diversity of habitat types, and a higher degree of urbanization and development as well as a higher propagule influx through ports (Hulme, 2004). Meanwhile, a higher local abundance in comparable communities may reflect higher susceptibility to invasion as a function of lower native species richness, the occurrence of unsaturated communities on islands or lower competitive abilities of native species on islands. Nevertheless, because a positive relationship has often been found between local abundance and regional distribution (occurrence) for a variety of organisms within their native range, these two variables should not be viewed in isolation (McGeoch & Gaston, 2002).

In this paper we examine, for the first time, whether the regional occurrence and local abundance of an invasive alien plant differs between insular and adjacent mainland areas. Our hypotheses are that the alien will have higher occurrence (i.e. found in more sites), invade a wider range of habitats, and within specific habitats occur at higher densities on islands than in adjacent mainland sites.

MATERIALS AND METHODS

Study species

Oxalis pes-caprae L. (Oxalidaceae) is a small geophyte from South Africa (Peirce, 1997). Shoots of *O. pes-caprae* (*Oxalis* hereafter) arise from an underground bulbil (usually < 2.5 cm in length). In the Mediterranean, *Oxalis* generally flowers from late autumn to early summer, but fruits and viable seed have not been observed. The principal means of reproduction and spread is vegetative, via bulbils (Pütz, 1994). Each plant is capable of producing over 20 bulbils annually (Vilà & Gimeno, in press). Bulbils can be moved by soil disturbance, wind, vehicles, water (bulbils float), and may be dispersed by birds. The bulbils remain dormant in the summer and sprout in the autumn.

In the Mediterranean Basin, *Oxalis* is invasive in Italy, Greece, the Iberian Peninsula, as well as in North Africa (Damanakis & Markaki, 1990; Brandes, 1991). It was introduced into the Mediterranean Basin in 1796, reaching mainland Spain by 1825 and the Balearic Islands by 1870 (D'Austria, 1884). It is often seen in disturbed and agricultural areas and can occur in all soil types. It tends to do best on heavy, well-drained fertile soil, especially in cultivated areas. *Oxalis* is a serious weed in fruit orchards of the Mediterranean region (Marshall, 1987). Additionally, it may cause oxalate poisoning in livestock if eaten in sufficient quantities (Hulme, 2004).

Study sites

The study was carried out in four administrative regions in Spain: two Balearic Islands (Mallorca and Menorca) and two adjacent coastal regions of mainland Spain (València and Murcia). The islands are approximately 200 km from València and Murcia and are found at comparable latitudes. All regions have a Mediterranean climate with warm summers and mild winters. Although the four regions encompass similar land uses, the relative proportions differ as does both the geology and topography (Table 1).

Field survey

The distribution of *Oxalis* was evaluated by sampling five, randomly chosen, 10 × 10 km UTM cells in each region located less than 20 km from the coast. We are confident that selected cells were representative of the total landscape variation within each region in which *Oxalis* is distributed. To stratify the sampling, each UTM cell was subdivided into one-hundred 1-km^2 squares, within each of which a single survey point was selected. Exact survey points at each quadrat were selected by stopping every kilometre along several communication networks (Table 2). At each of the 500 survey points per region, we classified the dominant habitats falling within a 50-m radius according to 10 categories: coastal, field margins, forest (pine, oak and mixed), urban, grassland, old field, orchard, ruderal (roadside, disturbed and open areas), shrubland and tree groves (almond, citrus and olive groves). Therefore, at each survey point we could obtain *Oxalis* occurrence values in each of several habitat types. For all habitats surveyed at each point, *Oxalis* cover was categorized using a six point abundance index based on percentage cover: dominant (≥ 75%) = 5, abundant (75–50%) = 4, frequent (50–25%) = 3, occasional

Table 1 Environmental characteristics of the four study regions where *Oxalis pes-caprae* was surveyed. Climatic values are mean values for 10 years at the main climatological station in each region

	Islands		Mainland	
Variable	Mallorca	Menorca	Murcia	València
Latitude (N)	39.3–39.9	39.8–40.1	38.5–37.2	37.5–40.5
Longitude	2.3–3.3 E	3.8–4.2 E	0.4–2.2 W	1.3 W–0.3 E
Human population density (km^{-2})*†	174.84	99.28	108.46	186.05
Mean annual temperature (°C)*†	18	19	19	18
Annual precipitation (mm)*†	397	642	330	400
Maximum elevation (m)*†	1443	357	1300	1836
Area (ha)*†	362,043	69,440	1,131,738	2,325,912
Forest area (%)‡	26.8	26.6	24.3	47.9
Agricultural area (%)‡	56.8	32.9	24.3	35.6
Pasture area (%)‡	0.2	17.2	1.5	1.0
Geology (%)*†	Calcareous	Calcareous silicic	Calcareous	Calcareous

*Environmental Department of Balearic Islands Government, 2001, http://www.caib.es/.
†Environmental Department of València Government, 2001, http://ive.infocentre.gva.es/.
‡National Statistical Institute, Spain, 2004, http://www.ine.es/.

Table 2 Sampling effort (percentage of survey points) along communication networks across the four study regions where *Oxalis pes-caprae* was surveyed

	Islands		Mainland	
Network	Mallorca	Menorca	Murcia	València
Motorway	0	0	2.7	0
Main road	52	39.3	49.9	50.3
Secondary road	0	21.1	24.8	28.4
Minor road	14.7	13.2	21.6	6
Track	32.4	23.4	0.9	14.8
Footpath	0.7	2.9	0.1	0.5

(25–5%) = 2, rare (≤ 5% to > 0%) = 1 and absent (0%) = 0.

Statistical analysis

Differences in the occurrence (presence/absence) of *Oxalis* among different habitats in each region weighted by the frequency of each particular habitat were tested using χ^2 goodness-of-fit analyses (Vilà *et al.*, 2003). Differences in *Oxalis* local abundance between habitats within each region were tested with ANOVA. Differences in *Oxalis* local abundance were also compared between the four regions with a two-way ANOVA, with region and habitat as independent variables. For this purpose, only ruderal, old field and tree grove habitats were included in the analysis because these were the three most frequently invaded habitats across the four regions. Pair-wise differences among habitats were evaluated by a Tukey–Kramer test. In order to analyse variation in local abundance independent of variations in regional incidence the 'absent' category was not included in this analysis. Statistical analyses were carried out using SAS (SAS Institute Inc. 1998).

RESULTS

Overall, *Oxalis* was found in 57.52% and 76.20% of the surveyed points in Mallorca and Menorca, respectively, which contrasts with 41.74% in Murcia and only 18.28% in València. *Oxalis* did not occur with similar frequency in the habitats examined (Mallorca $\chi^2 = 99.03$, d.f. = 8, $P < 0.001$; Menorca $\chi^2 = 164.62$, d.f. = 8, $P < 0.001$; Murcia $\chi^2 = 32.97$, d.f. = 8, $P < 0.001$; València $\chi^2 = 110.05$, d.f. = 8, $P < 0.001$, Table 3, Fig. 1). Although there was a positive correlation between the occurrence with which a habitat was encountered and *Oxalis* occurrence (linear regression analysis: Mallorca $r^2 = 0.97$, Menorca $r^2 = 0.90$, Murcia $r^2 = 0.94$, València $r^2 = 0.90$, $P < 0.001$), the most frequently encountered habitats were not always the most frequently invaded. For example, as it might be expected from a sampling regime along roadsides, ruderal habitats were most frequently encountered in all four regions (Fig. 1); however, except in Menorca, ruderal habitats were not significantly more invaded than expected by chance (Table 3). Similarly, at the other extreme, although urban areas were undersampled, they were not less invaded than expected. In all four regions, *Oxalis* was over-represented in tree groves, even though the actual crop differed among regions (almonds in Mallorca, olives in Menorca and citrus crops on the mainland). In contrast, forests and shrublands consistently featured lower *Oxalis* occurrence than expected; this difference was very noticeable on the mainland where these habitats were never invaded (Fig. 1). On both islands, *Oxalis* was also encountered more frequently than expected in field margins but this trend was not statistically significant on the mainland.

Table 3 Observed and expected frequency of *Oxalis pes-caprae* occurrence (presence/absence) in islands and mainland Spain. Bold values represent habitats within a region in which the occurrence of the invader was significantly different from expected (χ^2 goodness-of-fit analyses *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Expected values were obtained by the relative occurrence of habitats when conducting the field survey

	Island				Mainland			
	Mallorca		Menorca		Murcia		València	
Habitat	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
Coastal	**0**	**6***	**8**	**17***	0	1	0	3
Urban	17	16	17	13	8	5	3	3
Orchard	15	19	13	11	**5**	**10*****	**8**	**17***
Field margin	**92**	**52*****	**58**	**31*****	3	0	1	1
Shrubland	**21**	**11****	**26**	**88*****	**0**	**10*****	0	28
Forest	**0**	**43*****	**1**	**38*****	0	2	0	26
Grassland	**18**	**31***	**51**	**148*****	0	0	0	2
Old field	51	54	102	95	16	16	32	31
Tree groves	**194**	**164****	**271**	**196*****	**51**	**28*****	**158**	**84*****
Ruderal	292	304	**341**	**251*****	83	94	141	148

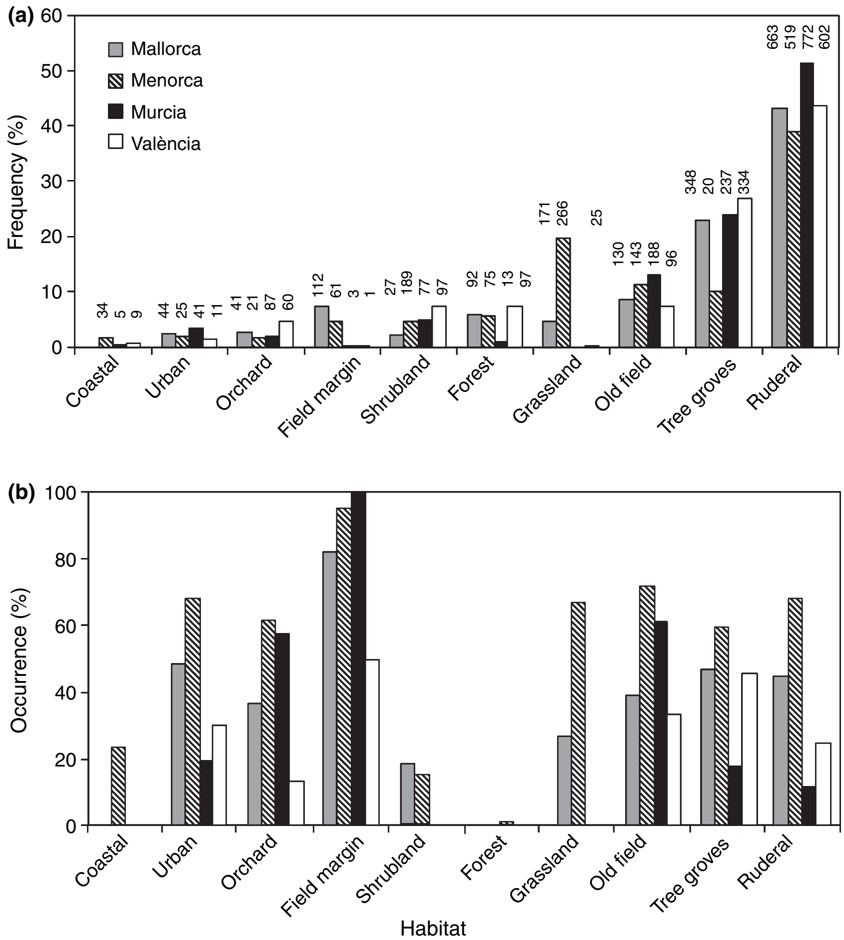

Figure 1 Trends among the different habitats in each of the four study regions where *Oxalis pes-caprae* was surveyed: (a) the relative frequency of habitats sampled (bar labels refer to the absolute number of times each habitat was encountered) and (b) the proportional *O. pes-caprae* occurrence in each habitat. Mallorca and Menorca are located in the Balearic Islands, València and Murcia are located on adjacent mainland Spain.

Local *Oxalis* abundance did differ among habitats within each region (Mallorca $F_{7,653} = 8.01$, $P < 0.001$; Menorca $F_{9,740} = 4.07$ $P < 0.001$; Murcia $F_{5,163} = 28.65$, $P < 0.001$; València $F_{4,343} = 48.32$, $P < 0.001$, Fig. 2). On the mainland, *Oxalis* abundance was highest in tree groves and least in old fields and ruderal habitats. In contrast, for islands, *Oxalis* abundance values were greatest in old fields and field margins but least in grasslands.

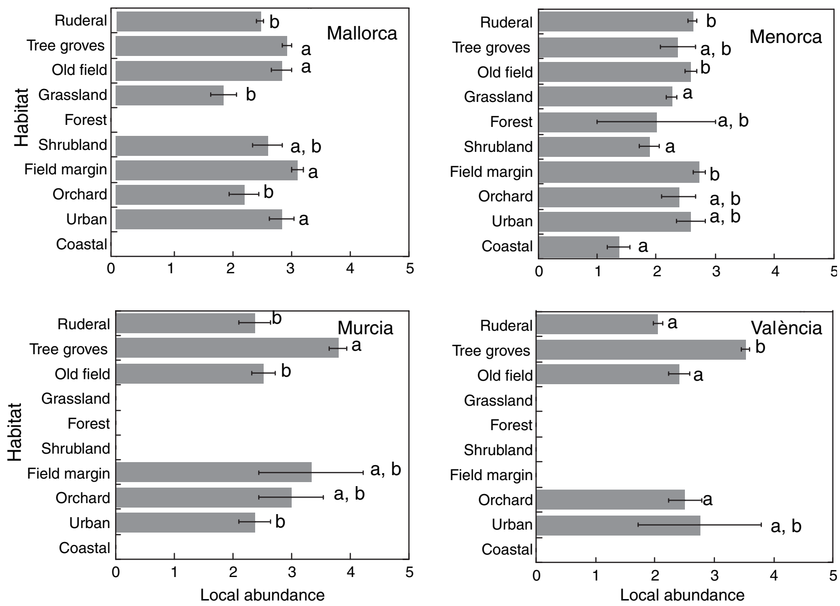

Figure 2 Trends in the mean abundance (± SE) of *Oxalis pes-caprae* in the habitats where found on the Balearic Islands of Mallorca and Menorca and in adjacent València and Murcia regions of mainland Spain. Abundance (percentage cover) was categorized according to the following point abundance index: dominant (≥ 75%) = 5, abundant (75–50%) = 4, frequent (50–25%) = 3, occasional (25–5%) = 2, rare (≤ 5 to > 0%) = 1. Bars labelled with the same letter are not significantly different from each other (Tukey–Kramer test, $P < 0.05$).

Local *Oxalis* abundance was not significantly different among regions ($F_{3,1457} = 1.55$, $P = 0.199$). However, there was a significant interaction between region and habitat ($F_{6,1457} = 17.44$, $P < 0.001$), indicating that in ruderal habitats *Oxalis* was more abundant on islands than on the mainland. For tree groves, *Oxalis* was actually more abundant on the mainland and there were no significant differences between regions for old fields. Most of the other habitats were too rarely invaded to allow robust comparisons to be made.

DISCUSSION

Overall, considering that the relative intensity of the impact of an invader (I) is positively related to both its distribution (D) and local abundance (A), we can estimate I for each region as $I = \sum(D_i \times A_i)$ where i refers to a specific habitat in each region (Parker *et al.*, 1999). Such a calculation reveals that the intensity of the impact on islands ($I = 1326.81$ and 881.45 on Menorca and Mallorca, respectively) is of the order of twice that for the mainland ($I = 461.99$ and 407.52 in Murcia and València, respectively).

If islands are more susceptible to invasion that mainland areas, *Oxalis* should invade a wider range of habitats, occupy a greater proportion of these vulnerable habitats and, within the invaded habitats, occur at higher densities (i.e. higher local abundance). This study presents support for the first two phenomena but not the third. Furthermore, although the characteristics of certain habitats differed between mainland and island regions (e.g. tree groves) this did not influence local abundance. It therefore appears that the greater susceptibility of the islands to invasion is not a result of factors operating at the community level, e.g. higher susceptibility of insular native species to invaders, the lack of natural enemies, unsaturated communities or the presence of empty niches (Carlquist, 1965; D'Antonio & Dudley, 1995; McDonald & Cooper, 1995; Hulme, 2004). If any of these factors were in operation, then we would expect a higher local abundance of *Oxalis* on the islands. In fact, plant communities that appear susceptible to *Oxalis* invasion are not less diverse on Mallorca and Menorca than in adjacent mainland areas. An extensive survey in these regions, following the same sampling protocols, found that while old fields have on average 148 plant species on the smallest island of Menorca, Mallorca and València had 78 and 121 species, respectively (M. Tessier, M. Vilà & I. Gimeno, unpubl. data). At the plot level (2 × 2 m, $n > 30$) Menorca (mean ± SE: 24.21 ± 1.34) had also significantly more species than Mallorca (19.45 ± 1.14) and València (17.56 ± 1.4). These results suggest that there is limited support for there being lower biotic resistance in islands than in mainland communities. To test correctly the null hypothesis of no differences in invasibility between island and mainland regions and the role of biotic resistance on *Oxalis* invasion, controlled field transplant experiments should be conducted in both regions while manipulating community species composition and diversity.

Oxalis invaded a wider range of habitats and occupied a greater proportion of these vulnerable habitats on the islands than in mainland regions. Although the island and mainland regions were chosen to be as comparable as possible, numerous variables operating at the regional scale are likely to differ between islands and the mainland. At least five factors may influence the occurrence of an invasive species: time since introduction, the disturbance regime, climate suitability, dispersal efficiency and propagule pressure (Mack *et al.*, 2000). Precise data on the time of introduction are sparse and there are no herbarium records documenting when *Oxalis* first arrived, but it appears that it was introduced to the Balearic Islands nearly 50 years after the introduction to the Spanish mainland (D'Austria, 1884).

Thus, even a conservative estimate of arrival time in Murcia and València would be unlikely to support the date of introduction as the determinant of the island–mainland differences.

Neither the extent of cultivation and soil disturbance or human population density (reflecting the degree of anthropogenic impacts) differs consistently between the islands and the mainland (Table 1). Furthermore, the likely similarity in disturbance regime on islands and on the mainland is borne out by the comparable frequency with which ruderal habitats were sampled (Fig. 1). In addition, *Oxalis* is a characteristic weed of human-modified habitats and thus the scope for differences between islands and mainland in the disturbance intensity in such habitats is relatively limited.

In addition to disturbance, *Oxalis* benefits from soil moisture occurring in partially shaded, irrigated (including roadside runoff) habitats. The lower annual precipitation and higher mean temperatures on the mainland (Table 1) imply greater evapotranspiration that could limit *Oxalis* occurrence. However, climate would be expected also to influence abundance. In addition, the mainland climate is unlikely to be a limiting factor given the widespread occurrence of *Oxalis* in the more xeric environments of North Africa and the eastern Mediterranean.

The role of dispersal in determining the relationship between species abundance and occurrence is unclear (McGeoch & Gaston, 2002; Pyšek & Hulme, 2005), although it may become more important for species with limited dispersal ability (Gaston & Blackburn, 2003). In the Mediterranean Basin, *Oxalis* is not known to produce viable seed and the dispersal unit is limited to underground bulbils. In general, humans are the major dispersal agent, with bulbils transported in soil and/or attached to agricultural machinery. Although anthropogenic transport of bulbils can spread *Oxalis* over long distances in a relatively short time, this form of dispersal has only become important in the last 50 years, following the mechanization of Mediterranean agriculture (P. Fraga, pers. comm.), and thus it is conceivable that *Oxalis* has not yet been dispersed throughout the larger mainland regions. Furthermore, Mediterranean islands often have a higher density of roads that can serve as invasion corridors (Hulme, 2004). Trampling by cattle and sheep can also transfer bulbils from one area to another. Livestock production, even when accounting for area, is much higher on the Balearic Islands than in either València or Murcia. For example, milk production in the Balearic Islands is 84×10^6 L year^{-1} compared to only 36×10^6 and 30×10^6 L year^{-1} in the two mainland regions, respectively. Similarly, wool production is 674×10^3 kg year^{-1} compared to 159 and 417×10^3 kg year^{-1} (http://www.ine.es for 2002). Moreover, island populations of *Oxalis* produce higher numbers of bulbils than mainland populations (Vilà & Gimeno, in press) and, therefore, propagule supply to new habitats could have been greater on islands than in mainland habitats.

We suspect that even assuming similar dispersal rates, habitat vulnerability, climate and dates of introduction on both islands and on the mainland, maximum occurrence will be reached sooner on islands simply due to the smaller total area and higher connectance through the landscape compared to mainland regions. A spatially explicit analysis of *Oxalis* distribution in association with landscape structure should be conducted to test the hypothesis of higher *Oxalis* spread within and between habitats on islands compared to the mainland.

In conclusion, *Oxalis* invaded a wider range of habitats and was observed to occupy a greater proportion of these vulnerable habitats on the two islands compared to the two mainland regions. However, the abundance of *Oxalis* within those sites where it occurs is similar for both regions. Therefore, at the local scale, island communities do not appear to be more easily invaded than mainland communities. We postulate that the greater spread of this species on the two islands is most parsimoniously explained by the strong dependence on domestic animal and human-mediated dispersal, which are probably greater on the islands than within the two mainland areas.

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BIOSKETCHES

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