BIODIVERSITY RESEARCH

Widespread resistance of Mediterranean island ecosystems to the establishment of three alien species

Montserrat Vilà[1]*, Akis-Stavros D. Siamantziouras[2], Giuseppe Brundu[3], Ignazio Camarda[3], Philip Lambdon[4], Frédéric Médail[5], Eva Moragues[6], Carey M. Suehs[5], Anna Traveset[6], Andreas Y. Troumbis[2] and Philip E. Hulme[7]

[1]*Estación Biológica de Doñana, Centro Superior de Investigaciones Científicas (EBD-CSIC), Avda/María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain,* [2]*Biodiversity Conservation Laboratory, Department of Environment, University of the Aegean, GR-811 00 Mytilene, Greece,* [3]*Dipartimento di Botanica ed Ecologia vegetale, Università degli Studi di Sassari, Sardinia, Italy,* [4]*NERC Centre for Ecology & Hydrology, Banchory, Kincardineshire, AB31 4BW UK,* [5]*Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP, UMR CNRS 6116), Université Paul Cézanne/Aix-Marseille III, Europôle méditerranéen de l'Arbois, BP 80. F-13545 Aix-en-Provence cedex 04, France,* [6]*Institut Mediterrani d'Estudis Avançats (CSIC-UIB), University of the Balearic Islands, Miquel Marquès, 21, 07190 Esporles (Mallorca), Spain,* [7]*National Centre for Advanced Bio-Protection Technologies, PO Box 84, Lincoln University, Canterbury, New Zealand*

*Correspondence: Estación Biológica de Doñana Centro Superior de Investigaciones Científicas (EBD-CSIC), Avda/María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain. Tel.: +954-232340; Ext. 123; Fax: +954-621125; E-mail: montse.vila@ebd.csic.es

ABSTRACT

Although some invasive plants are cosmopolitan, not all ecosystems are invaded to the same degree. Yet there is little experimental work on how ecosystem resistance to invasion at the establishment phase differs among ecosystems. We conducted two field sowing experiments in two consecutive years to examine establishment of the deciduous tree *Ailanthus altissima*, the succulent subshrub *Carpobrotus* spp. and the annual geophyte *Oxalis pes-caprae* in coastal dunes, shrublands and oldfields in more than 200 sites across six Mediterranean Basin islands differing in climatic conditions and local species richness.

Establishment success (i.e. percentage of plots with at least one seedling) and rates (i.e. seedling to sown seed ratio) were low, especially for *Ailanthus* even when accounting for differences in seed viability. *Oxalis* was capable of producing a new cohort of seedlings the year following planting. By contrast, all *Ailanthus* seedlings and half the *Carpobrotus* seedlings died following the first summer. Differences in establishment success and rates among ecosystems were species-, island- and year-dependent.

Differences in precipitation and mean temperature were associated with differences in establishment rates across sites. Establishment rates tended to be positively correlated with cumulative precipitation and negatively with mean Tª. Unexpectedly, native species richness was not a good predictor of seedling establishment, except for higher *Oxalis* establishment success in species rich habitats.

By conducting field sowing tests at multiple sites across a region we found that except for *Oxalis*, Mediterranean island ecosystems are quite resistant to invader establishment. These results suggest that differences in the degree of invasion between ecosystems and islands might be more dependent upon the influence of invasion event factors (e.g. propagule pressure) or factors acting at a later life-history stages rather than differences in the resistance imposed by ecosystems to invader recruitment. Moreover, our results support the notion that in Mediterranean ecosystems invasions are highly idiosyncratic events and strongly dependent on water availability conditions.

Keywords
Ailanthus altissima, biological invasions, *Carpobrotus* spp., invasibility, *Oxalis pes-caprae*, plant invader, species richness.

INTRODUCTION

Many ecosystems around the world are invaded by non-native species that have been introduced deliberately or accidentally by humans. The local and regional abundance of aliens (i.e. degree of invasion) depends upon historical factors (e.g. number, frequency and time since introduction), the species potential to invade (i.e. invasiveness) and ecosystem resistance to invasion (i.e. invasibility). Disentangling these three components is essential, as observed patterns may mistakenly suggest ecosystem resistance when in fact the absence of invasive species is a result of low propagule pressure (Lonsdale, 1999). Moreover, there is evidence that there is only a limited overlap in alien species identity across ecosystems and regions (Lloret *et al.*,

2004) despite a high similarity in the degree of invasion across habitats (Chytrý *et al.*, 2008), suggests that invasibility has to be tested for different species independently of their propagule pressure.

Ecosystem invasibility is determined by biotic and environmental factors (Lonsdale, 1999). Species richness has received high attention as a biotic predictor of invasibility (Levine & D'Antonio, 1999; Shea & Chesson, 2002; Levine *et al.*, 2004), and most manipulative studies have found that establishment of non-resident species (i.e. not necessarily alien species) to an ecosystem is constrained by local species richness (Robinson *et al.*, 1995; Levine, 2000). Experiments have been performed in particular ecosystem types by assembling a gradient of species richness from a selected species pool. Consequently, it is not known whether species richness might also drive differences in invasibility across ecosystems.

Another factor determining invasibility is climate. Most successful introduced plants are pre-adapted to the climatic conditions in the recipient ecosystem. In Mediterranean ecosystems where climate is characterized by hot, dry summers, water availability often limits plant establishment and biomass production (Thompson, 2005). Moreover, Mediterranean ecosystems are predicted to be very susceptible to water availability fluctuations caused by climate change (Lavorel *et al.*, 1998), which will possibly modify species distributions and plant–plant interactions. In this scenario, differences in climatic conditions within ecosystems might be relevant for plant invader establishment.

Furthermore, the influence of species traits on the ability to invade certain ecosystems suggests that invasibility is dependent on invader identity and therefore invasibility is not a fixed attribute of an ecosystem (Lloret *et al.*, 2005). Rather, because invasibility is determined by the interaction of the introduced species with the resident biota and the limits imposed by environmental constraints, invasibility of a particular ecosystem seems to be context and time specific (Thomsen *et al.*, 2006). Only by comparing how a range of different species invade the same set of ecosystems might we be able to discern how much differences in the degree of invasion among ecosystems depend upon the characteristics of the receptor ecosystem or of the invader species (Mitchell *et al.*, 2006).

Invasibility depends on the likelihood of alien species establishing and dominating in the long term (Huston, 2004). Several field experiments have tested how invasibility differs among ecosystems using sowing or transplant experiments in different ecosystems across sites (D'Antonio, 1993; Larson *et al.*, 2001; Lambrinos, 2002; Kollmann *et al.*, 2007). However, most of these studies were restricted to particular landscapes with very few replicates or even with pseudoreplicated experimental designs (Hurlbert, 1984).

Islands are highly vulnerable to invasions (Elton, 1958; McDonald & Cooper, 1995) compared to adjacent mainland areas, and Mediterranean Basin islands are no exception (Hulme, 2004; Gimeno *et al.*, 2006; Hulme *et al.*, 2008). For example, Lloret *et al.* (2004) found over 400 introduced plant species on only eight principal islands of the Mediterranean Basin. Nevertheless,

considerable differences occur in the number of alien species found among ecosystems. Notably, Mediterranean woodlands, even if extensive and exposed to invader pressure, contain a low proportion and abundance of invaders compared to grasslands, oldfields and ruderal ecosystems (Vilà *et al.*, 2007). However, despite the wide distribution and frequent proximity of such ecosystems, no study has experimentally compared the extent to which Mediterranean ecosystems differ in their invasibility.

Mediterranean Basin islands are a hotspot of biodiversity (Médail & Quézel, 1997), with the climate determining high variability in plant establishment between areas and years (Cowling *et al.*, 2005). Mediterranean islands therefore represent an outstanding opportunity to assess variation in ecosystem resistance to invasions within a single biome and to scale up from local to regional implications (Hierro *et al.*, 2005). We conducted identical, multiple propagule, sowing experiments to assess the regional consistency in early establishment of plant invaders as a proxy for invasibility. We focused on invaders with contrasting life-forms: the deciduous tree *Ailanthus altissima* (P. Mill) Swingle (Simaroubaceae), the succulent subshrubs *Carpobrotus* spp. (Aizoaceae) and the annual geophyte *Oxalis pes-caprae* L. (Oxalidaceae).

The main goal of this study is to test to what extent the degree of invasion can be attributed to differences in plant establishment and whether differences among ecosystems are spatially and temporally consistent. Specifically, we addressed the following questions: (1) Are there differences in early establishment among ecosystems? (2) Are differences dependent on species identity? (3) Are ecosystem differences consistent across islands? (4) Are spatial differences related to climatic conditions and to local species richness? Based on observed ecosystem differences in the occurrence of invaders across Mediterranean Basin islands (Table 1), we anticipate *Oxalis* to be the most invasive, followed by *Carpobrotus* and then *Ailanthus*; and we expect seedling establishment to be the highest in oldfields, the lowest in shrublands and intermediate in coastal dunes. To our knowledge, this is the most extensive field sowing experiment testing seedling establishment across a region.

METHODS

Study area and invasive taxa

Of the nearly 5000 islands in the Mediterranean Basin, six were chosen as representative in terms of range of island size, isolation and geographical location according to an East-West gradient: Crete and Lesbos in Greece, Sardinia in Italy, Porquerolles in France, as well as Mallorca and Menorca in Spain.

Three of the most common and widespread invasive alien plant taxa in Mediterranean ecosystems (Hulme, 2004; Hulme *et al.*, 2008) were selected for study and are known to occur in different ecosystems and have a range of possible impacts on native systems (Vilà *et al.*, 2006b):

Ailanthus altissima (P. Mill.) Swingle, native to China and mainly used for ornamental and landscaping purposes, is able to resprout and develop root networks that form dense clonal

Table 1 Trends in the occurrence (% of presences in a cross-island survey) of invaders in three different ecosystems across six Mediterranean Basin islands. Occurrence was categorized according to a 0–5 categorical scale as 5: widespread (≥ 75%), 4: abundant (50–25%), 3: frequent (50–25%), 2: occasional (25–5%), 1: rare (≤ 5 > 0) and 0: not present (EPIDEMIE, unp. data). Values are based on 500 field survey points by sampling 5 randomly chosen 10 × 10 km UTM cells in each island (see Gimeno *et al.*, 2006 for methodology).

	Ailanthus			*Carpobrotus*			*Oxalis*		
Island	Dunes	Shrublands	Oldfields	Dunes	Shrublands	Oldfields	Dunes	Shrublands	Oldfields
Crete	0	2	2	3	3	2	1	4	4
Lesbos	0	2	2	1	0	0	1	1	4
Mallorca	0	1	3	3	1	0	0	2	5
Menorca	0	1	2	4	1	1	1	2	5
Porquerolles	0	0	0	4	4	4	1	2	2
Sardinia	1	3	4	5	4	0	1	4	4

stands (Kowarik, 1995). Seedling recruitment also occurs from wind dispersed samaras (Kowarik & Säumel, 2007). It is common in disturbed urban areas, oldfields, along roadsides, woodland edges and forest openings throughout Europe (Kowarik & Säumel, 2007).

Carpobrotus acinaciformis (L.) Bol. and *C. edulis* (L.). N.E. Br. are succulent, mat-forming perennial herbs native to South Africa and introduced as ornamentals (Wisura & Glen, 1993). These two species and their hybrids (Suehs *et al.*, 2004) are now widely naturalized in Mediterranean coastal habitats, and are considered as a serious threat to several endemic and rare plant species (Draper *et al.*, 2003). Successful seed establishment is highly dependent on seed dispersal by native or introduced mammals and a lack of competition with the resident vegetation (Vila & D'Antonio, 1998; Bourgeois *et al.*, 2005).

Oxalis pes-caprae L. was accidentally introduced from South Africa in many Mediterranean regions of the world since the beginning of the 19th century (Peirce, 1997; Rottenberg & Parker, 2004). It is the most widespread and abundant invader across the Mediterranean Basin (Gimeno *et al.*, 2006; Hulme *et al.*, 2008). *Oxalis* spreads vegetatively by means of underground bulbs. No sexual reproduction has been observed in the introduced range (Galil, 1968). The probability of bulb establishment and seedling survival is high (Vilà *et al.*, 2006a). In the Mediterranean Basin, it is mostly present in oldfields, olive groves, irrigated crops, orchards, pastures and ruderal areas (Gimeno *et al.*, 2006).

The sowing experiments were conducted in typical shrublands, coastal dunes and oldfields from which the three focal species were absent. To avoid pseudoreplication and lack of independence, the minimum distance between replicate sites within an island was 1 km. Coastal dunes were located less than 500 m from the beach and had a low cover of maritime shrubs and perennial grasses; oldfields were in general early successional ecosystems with a high cover of annual grasses and herbs appearing after recent (2–5 year old) agricultural or pasture abandonment. Finally, shrublands were areas dominated on average by between 40% and 80% shrub cover and less than 2 m in height.

Seeding experiments

In fall 2001, we selected up to 10 sites per ecosystem and island. In each site, four 1 m² plots were established at least 2 m apart from each other. To homogenize experimental conditions across sites as much as possible we tried to place plots in open undisturbed areas within the vegetation matrix. Each plot was randomly assigned to one of the following propagule addition treatments: 1000 *Carpobrotus* seeds, 100 *Ailanthus* seeds or 100 *Oxalis* bulbs, no propagules added (control). These values were of a similar order to the propagule banks in invaded areas or previously conducted seed addition experiments (Vilà *et al.*, 2006a for *Oxalis*, Kowarik & Säumel, 2007 review for *Ailanthus*; D'Antonio, 1993 for *Carpobrotus*). Propagules were collected from several locations within each island in which they were sown but prior to sowing aborted or damaged propagules were discarded. Before experimentation we tested seed and bulb viability by greenhouse germination tests. On average, germination was 37% for *Ailanthus*, 39% for *Carpobrotus* and 95% for *Oxalis*. Propagules were sown within 1 cm of the soil surface and to ensure an even distribution across the plots one quarter of the propagules were sown in a central 50 cm² square, whereas the remainder was spread over the remainder of the plot. For conservation reasons, *Oxalis* bulbs were not planted in dunes either in Mallorca or in Menorca (Table 2). We counted seedling density in April–May 2002 and 2003. We did not label seedlings but by comparing the size of the seedlings during our surveys we think that seedlings present in the second year after sowing were survivors rather than new germinants from the sown seeds except for *Oxalis* (see succeeding discussions).

In fall 2002, the experiment was repeated in most sites. New plots were established 2 m apart from those of the previous year and seedling density was recorded in April–May 2003. In January 2003 (only first experiment), 2004, 2005 and 2006 we revisited the sites, pulled up and killed all emerged seedlings to prevent invasion of the sites by the three planted species.

For both experiments we estimated early establishment success and establishment rates. Establishment success was calculated as the percentage of plots with at least one seedling. Establishment rates were measured as the ratio between the

Table 2 Percentage of plots with seedlings established one year after each experimental sowing (2001/2002) in three different ecosystems across six Mediterranean Basin islands. Missing values are indicated (−).

	Ailanthus			Carpobrotus			Oxalis		
Island	Dunes	Shrublands	Oldfields	Dunes	Shrublands	Oldfields	Dunes	Shrublands	Oldfields
Crete	20/30	0/10	0/11	60/80	0/40	0/10	40/60	30/60	60/78
Lesbos	29/20	25/10	25/10	0/90	0/80	0/10	0/20	75/50	88/90
Mallorca	43/10	0/13	11/11	71/90	14/38	56/44	−/−	−/56	−/89
Menorca	0/−	0/20	0/0	14/−	44/80	33/10	−/−	67/90	67/100
Porquerolles	0/0	0/40	0/0	30/30	40/90	50/30	0/90	10/80	0/70
Sardinia	0/0	0/0	0/0	0/100	0/100	−/40	0/100	0/100	10/100

number of seedlings in the first or second spring after sowing and the number of propagules sown at the beginning of the experiment. As *Oxalis* is an annual geophyte and could produce a bulb bank one year after sowing, in spring 2002 we counted the number of seedlings, and seedling density was considered as an equivalent measure of establishment rate for the second year after sowing.

Before setting up the 2001 experiment, for most sites we conducted a floristic survey and quantified species richness as the local number of species. During both experiments we recorded island precipitation and mean temperature for the period between sowing and sampling (September–May). Where available, climate data were recorded from the nearest weather station to each site.

Statistical analysis

By the end of the experiments some plots and sites had been destroyed or lost due to disturbance and vandalism resulting in an unbalanced data set that consisted of 925 plots.

Differences among species, ecosystems and islands in establishment success (i.e. percentage of plots with at least one seedling) one year after sowing were compared with a χ^2 goodness-of-fit test. Differences in establishment rates and seedling density for *Oxalis* for islands with successful establishment were analysed using generalized linear models (GLM) with island included as a random factor and ecosystem nested within island as a fixed factor. A different analysis was conducted for each species and year. Where differences among ecosystems were significant, differences within islands were tested using ANOVA or *t*-tests if data met the assumptions of parametric analysis after data transformation or by Kruskall–Wallis or Mann–Whitney's tests when data did not meet such assumptions. When a significant ecosystem effect was detected, pairwise comparisons were performed using a Tukey test. All tests were performed with SPSS, Inc. software.

For each species and experiment, we tested if there was a relationship between species establishment success as a binary dependent variable (seedlings present or absent) and cumulative precipitation, mean temperature and local species richness as independent variables in logistic regressions. Correlations were also conducted between establishment rates and the three previously mentioned independent variables. Because species

richness of the sites was only assessed during the first experiment, this variable was only included in models for 2001 data. Species richness was log transformed before analysis to meet the assumptions of parametric statistics. Throughout the text all mean values are accompanied by their standard errors unless otherwise indicated.

### RESULTS

Climatic conditions across islands

On average, cumulative precipitation and temperature were higher in the second than in the first year (precipitation: paired t-test = −2.76, d.f. = 149, $P = 0.006$; Tª: paired t-test = −11.87, d.f. = 149, $P < 0.0001$). Both years, were wetter but warmer than average (compared to mean values from late XIX to late XX century at http://www.worldclimate.com). Both variables were significantly different among islands (Fig. 1). For precipitation, the pattern among islands was different between years (2001: $F_{4,145} = 57.81$, $P < 0.0001$; 2002: $F_{5,174} = 37.77$, $P < 0.0001$). For example, in 2001 Crete had the lowest precipitation record while in 2002 it had one of the highest. Differences in Tª among islands followed a more consistent pattern between years (2001: $F_{4,145} = 318.98$, $P < 0.0001$; 2002: $F_{5,174} = 327.79$, $P < 0.0001$) being always lowest in Porquerolles and highest in Crete (Fig. 1).

Species richness across islands

Species richness was significantly different across islands ($F_{5,162} = 30.02$, $P < 0.0001$) being highest in Crete and Lesbos and lowest in Mallorca, Porquerolles and Sardinia. Differences were also significant between habitats (ANOVA with habitats nested within islands: $F_{5,162} = 10.67$, $P < 0.0001$). On average, oldfields followed by shrublands were significantly more species rich than dunes but this pattern was not consistent across islands (Fig. 3).
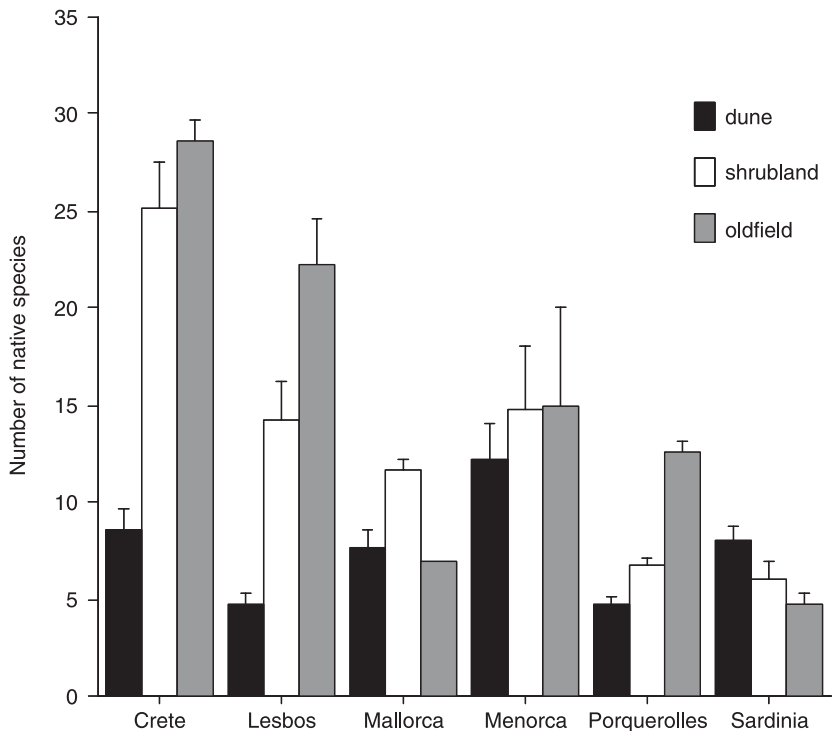
Establishment success

On average and for all three species, establishment success was larger in the second (49.74%) than in the first experimental sowing (21.21%) matching the higher precipitation and Ta recorded in the second period compared with the first (Figs 1 & 2). However,
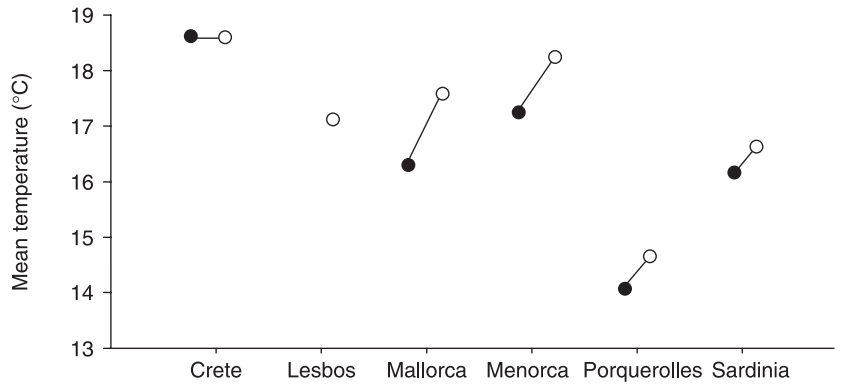
Figure 1 Mean Tᵃ and cumulative precipitation for the 2001 (black) and 2002 (white) sowing experiment in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia.
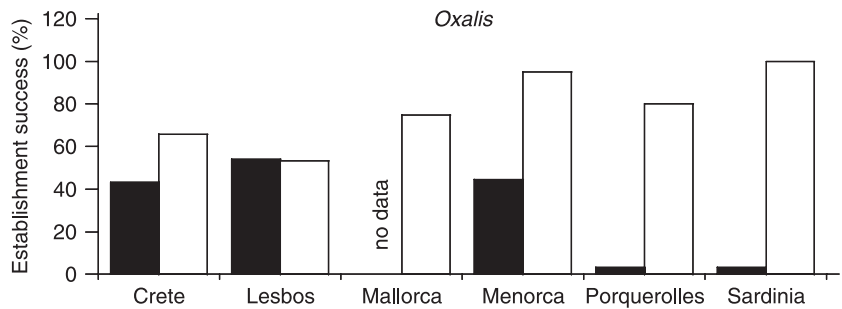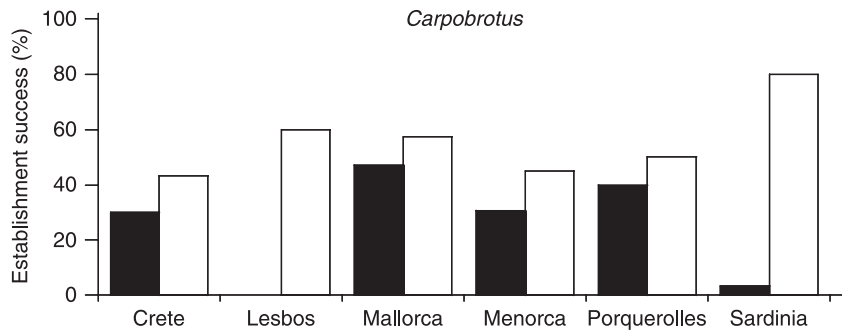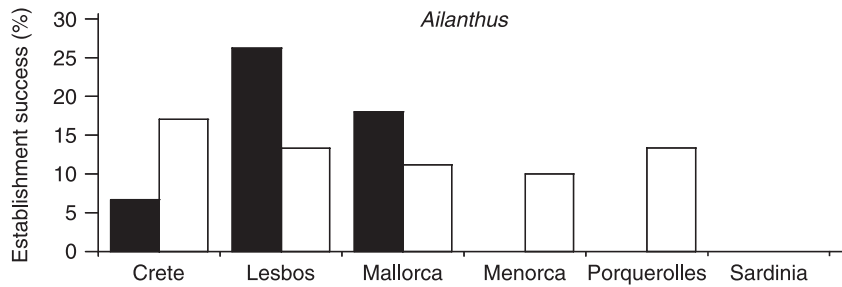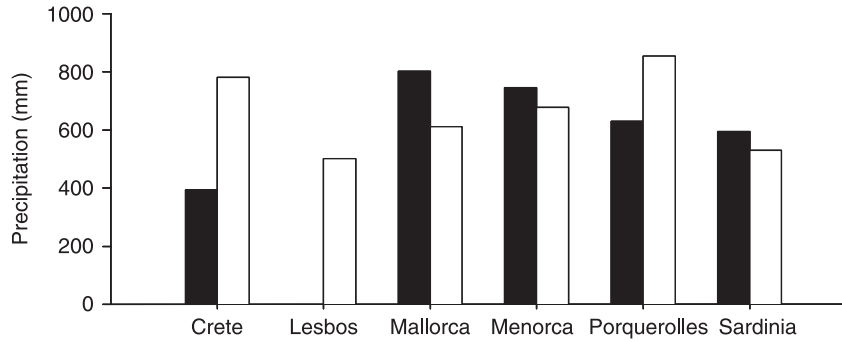
Figure 2 Establishment success (i.e. percentage of plots with at least one seedling) for the 2001 (first column) and 2002 (second column) sowing experiment in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia. Notice that scales are not the same for the three species.

Figure 3 Mean (+ standard error) species richness in different ecosystem types in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia.

except for a positive relationship between T^a and *Oxalis* establishment success for the first experiment, there was no significant association between establishment success and climatic conditions for any species or experiment (Appendix 1). Successful establishment was positively related to species richness only for *Oxalis* (Appendix 1).

Independent of the initial year of sowing there were also significant differences among species (2001: $\chi^2 = 24.49$, 2002: $\chi^2 = 76.37$, both $P < 0.0001$). *Ailanthus* always had the lowest establishment success (2001: 7.41%; 2002: 10.84%). In fact, in the first experiment, no *Ailanthus* establishment occurred at all in Menorca, Porquerolles and Sardinia (Table 2). In the first year, establishment success was not significantly different between *Carpobrotus* (25%) and *Oxalis* (28.57%). In contrast, for the 2002 sowing, it was lower for *Carpobrotus* (56.89%) than for *Oxalis* (76.25%).

Although in the 2001 sowing there were no significant differences in establishment success among ecosystems ($\chi^2 = 0.41$, $P = 0.82$), for the 2002 sowing it was significantly lower in oldfields than in dunes and shrublands ($\chi^2 = 6.34$, $P < 0.05$). Significant island differences were found only in the first experiment (2001: $\chi^2 = 33.89$, $P < 0.0001$; 2002: $\chi^2 = 3.43$, $P < 0.64$). For the 2001 sowing the lowest establishment success occurred in Sardinia and there were no significant differences among the rest of the islands.

Establishment rates

On average, establishment rates were rather low, and especially so for *Ailanthus* (Fig. 4). For this species, there were no significant differences among islands and among ecosystems in either

experiment (Table 3), probably due to its low establishment success. Two years after sowing, seedling mortality was high. By spring 2003, all *Ailanthus* seedlings from the 2001 sowing had died except for a single seedling in each of three plots (one plot in a dune in Crete, and two plots in oldfields in Mallorca and Menorca).

For *Carpobrotus*, there were no significant differences among islands but ecosystems differed (Table 3): overall, oldfields had higher values than dunes and shrublands in the 2001 experiment, but in the 2002 experiment oldfields had the smallest establishment rates (Fig. 5). One year after sowing, seedling density decreased more than 50%; dunes were the habitat with the smallest establishment (data not shown).

For *Oxalis*, establishment rates were significantly different among islands and ecosystems (Table 3), being highest in Lesbos and lowest in Porquerolles and Sardinia in the 2001 experiment; and higher in Porquerolles and Sardinia than in the other islands in the 2002 experiment. On average, establishment rates were significantly higher in oldfields than in the other ecosystems, but in some islands these differences were not significant (Fig. 6).

Oxalis produced a new cohort of seedlings the following year after planting (Fig. 7). Seedling density almost doubled in Crete and Menorca. In spring 2003, seedling density was higher in oldfields and shrublands than in dunes, and this was consistent among islands (Table 3).

Except for *Ailanthus*, which had an extremely low establishment success as well as low establishment rates, establishment rates tended to be positively correlated with cumulative precipitation and negatively with mean T^a (Appendix 2). However, there was no significant association with local species richness (Appendix 2).
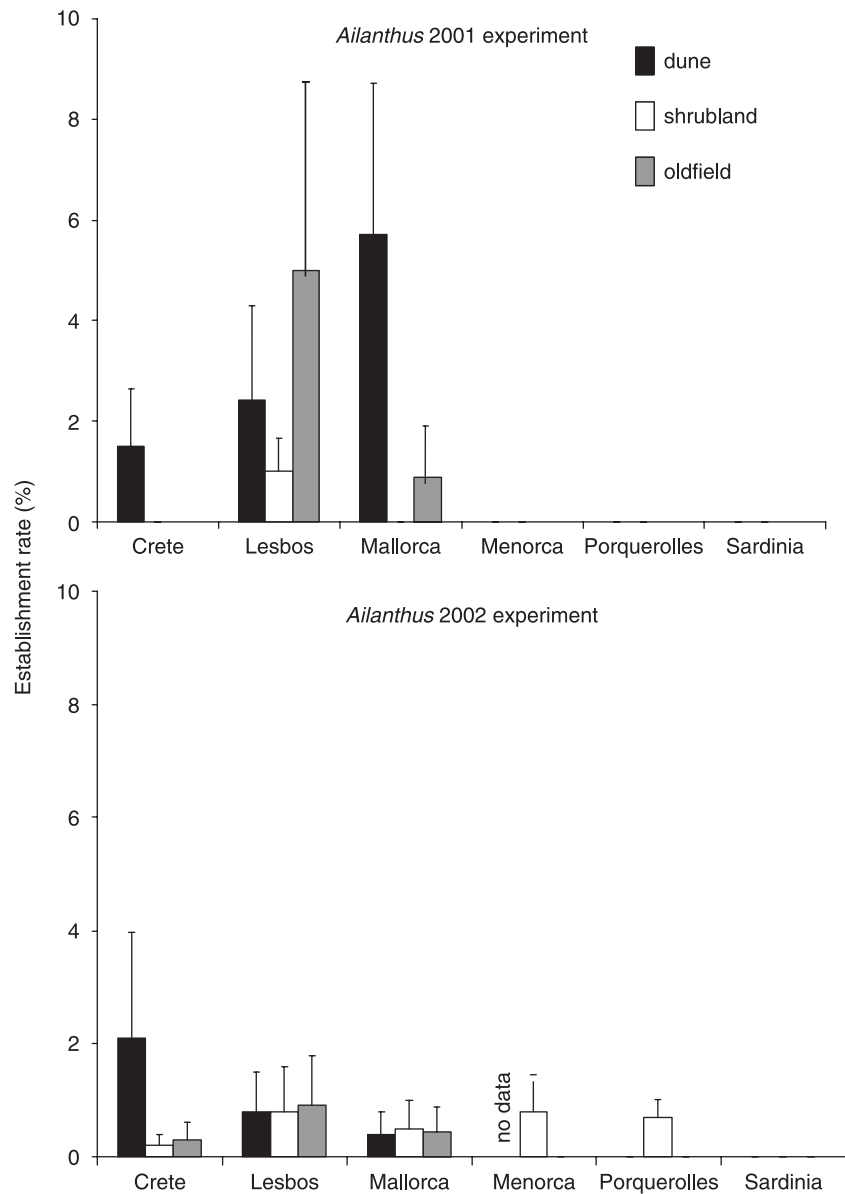
Figure 4 Means (+ standard error) for *Ailanthus* spring establishment rates in different ecosystem types in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia arising from experimental sowing of 100 seeds in 2001 and 2002. There were no significant ecosystem differences.

Table 3 ANOVA results for the influence of ecosystem on establishment rates across six Mediterranean Basin islands (sowing year/sampling year). The ANOVA for *Oxalis* sown in 2001 and sampled in 2003 corresponds to seedling density.

	Ailanthus		*Carpobrotus*		*Oxalis*	
	F value$_{(d.f.)}$	P	F value$_{(d.f.)}$	P	F value$_{(d.f.)}$	P
(2001/2002)						
Island	$F_{(5,12)} = 2.140$	0.130	$F_{(5,12)} = 2.217$	0.120	$F_{(4,10)} = 3.529$	**0.047**
Ecosystem (Isl.)	$F_{(12,144)} = 1.741$	0.064	$F_{(12,144)} = 3.707$	**< 0.001**	$F_{(10,111)} = 5.666$	**< 0.001**
(2002/2003)						
Island	$F_{(5,11)} = 0.518$	0.758	$F_{(5,11)} = 1.316$	0.326	$F_{(5,11)} = 5.081$	**0.011**
Ecosystem (Isl.)	$F_{(11,150)} = 1.085$	0.377	$F_{(11,150)} = 3.871$	**< 0.001**	$F_{(11,143)} = 2.946$	**0.002**
(2001/2003)						
Island	$F_{(4,10)} = 0.696$	0.611	$F_{(4,10)} = 1.071$	0.420	$F_{(4,10)} = 3.633$	**0.043**
Ecosystem (Isl.)	$F_{(10,114)} = 1.094$	0.372	$F_{(10,113)} = 3.032$	**0.002**	$F_{(10,106)} = 3.188$	**0.001**
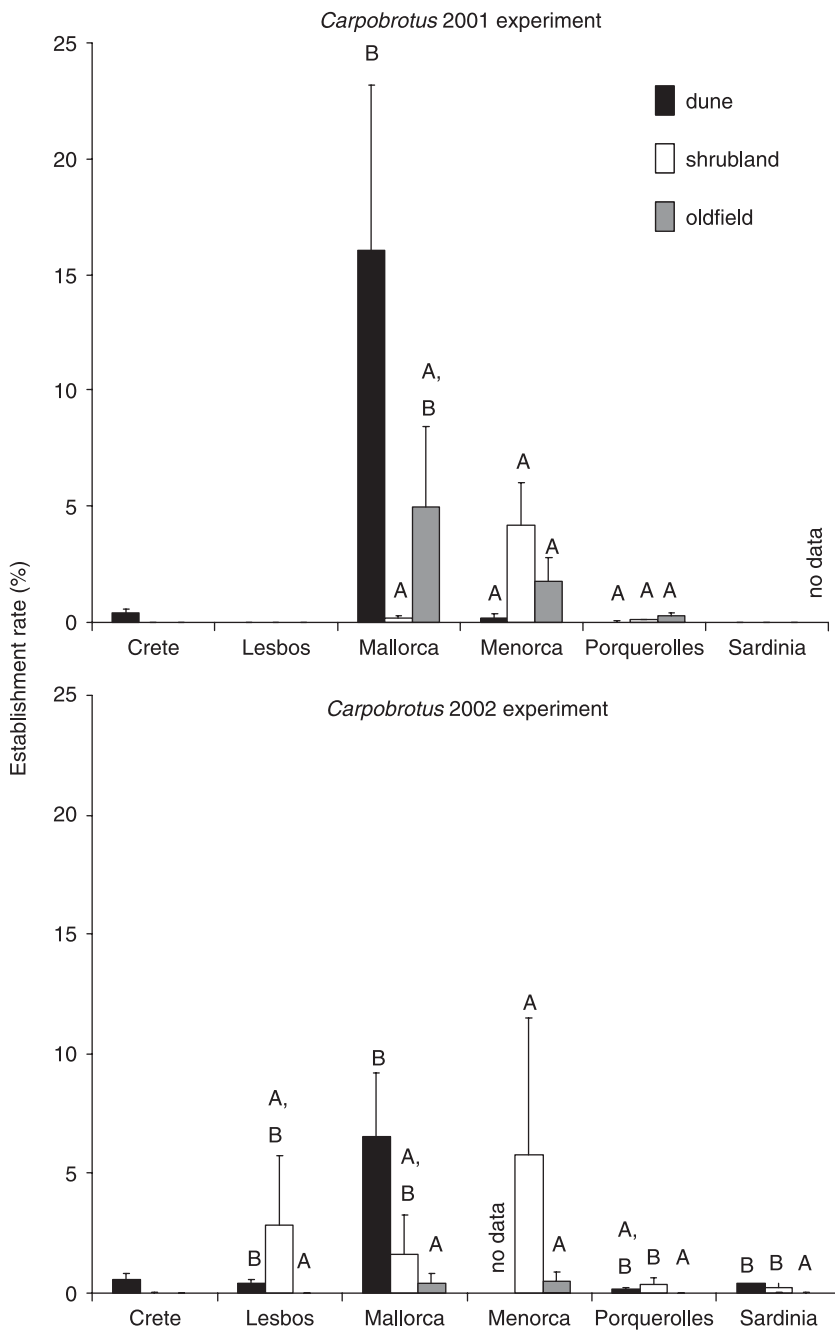
Figure 5 Means (+ standard error) for *Carpobrotus* spring establishment rates in different ecosystem types in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia arising from experimental sowing of 1000 seed in 2001 and 2002. Significant ecosystem differences within islands are indicated by letters (Tukey test, $P < 0.05$).

DISCUSSION

We found spatially and temporally consistent differences in invasiveness between the three species. As expected, the likelihood of establishment and seedling survival was extremely poor in *Ailanthus*, poor in *Carpobrotus* and good in *Oxalis*. In fact, during our removal visits the following three years after the experiments, no *Ailanthus* or *Carpobrotus* seedling were found, whereas *Oxalis* persisted. These low establishment rates, especially for *Ailanthus* contrast with other field sowing experiments conducted in less water limited ecosystems (e.g. Kowarik & Säumel, 2007 review for *Ailanthus*; D'Antonio, 1993 for *Carpobrotus*).

These species differences in establishment rates could be explained by both differences in seed viability (see Methods: Seedling experiment section) and failure to establish. When accounting for differences in the proportion of viable propagules sown, establishment rates still remained lower for *Ailanthus* (mean value between the two experiments: 1.93%) and *Carpobrotus* (10.98%) than for *Oxalis* (19.68%).

We acknowledge that our study only explored early seedling establishment and the analysis of invasibility for long-lived species should also include the probability to dominate over a longer time frame (Huston, 2004). Despite this, differences in invasiveness between the three species match both the local and regional
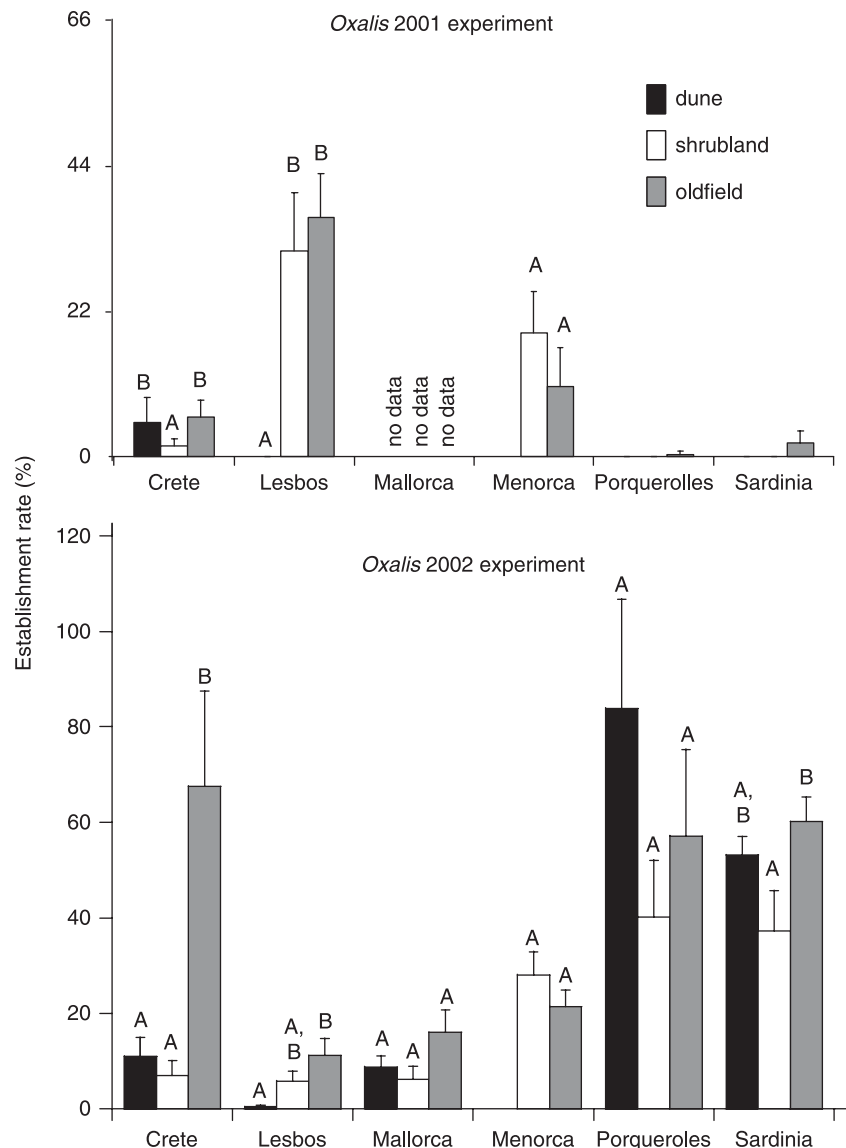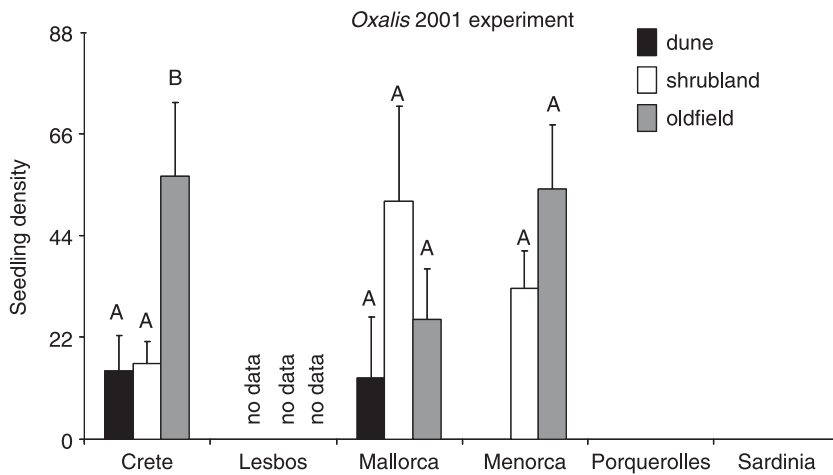
Figure 6 Means (+ standard error) for *Oxalis* spring establishment rates in different ecosystem types in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia arising from experimental sowing of 100 bulbs in 2001 and 2002. Significant ecosystem differences within islands are indicated by different letters (Tukey test, $P < 0.05$). Notice that scales are not the same for both experiments.

abundance of the three species across these islands (Table 1). *Oxalis* is the most locally abundant and widespread species of the three in the Mediterranean Basin islands, invading a wide range of ecosystems (Gimeno *et al.*, 2006; Hulme *et al.*, 2008). *Carpobrotus* is also a rather widespread species across islands, but mainly found in coastal areas (Hulme *et al.*, 2008) where it has high clonal growth. Finally, although *Ailanthus* can become locally dominant forming dense clonal stands, it is not frequently found into undisturbed natural ecosystems. As we only compared three phylogenetically very distinct species, it would be inappropriate to relate differences in establishment to specific species traits such as seed size or growth form.

Except for *Ailanthus*, which was consistent in dying in most sites, establishment differed among ecosystems. However, our results do not support that oldfields are consistently more invasible than coastal dunes and shrublands. Mediterranean woody ecosystems generally have a low degree of invasion (Brundu *et al.*, 2003; Pino *et al.*, 2005; Vilà *et al.*, 2007). However, we have found

that the likelihood of shrubland invasion might not differ from oldfields, even for species usually not found there. This result suggests that the general low degree of invasion in Mediterranean shrublands might not be related to low invasibility of this ecosystem type *per se* but to low propagule supply or to limiting ecological factors acting at later life-history stages (Williamson & Harrison, 2002; von Holle & Simberloff, 2005).

Ecosystem differences were spatially and temporally variable. For example, establishment rates for *Oxalis* in dunes were lower than in oldfields in Lesbos and Mallorca, but not in Sardinia. These differences could not be explained by resistance imposed by local species richness except for higher *Oxalis* establishment success in species-rich ecosystems. Studies that have found a negative effect of native species richness on invader establishment have been conducted at small spatial scales, using herbaceous target species, ensuring that the invader interacts with immediate neighbours (Fridley *et al.*, 2004). Only when the neighbourhood setting influences the invader recruitment by modifying cover or

Figure 7 Means (+ standard error) for *Oxalis* seedling density (seedlings/m^2) one year after experimental sowing of 100 bulbs in different ecosystem types in Crete, Lesbos, Mallorca, Menorca, Porquerolles and Sardinia. Significant ecosystem differences within islands are indicated by different letters (Tukey test, $P < 0.05$).

root overlap is a negative relationship likely to be found (Levine, 2000). Our experiment did not manipulate native species identity and species richness in the recipient ecosystems; in fact, many plots were located in open microsites outside a major influence of mature native plants. Therefore, our study does not reflect the intrinsic effects of diversity operating at neighbourhood scales, rather results are more in accordance with results found in floristic surveys than in experimental setting (Levine & D'Antonio, 1999). Our study supports results from observational studies that have found native rich habitats not to be immune to plant invaders (Stohlgren *et al.*, 1999; Stohlgren & Chong, 2002). Differences within and between ecosystems might be modulated by microsite heterogeneity with regard to soil quality, compaction or water and nutrient availability; as well as biotic constraints such as seed predators or herbivores interacting in complex ways (Mazia *et al.*, 2001; Renne *et al.*, 2006).

Similarly, we found large inter-annual variations. The lower establishment success and establishment rates from the sowing undertaken in 2001 compared to the 2002, and the high summer mortality were most likely caused by strong water limitation. In Mediterranean ecosystems, high summer water stress is known to decrease the likelihood of invasion (Thomsen *et al.*, 2006). These findings suggest that timing and ecosystem vulnerability to invasion might be largely dependent on water availability conditions triggering plant recruitment as proposed by the resource pulse hypothesis (Davis *et al.*, 2000; Renne *et al.*, 2006). Therefore, microsite soil differences in water retention as well as extreme events might play an important role in determining seedling establishment.

Although our study was conducted over a short time frame it highlights a high resistance of Mediterranean ecosystems to invasion (di Castri, 1990) in terms of recruitment limitation even to common invaders already occurring in the region. The establishment of invaders seem not to be an intrinsic property of a particular ecosystem type (Renne *et al.*, 2006) because seedling establishment differences between ecosystems were not consistent across islands nor years, and were dependent on invader identity and climatic constraints. Furthermore, our results suggest that there is not an association between the degree of invasion and the resistance imposed by the ecosystem to invasion, indicating that the variation in the degree of invasion is probably highly related to historical events such as propagule pressure or time since introduction (Pyšek & Jarosík, 2005; von Holle *et al.*, 2005). Our study represents the worst case scenario in terms of the species, the climatic conditions experienced and the geographical area assayed. That is, the three species are some of the most widespread invasive plants in Mediterranean islands. Precipitation in both years was moderately high compared to average long-term series. Finally, according to the received wisdom on plant invasions (Rejmanek *et al.*, 2005), even lower recruitment success would be expected if less invasive species were tested and if the experiment were conducted in mainland Mediterranean areas. More generalities could be drawn if the study was conducted over a longer timeframe, essaying more species in parallel mainland ecosystems.

REFERENCES

Bourgeois, K., Suehs, C.M., Vidal, E. & Médail, F. (2005) Invasional meltdown potential: facilitation between introduced plants and mammals on French Mediterranean islands. *Ecoscience*, **12**, 248–256.

Brundu, G., Camarda, I. & Satta, V. (2003) A methodological approach for mapping alien plants in Sardinia (Italy). *Plant*

invasions: ecological threats and management solutions (ed. by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, M. Wade and M. Williamson), pp. 41–62. Backhuys Publishers, Leiden, The Netherlands.

di Castri, F. (1990) On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. di Castri, A.J. Hansen and M. Debussche), pp. 3–16. Kluwer Academic Publishers, Dordrecht.

Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X. & Smart, S.M. (2008) Habitat invasions by alien plants: a quatitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.

Cowling, R.M., Ojeda, F., Lamont, B.B., Rundell, P.W. & Lechmere-Oertel, R. (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone Mediterranean-climate ecosystems. *Global Ecology and Biogeography*, **14**, 509–519.

D'Antonio, C.M. (1993) Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology*, **74**, 83–95.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

Draper, D., Rosselló-Graell, A., García, C., Gomes, C.T. & Sérgio, C. (2003) Application of GIS in plant conservation programmes in Portugal. *Biological Conservation*, **113**, 337–349.

Elton, C.S. (1958) *The ecology of invasions*. Methuen, London.

Fridley, J.D., Brown, R.L. & Bruno, J.F. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, **85**, 3215–3222.

Galil, J. (1968) Vegetative dispersal in *Oxalis cernua*. *American Journal of Botany*, **55**, 68–73.

Gimeno, I., Vilà, M. & Hulme, P.E. (2006) Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* in the western Mediterranean. *Journal of Biogeography*, **33**, 1559–1565.

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5–15.

Hulme, P.E. (2004) Islands, invasions and impacts: a Mediterranean perspective. *Ecología insular / island ecology* (ed. by J.M. Fernández-Palacios and C. Morici), pp. 359–383. Asociación Española de Ecologia Terrestre (AEET), Cabildo Insular de la Palma.

Hulme, P.E., Brundu, C., Camarda, I., Dalias, P., Lambdon, P., Lloret, F., Medail, F., Moragues, E., Suehs, C., Traveset, A., Troumbis, A. & Vilà, M. (2008) Assessing the risks to Mediterranean islands ecosystems from non-native plant introductions. *Plant invasions: human perception, ecological impacts and management* (ed. by B. Tokarska-Guzik, J.H., Brock, G. Brundu, L.E. Child, C. Daehler and P. Pyšek), pp. 39–56. Backhuys Publishers, Leiden, The Netherlands.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monograph*, **54**, 187–211.

Huston, M.A. (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. *Diversity and Distribution*, **10**, 167–178.

Kollmann, J., Frederiksen, L., Vestergaard, P. & Bruun, H.H. (2007) Limiting fators for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biological Invasions*, **9**, 31–42.

Kowarik, I. (1995) Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *Journal of Vegetation Science*, **6**, 853–856.

Kowarik, I. & Säumel, I. (2007) Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 207–237.

Lambrinos, J.G. (2002) The variable invasive success of *Cortaderia* species in a complex landscape. *Ecology*, **83**, 518–529.

Larson, D.L., Anderson, P.J. & Newton, W. (2001) Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications*, **11**, 128–141.

Lavorel, S., Canadell, J., Rambal, S. & Terradas, J. (1998) Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology and Biogeography Letters*, **7**, 157–166.

Levine, J.M. (2000) Species diversity and biological invasions: Relating local process to community pattern. *Science*, **288**, 852–854.

Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.

Lloret, F., Médail, F., Brundu, G. & Hulme, P.E. (2004) Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? *Global Ecology and Biogeography*, **13**, 37–45.

Lloret, F., Médail, F., Brundu, G., Camarga, I., Moragues, E., Rita, J., Lambdon, P. & Hulme, P.E. (2005) Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology*, **93**, 512–520.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.

Mazia, C.N., Chaneton, E.J., Ghersa, C.M. & León, R.J.C. (2001) Limits to tree species invasion in Pampean grassland and forest plant communities. *Oecologia*, **128**, 594–602.

McDonald, I.A.W. & Cooper, J. (1995) Insular lessons for global biodiversity conservation with particular reference to alien invasions. *Islands: biological diversity and ecosystem function* (ed. by P.M. Vitousek, L.L. Loope and H. Andersen), pp. 189–204. Springer-Verlag, Berlin.

Médail, F. & Quézel, P. (1997) Hot spots analysis for conservation of plant biodiversity in the Mediterranean basin. *Annals of the Missouri Botanical Garden*, **84**, 112–127.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E. &

Vázquez, D.P. (2006) Biotic interactions and plant invasions. *Ecology Letters*, **9**, 726–740.

Peirce, J.R. (1997) The biology of Australian weeds: 31. *Oxalis pes-caprae* L. *Plant Protection Quarterly*, **12**, 110–119.

Pino, J., Font, X., Carbó, J., Jové, M. & Pallarès, L. (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological Conservation*, **122**, 339–350.

Pyšek, P. & Jarosík, V. (2005) Residence time determines the distribution of alien plants. *Invasive plants: ecological and agricultural aspects* (ed. by S. Inderjit), pp. 77–96. Birkhäuser Verlag, Switzerland.

Rejmanek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M. & Grotkopp, E. (2005) Ecology of invasive plants: state of the art. *Invasive alien species: a new synthesis* (ed. by H.A. Mooney, J.A. McNeely, L. Neville, P.J. Schei and J. Waage), pp. 104–162. Island Press, Washington DC.

Renne, I.J., Tracy, B.F. & Colonna, I.A. (2006) Shifts in grassland invasibility: effects of soil resources, disturbance, composition, and invader size. *Ecology*, **87**, 2264–2277.

Robinson, G.R., Quinn, J.F. & Stanton, M.L. (1995) Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology*, **76**, 786–794.

Rottenberg, A. & Parker, J.S. (2004) Asexual populations of the invasive weed *Oxalis pes-caprae* are genetically variable. *Proceedings of the Royal Society B: Biological Sciences*, **271**, S206–S208.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999) Exotic plant species invade hot spots of native plant diversity. *Ecological Monograph*, **69**, 25–46.

Stohlgren, T.J. & Chong, G.W. (2002) Assessing vulnerability to invasion by non-native plant species at multiple spatial scales. *Environmental Management*, **29**, 566–577.

Suehs, C.M., Affre, L. & Médail, F. (2004) Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: II. Reproductive strategies. *Heredity*, **92**, 550–556.

Thompson, J.D. (2005) *Plant evolution in the Mediterranean*. Oxford University Press, Oxford, UK.

Thomsen, M.A., D'Antonio, C.M., Suttle, K.B. & Sousa, W.P. (2006) Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecology Letters*, **9**, 160–170.

Vila, M. & D'Antonio, C.M. (1998) Fruit choice and seed dispersal of invasive vs. noninvasive *Carpobrotus* (Aizoaceae) in coastal California. *Ecology*, **79**, 1053–1060.

Vilà, M., Bartomeus, I., Gimeno, I., Traveset, A. & Moragues, E. (2006a) Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. *Annals of Botany*, **97**, 1055–1062.

Vilà, M., Pino, J. & Font, X. (2007) Regional assessment of plant invasions across different habitat types. *Journal of Vegetation Science*, **18**, 35–42.

Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Médail, F., Moragues, E., Traveset, A., Troumbis, A.Y. & Hulme, P.E. (2006b) Regional assessment of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography*, **33**, 853–861.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.

Williamson, J. & Harrison, S. (2002) Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications*, **12**, 40–51.

Wisura, W. & Glen, H. (1993) The South African species of *Carpobrotus* (Mesenbryanthema – Aizoaceae). *Contributions from the Bolus Herbarium*, **15**, 76–107.

Editor: Michael Huston

Appendix 1 Mean (± SE) cumulative precipitation, Tª and local species richness in plots with and without seedling establishment after the 2001 and 2002 sowing experiment across six Mediterranean islands. Differences between plots according to a logistic regression are indicated for each invasive species and experiment. The influence of local species richness was only tested for the first experiment.

Species	2001				2002			
	Establishment	No establishment	χ^2	P	Establishment	No establishment	χ^2	P
Precipitation								
Ailanthus	744.65 ± 69.50	609.32 ± 15.11	3.19	0.07	695.86 ± 49.20	653.88 ± 17.46	0.06	0.81
Carpobrotus	648.06 ± 27.07	601.39 ± 17.75	2.05	0.15	643.87 ± 18.75	675.50 ± 21.54	1.24	0.26
Oxalis	508.96 ± 32.60	537.16 ± 20.62	0.55	0.46	648.90 ± 18.87	687.81 ± 34.30	0.76	0.38
Temperature								
Ailanthus	17.08 ± 0.65	16.38 ± 0.14	1.15	0.28	16.97 ± 0.36	16.86 ± 0.13	0.01	0.92
Carpobrotus	16.32 ± 0.25	16.45 ± 0.16	0.19	0.66	16.85 ± 0.14	17.25 ± 0.16	3.45	0.06
Oxalis	18.11 ± 0.26	17.01 ± 0.16	12.55	**0.0004**	16.87 ± 0.14	16.82 ± 0.25	0.023	0.88
Species richness								
Ailanthus	9.70 ± 2.64	12.27 ± 0.78	0.98	0.32				
Carpobrotus	10.55 ± 1.57	12.51 ± 0.84	1.29	0.26				
Oxalis	21.70 ± 1.72	10.68 ± 1.21	23.35	**< 0.001**				

Appendix 2 Correlation analysis between establishment rates and cumulative precipitation, Tª and local species richness in plots with successful seedling establishment after the 2001 and 2002 sowing experiment across six Mediterranean islands. The influence of local species richness was only tested for the first experiment.

Species	2001		2002	
	z value	P	z value	P
Precipitation				
Ailanthus	0.84	0.40	−0.99	0.32
Carpobrotus	3.64	**0.0003**	−0.90	0.37
Oxalis	2.62	**0.009**	2.79	**0.005**
Temperature				
Ailanthus	−0.80	0.42	0.08	0.94
Carpobrotus	0.75	0.45	−2.87	**0.004**
Oxalis	−2.66	**0.008**	−4.42	**< 0.0001**
Species richness				
Ailanthus	−0.24	0.81		
Carpobrotus	−0.18	0.86		
Oxalis	−0.75	0.45		