



# Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands

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## ABSTRACT

**Aims** Although biological invasions occur throughout the world, and some invaders are widespread in many habitats, few studies on the ecological impact of invaders have examined multiple sites. We tested how the impact of three widespread plant invaders changed depending on the identity of the species and the invaded island. We also tested whether relative species loss was lower in species-rich communities than in species-poor ones.

**Location** We conducted floristic surveys and soil analyses in eight Mediterranean Basin islands: Crete and Lesbos (Greece), Sardinia (Italy), Corsica, Bagaud and Porquerolles (France), and Mallorca and Menorca (Spain).

**Methods** We compared native species richness and diversity, proportion of life forms, soil percentage nitrogen, percentage organic carbon, C/N, and soil pH in nearby paired plots of 2 × 2 m: one control and one invaded by either the deciduous tree *Ailanthus altissima*, the succulent subshrubs *Carpobrotus* spp. or the annual geophyte *Oxalis pes-caprae*, across eight Mediterranean Basin islands.

**Results** On average, the presence of invaders reduced species diversity, *Carpobrotus* spp. exhibiting the largest impact and *Oxalis* the least. However, the relative impact was island-dependent, and was positively but weakly associated with the species richness of the recipient community. Therophytes were the life form that experienced the largest decrease across islands. The effects of invasion on soil properties were very variable. Total N changed (increased) only in plots invaded by *Ailanthus*, significantly decreasing the C/N ratio. The presence of this tree increased soil pH, whereas the opposite was found in plots invaded by the other two species. Organic C increased in plots invaded by *Ailanthus* and *Carpobrotus* species.

**Main conclusions** By conducting an analysis at multiple sites, we found that the three plant invaders had an impact on plant community structure not entirely concordant with changes in soil properties. The impacts depended on the identity of the species and of the invaded island, suggesting that impact of invaders is context-specific. The impact in terms of species loss was not lower in species-rich than in species-poor communities.

## Keywords

*Ailanthus altissima*, alien plants, *Carpobrotus* spp., ecosystem functioning, invasibility, invasion impact, Mediterranean ecosystems, *Oxalis pes-caprae*, species diversity.

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## INTRODUCTION

Biological invasions by non-native plant species are regarded as among the most important drivers of environmental change in Mediterranean ecosystems (Sala *et al.*, 2000). Although the potential consequences of non-native plant invasion include changes in native species composition, community structure, nutrient and water fluxes as well as disturbance regimes, only limited information exists as to the nature of impacts on Mediterranean ecosystems (Levine *et al.*, 2003). There is an urgent need for comparative studies that assess the impacts of different invasive species in Mediterranean ecosystems.

Mediterranean Basin islands are most at risk from invasive species threatening endemic species, especially in coastal areas (Hulme, 2004 and references therein). The alien flora of Mediterranean islands comprises a small number of species present in many islands, while most are found on only one or a few islands (Lloret *et al.*, 2004). Therefore Mediterranean islands represent an outstanding opportunity to assess the relative magnitude of invasive species impacts within a single biome, and to scale-up from local impacts to regional implications (Pauchard *et al.*, 2004). For this purpose, large-scale surveys can provide insights and generalizations not obtained from more localized studies. For example, observational studies across many sites and vegetation types have found that the relationship between native and alien species richness is generally positive (Stohlgren *et al.*, 1999; Stohlgren & Chong, 2002; Gilbert & Lechowicz, 2005), contradicting early theories that communities with high species diversity were less vulnerable to invasions (Elton, 1958).

We conducted a large-scale survey adopting similar protocols to assess regional consistency in the magnitude and direction of the impacts of three widely distributed plant invaders on changes in plant community structure (such as species diversity) and soil properties, across eight Mediterranean Basin islands. We focused on soil properties because changes in these are symptomatic of changes in ecosystem processes. Assessments of invasive plant impacts on ecosystem processes have tended to be biased towards species possessing specific traits, such as nitrogen fixation (Ehrenfeld, 2003; Levine *et al.*, 2003). To avoid such biases, our case study selection of invasive species was based on prevalence and contrasting life forms, rather any *a priori* expectation of impacts. The alien species chosen were the clonal deciduous tree *Ailanthus altissima* (P. Mill) Swingle (Simaroubaceae); the succulent clonal subshrubs *Carpobrotus* spp. L. (Aizoaceae); and the clonal geophyte *Oxalis pes-caprae* L. (Oxalidaceae). Specifically, we addressed the following questions: (1) Are alien plants associated with a change in native species diversity or functional group representation? (2) Are alien plants associated with changes in soil properties (percentage organic C; percentage total N; C/N ratio) or soil pH? (3) Are associations consistent across islands, or are some islands more susceptible than others? (4) Are species-rich communities more resistant than species-poor communities to species loss due to the

presence of an invader? Our hypothesis is that the presence of aliens is associated with a reduction in species diversity, changes in the proportion of life forms and changes in soil properties. We expect species-rich communities to be more resistant to the impact of the invader. To our knowledge, this is the most extensive comparative analysis examining the effect of the same invader plant species on vegetation structure and ecosystem functioning across a single region.

## METHODS

### Study area and invasive taxa

Of the nearly 5000 islands in the Mediterranean Basin (Hulme, 2004 and references therein), eight were chosen as representative in terms of range of island size, isolation and geographical distribution from a west–east gradient: Crete and Lesbos in Greece; Sardinia in Italy; Corsica and the Hyères Archipelago (Bagaud and Porquerolles) in France; and Mallorca and Menorca in Spain (Table 1). The selection of these islands was also based on researcher affiliation and expertise.

According to their occurrence in the focal islands (Table 1), three invasive plant taxa listed as common, widespread, naturalized plants in Mediterranean ecosystems (Quézel *et al.*, 1990; Hulme, 2004) were chosen to represent different life forms (a tree, a perennial succulent and an annual, respectively), different types of communities invaded, and therefore a range of possible impacts on native systems: *A. altissima*, *Carpobrotus* spp. and *O. pes-caprae*. These three taxa are hereafter collectively referred to as the invader, or referred to individually by genus.

*Ailanthus* is a deciduous tree native to China, planted mainly as an ornamental and in landscaping. It is able to resprout and develop root networks that form dense clonal stands (Hu, 1979; Kowarik, 1995). It is common in disturbed urban areas, old fields, along roadsides, woodland edges and forest openings all around Europe. *Carpobrotus acinaciformis* (L.) Bolus and *C. edulis* (L.) N.E. Br. are

**Table 1** The Mediterranean Basin study islands and their area, distance to nearest mainland, and number of experimental replicates for each invader per island

Island (country)	Area (km <sup>2</sup> )	Distance from mainland (km)	Number of plots per invader		
			<i>Carpobrotus</i>	<i>Ailanthus</i>	<i>Oxalis</i>
Bagaud (France)	6	8	13	0	0
Porquerolles (France)	12	2	21	0	24
Corsica (France)	8682	82	0	27	0
Crete (Greece)	8700	100	14	12	10
Lesbos (Greece)	1632	18	0	0	30
Mallorca (Spain)	3656	170	25	23	22
Menorca (Spain)	702	200	24	19	12
Sardinia (Italy)	24,090	230	30	25	30

chamaephyte, mat-forming succulents native to South Africa (Wisura & Glen, 1993), which were introduced as ornamentals and for erosion prevention. These two species and their hybrids (Vilà & D'Antonio, 1998; Suehs *et al.*, 2004a,b) are now widely naturalized on coastal rocks, cliffs and sand dunes, and are considered a serious threat to several plant species and coastal habitats (D'Antonio & Mahall, 1991; Draper *et al.*, 2003). Finally, *Oxalis* is an annual geophyte introduced accidentally from South Africa, which has invaded many Mediterranean regions of the world since the beginning of the nineteenth century (Peirce, 1997; Rottenberg & Parker, 2004). In the Mediterranean Basin, it is mostly present in disturbed areas such as olive groves, orchards, pastures and ruderal areas. *Oxalis* spreads vegetatively by means of underground bulbs. No sexual reproduction has been observed in the introduced range (Galil, 1968). *Oxalis* aboveground biomass contains oxalic acid, which is toxic to large herbivores (livestock) when consumed in large quantities (Libert & Franceschi, 1987).

### Vegetation surveys

Vegetation surveys were carried out between 2001 and 2003 in spring, at the peak of vegetative cover and species richness. For each of the three invaders, a 2 × 2-m paired-plot design was repeated between 10 and 30 times per island across the different habitats where each taxon occurred, resulting in a total of 361 paired plots (Table 1). Based on the fact that individual plants interfere with their closest neighbours (Harper, 1977), plot size was chosen as a compromise between the minimum area of interference while avoiding spatial scale sampling differences between species. One plot of each pair was centred on spontaneously established clones of the invader taxon (invaded plot). The other plot of each pair was subsequently placed at *c.* 2 m distance from the edge of the invaded plots for *Carpobrotus* and *Oxalis*, and at > 5 m from the edge for *Ailanthus*, both in a randomly chosen cardinal direction (control plot). Paired plots were selected after dedicated land surveys to ensure that the two paired plots shared similar substrate and habitat characteristics, and that the minimum distance between sites within an island was 1 km.

Each plot was divided into 16 subplots, each of 50 × 50 cm, within which the presence/absence of all plant species was recorded. Abundance was scored as the number of subplots in which a species occurred, and was used to derive plot estimates of species richness (number of species per plot); diversity (Shannon's *H'* index); and the percentages of therophytes, hemicryptophytes, geophytes, chamaephytes and phanerophytes based on number of counts (*sensu* Raunkiaer, 1934). The invasive taxon was excluded from these estimates in order to have parameter values independent of invader abundance (Wearne & Morgan, 2004). To reduce within- and between-island variability, the invaded plots were selected on the basis of having a high cover of the invader (present in ≥ 14 subplots).

### Soil sampling and analysis

Soil was collected at random from three different subplots and subsequently pooled for each plot. For each sample, surface litter (if present) was removed and the top 12 cm of soil was sampled to a total bulked volume of 0.0005–0.001 m<sup>3</sup> per plot. Samples were air-dried to constant mass, sieved with a 2-mm pore-size sieve, and ground in a standard ball mill grinder. Samples were analysed for pH; for carbonate (CaCO<sub>3</sub> %) using the Bernard calcimeter method; and for total C and N using a CHN analyser (EA1108, Carlo Erba Instruments, Milan, Italy). The percentage of organic C was calculated as the difference between total C and CaCO<sub>3</sub> % (Klute, 1986). The ratio of total % C to total % N (C/N) was also calculated as an estimate of soil quality.

### Statistical analysis

Because our study was performed at multiple sites, we could test for the consistency of impacts within islands and among islands (Meiners *et al.*, 2001). Within-island differences in plant community structure and soil properties between paired invaded and control plots were analysed with paired *t*-tests or Wilcoxon signed-rank tests if data did not meet the assumptions of parametric analysis (Zar, 1984; Daniel, 1990). Certain Raunkiaer life forms occurred too infrequently to be included in the analysis.

Among-island patterns in plant community structure and soil properties were analysed using generalized linear mixed models (GLMM). Percentage N, C/N and pH were initially included in the model as covariates to explain species richness and species diversity. However, they accounted for insignificant amounts (*P* > 0.10) and were subsequently excluded from the analysis. The final model was: response variable = presence of the invader (yes or no) + island + site nested within island + error. Sites and islands were considered random factors. Moreover, sites were nested within island to account for non-independence in standard error estimates (SAS, 2001). The presence/absence of the invader was a fixed factor. Separate analyses were performed for each invader.

When the GLMM found significant differences between invaded and control plots for a dependent variable, we tested for differences between islands in the relative impact (RI) of the presence of the invader. Such relative impact was estimated with an index adapted from the relative interaction index (RII) (Armas *et al.*, 2004). The RII is an index that measures the relative intensity of an interaction between plant species (competition or facilitation). The RII has better mathematical and statistical properties compared with classical indices such as the relative neighbour effect or the log response ratio (Goldberg *et al.*, 1999). For example, RII distribution is approximately normal, it is linear and does not have discontinuities, it is symmetrical around zero, and it has defined limits [−1; +1]. In our case, we calculated the RI of the presence of the invader on a dependent variable (*V*) as follows:

$$RI = \frac{V_{Control} - V_{Invaded}}{V_{Control} + V_{Invaded}}$$

A negative RI value means an increase of the parameter, associated with the presence of the invader; in contrast, a positive value means that the presence of the invader decreases the parameter. A zero value means that the presence of the invader has a non-significant effect on the parameter in question.

Where differences between invaded and control plots were significant, differences in RI between islands were tested using one-way ANOVA. All data met the assumptions of ANOVA and therefore were not transformed. When a significant island effect was detected, pairwise comparisons were performed using a Tukey test (Zar, 1984).

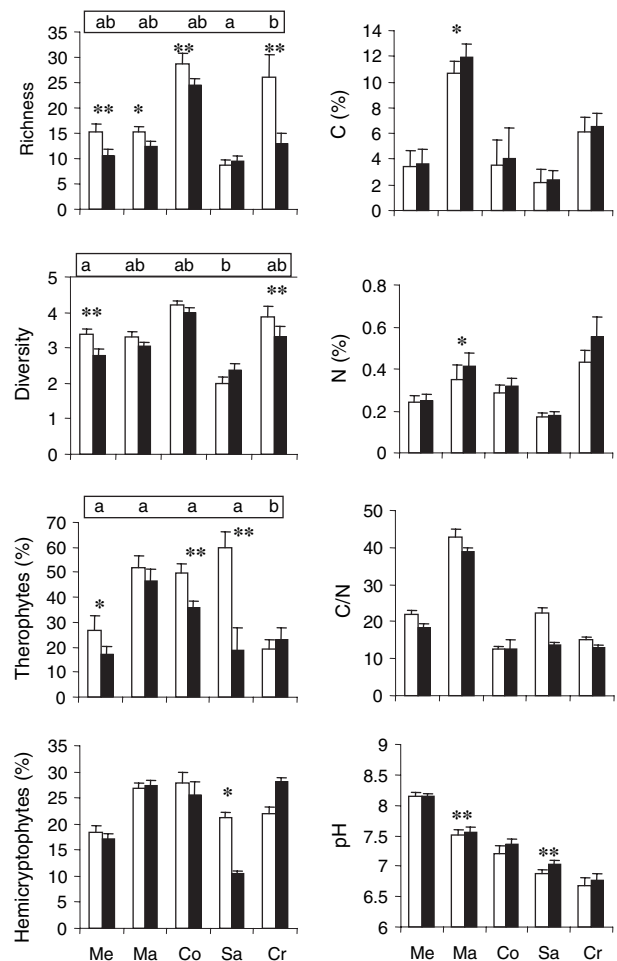
To test if the RI on species richness differed among the three invaders and the eight islands, we performed two one-way ANOVAs with invader and island as main effects, respectively. The potential for more species-rich communities to be more resistant to the impacts of the invader on species loss was explored using simple linear regression between species richness in control plots and the RI on species richness.

## RESULTS

A consistent and significant trend of lower species richness was found in plots invaded by each of the three non-native species (Figs 1–3). Invasion by *Carpobrotus* had the largest impact (mean  $\pm$  SE), with  $36.4 \pm 4.4\%$  decline in species richness in the invaded plots; *Ailanthus* was intermediate at  $23.8 \pm 3.1\%$ ; while *Oxalis* had the least impact leading only to  $10.2 \pm 4.4\%$  fewer species. While for *Carpobrotus* this impact (RI) was consistent in both magnitude and direction among islands (Table 3), this was not the case for the other invaders (Tables 2 & 4). For *Ailanthus* and *Oxalis*, the reduction in species richness was not significant in all islands (Figs 1 & 3). Patterns in both species diversity and RI among islands were broadly comparable with those found for species richness (Figs 1–3).

As regards life forms, therophytes appeared to be the most negatively influenced by the presence of an invader, but the effect among islands was significant only for *Ailanthus* and *Carpobrotus* (Tables 2 & 3). Reductions in the percentage of therophytes varied among islands (Figs 1 & 2). Hemicryptophytes showed an inconsistent pattern of increases and decreases in some islands (Figs 1–3). On average, chamaephytes increased in the plots invaded by *Carpobrotus*, but again the magnitude and direction were not consistent among islands (Fig. 2). The same inconsistency of pattern was found for geophytes in plots invaded by *Oxalis* (Fig. 3).

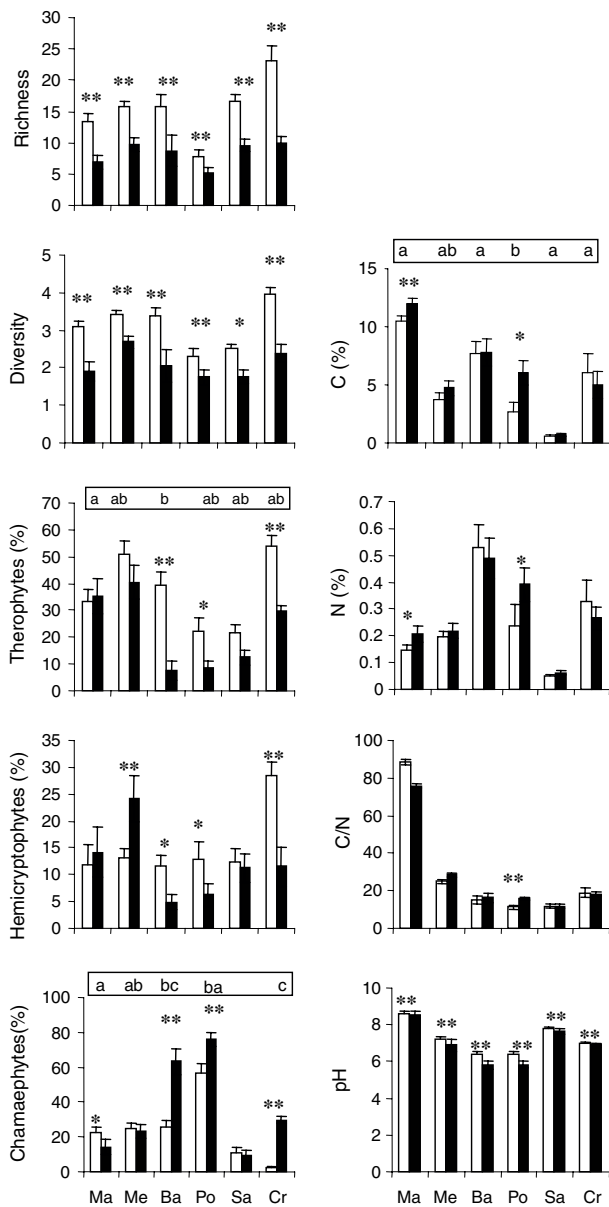
*Ailanthus*-invaded plots were also associated with significant increases for percentage C and especially percentage N, such that there was an overall significantly decreasing C/N (Table 2, Fig. 1). *Carpobrotus* was also associated with an accumulation of soil organic matter, but only the response in percentage C, and not percentage N or the C/N ratio, was significant (Table 3, Fig. 2). *Oxalis* did not influence these soil parameters (Table



**Figure 1** Means ( $\pm$ SE) for species richness, diversity (Shannon's  $H'$  index), percentage therophytes, percentage hemicryptophytes, percentage soil organic carbon, percentage total soil nitrogen, C/N ratio, and soil pH in *Ailanthus*-invaded (black) and control (white) plots on the islands of Menorca (Me), Mallorca (Ma), Corsica (Co), Sardinia (Sa) and Crete (Cr). Asterisks indicate significant differences between pairwise invaded and control plots within an island (\* $P < 0.05$ ; \*\* $P < 0.01$ ). Significant differences between islands for the relative impact (RI) index are indicated by lower-case letters (Tukey test,  $P < 0.05$ ). The RI was compared statistically only if there were overall differences between invaded and control plots across islands.

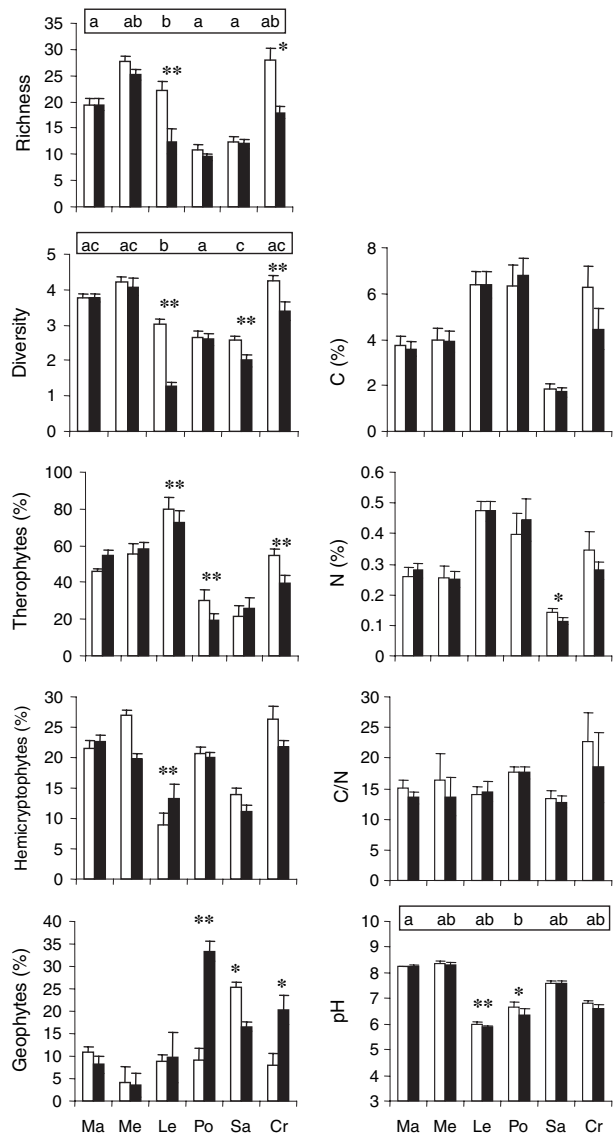
4, Fig. 3). All three species altered soil pH: whereas soils beneath *Ailanthus* were more basic, those under *Carpobrotus* and *Oxalis* were significantly more acid. These patterns were found consistently across islands for *Carpobrotus* and *Ailanthus*, but not for *Oxalis* (Tables 2–4).

*Carpobrotus* had a greater RI on species loss than the other two invaders studied ( $F_{2,353} = 18.97$ ,  $P < 0.0001$ ; Fig. 4). The average RI of the three species also differed between islands ( $F_{7,348} = 4.84$ ,  $P < 0.0001$ ) being larger in Bagaud (the smallest island), Crete and Lesbos, and lowest in Corsica (Fig. 4). However, there is no relationship between RI and either island area (Spearman's rank correlation,  $\rho = -0.43$ ,



**Figure 2** Means (+SE) for species richness, diversity (Shannon’s  $H'$  index), percentage therophytes, percentage hemicytopytes, percentage chamaephytes Percentage soil organic carbon, percentage total soil nitrogen, C/N ratio, and soil pH in *Oxalis*-invaded (black) and control (white) plots on the islands of Mallorca (Ma), Menorca (Me), Bagaud (Ba), Porquerolles (Po), Sardinia (Sa) and Crete (Cr). Asterisks indicate significant differences between pairwise invaded and control plots within an island (\* $P < 0.05$ ; \*\* $P < 0.01$ ). Asterisks indicate significant differences between pairwise invaded and control plots within an island (\* $P < 0.05$ ; \*\* $P < 0.01$ ). Significant differences between islands for the relative impact (RI) index are indicated by lower-case letters (Tukey test,  $P < 0.05$ ). The RI was compared statistically only if there were overall differences between invaded and control plots across islands.

$P = 0.26$ ) or distance to the mainland (Spearman’s rank correlation,  $\rho = -0.26$ ,  $P = 0.49$ ). Finally, a positive but weak relationship was detected between RI and species richness in control plots (Fig. 5).



**Figure 3** Means (+SE) for species richness, diversity (Shannon’s  $H'$  index), percentage therophytes, percentage hemicytopytes, percentage geophytes, percentage soil organic carbon, percentage total soil nitrogen, C/N ratio, and soil pH in *Oxalis*-invaded (black) and control (white) plots on the islands of Mallorca (Ma); Menorca (Me), Lesbos (Le), Porquerolles (Po), Sardinia (Sa) and Crete (Cr). Asterisks indicate significant differences between pairwise invaded and control plots within an island (\* $P < 0.05$ ; \*\* $P < 0.01$ ). Significant differences between islands for the relative impact (RI) index are indicated by lower-case letters (Tukey test,  $P < 0.05$ ). The RI was compared statistically only if there were overall differences between invaded and control plots across islands.

## DISCUSSION

We conducted floristic surveys in invaded and non-invaded plots following the same protocol at multiple sites within and across islands. We found that although, on average, the

**Table 2** Generalized linear mixed model (GLMM) results for parameter differences between *Ailanthus*-invaded and control plots across Mediterranean Basin islands, and ANOVA results for insular differences in relative impact (RI) index for parameters with significant differences across islands

Dependent variable	GLMM			ANOVA		
	df	F	P	df	F	P
Species richness	1, 10	21.8	0.01	4, 98	6.4	0.02
Species diversity	1, 10	5.1	0.01	4, 98	4.4	0.04
Therophytes (%)	1, 98	15.9	0.01	4, 10	7.6	0.01
Hemicryptophytes (%)	1, 98	0.2	0.67			
Organic carbon (%)	1, 99	5.1	0.03	4, 95	0.8	0.99
Total nitrogen (%)	1, 99	4.1	0.04	4, 95	1.1	0.80
C/N ratio	1, 99	4.37	0.04	4, 95	0.8	0.94
pH	1, 10	6.12	0.01	4, 96	0.6	0.65

**Table 3** Generalized linear mixed model (GLMM) results for parameter differences between *Carpobrotus*-invaded and control plots across Mediterranean Basin islands, and ANOVA results for insular differences in relative impact (RI) index for parameters with significant differences across islands

Dependent variable	GLMM			ANOVA		
	df	F	P	df	F	P
Species richness	1, 12	134.07	0.01	5, 12	5.5	0.30
Species diversity	1, 12	87.53	0.01	5, 12	2.3	0.21
Therophytes (%)	1, 12	27.24	0.01	5, 12	3.1	0.04
Hemicryptophytes (%)	1, 12	0.68	0.41			
Chamaephytes (%)	1, 12	12.46	0.01	5, 12	16.0	0.01
Organic carbon (%)	1, 11	7.11	0.01	5, 10	3.4	0.01
Total nitrogen (%)	1, 11	2.27	0.13			
C/N ratio	1, 11	0.60	0.44			
pH	1, 12	9.32	0.01	5, 11	1.2	0.38

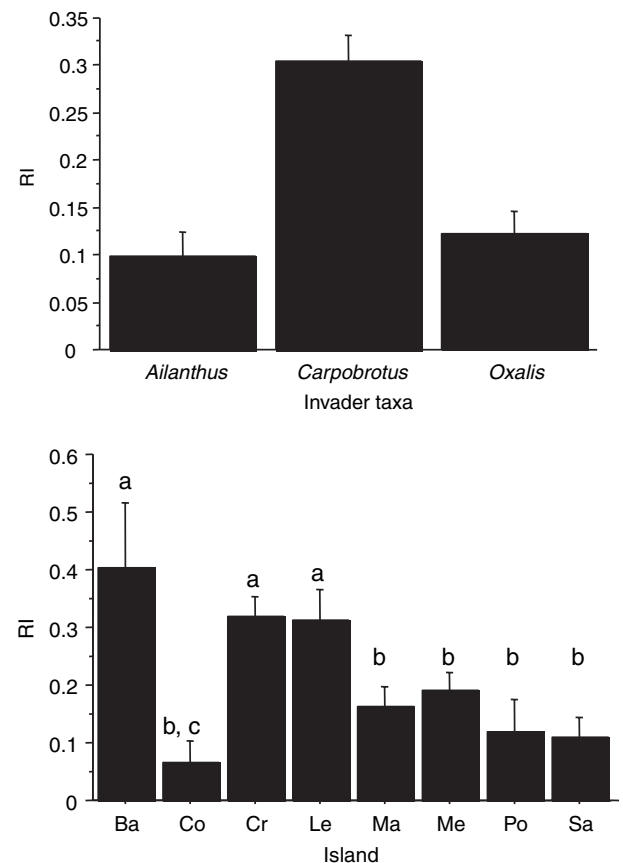
presence of the invader affects the vegetation structure and soil properties, the magnitude of this impact is very much dependent on the identity of the species and the island.

### Diversity loss

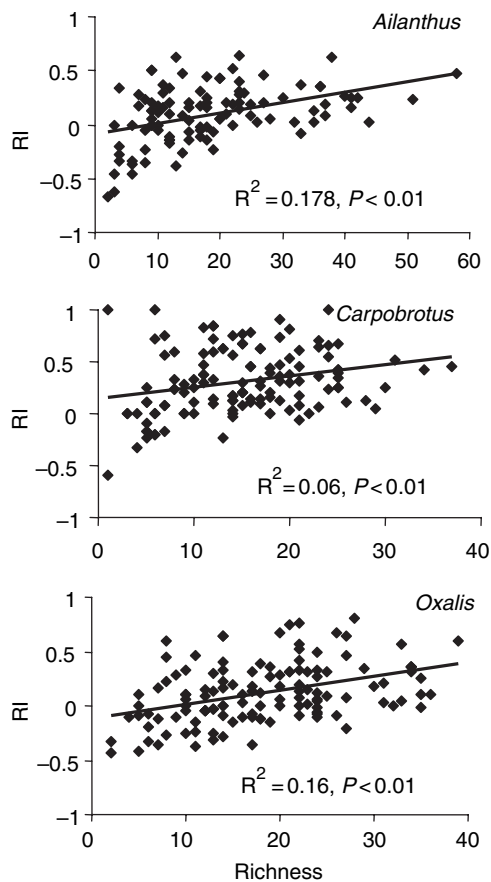
On average, we found a reduction in native plant species diversity and richness associated with the invasion by *Ailanthus*, *Carpobrotus* or *Oxalis*. However, as might be expected, the magnitude of the impact differed among the three species, with *Carpobrotus* exhibiting the largest impact (36% in species loss) and *Oxalis* the least (10%). Furthermore, the magnitude of the impact was very variable among islands, especially for *Oxalis*, but was not dependent on island size or distance to the mainland. Differences in species diversity changes across sites (islands in our study) have been observed in other ecosystems (Woods, 1993) and have been related to differences in invader infestation. In our case, selected invaded plots for all species and islands are considered to be highly infested. Several other

**Table 4** Generalized linear mixed model (GLMM) results for parameter differences between *Oxalis*-invaded and control plots across Mediterranean Basin islands, and ANOVA results for insular differences in relative impact (RI) index for parameters with significant differences across islands

Dependent variable	GLMM			ANOVA		
	df	F	P	df	F	P
Species richness	1, 13	23.54	< 0.01	5, 12	7.82	0.01
Species diversity	1, 13	41.23	< 0.01	5, 12	15.39	0.01
Therophytes (%)	1, 13	1.15	0.28			
Hemicryptophytes (%)	1, 13	0.11	0.74			
Geophytes (%)	1, 13	3.44	0.07			
Organic carbon (%)	1, 13	0.44	0.51			
Total nitrogen (%)	1, 13	0.00	0.97			
C/N ratio	1, 13	1.68	0.20			
pH	1, 14	5.94	0.02	5, 14	2.61	0.02

**Figure 4** Average relative impact (RI) in species loss according to the identity of the invader and the island. Bagaud (Ba), Corsica (Co), Crete (Cr), Mallorca (Ma), Menorca (Me), Porquerolles (Po) and Sardinia (Sa). RI has defined limits  $[-1; +1]$ . Higher values indicate that more species are lost in the invaded plots.

factors might limit our understanding of differences among islands. It is plausible that longer-established stands of invaders have greater effects in changing species diversity than recently



**Figure 5** Relationship between species richness in control plots and the relative impact (RI) of species loss of invasion by *Ailanthus altissima*, *Oxalis pes-caprae* and *Carpobrotus* spp. across eight Mediterranean Basin islands. A negative RI value means an increase in species richness associated with the presence of the invader; in contrast, a positive value means that the presence of the invader decreases species richness. A zero value means that the presence of the invader has a non-significant effect on the parameter in question.

invaded stands, as has been shown in chronosequence studies (Wearne & Morgan, 2004). Communities might also differ in their successional stages, especially those invaded by *Ailanthus* and *Oxalis*, which are mainly located at sites that are frequently disturbed anthropogenically. Long-term studies of permanent plots on lands released from agriculture have reported invasion-impact differences for species richness along seral stages (Meiners *et al.*, 2001). Unfortunately, information is lacking regarding both invasion history and disturbance regime across sites and islands in this study.

Island differences on the impact of invaders may also be related to biotic factors, such as differences in the vegetation structure of the recipient community. Species loss was not lower when the community was poor in species, as shown by the marginally positive relationship between species richness in control plots and the RI on species loss. This finding suggests that areas of higher native plant diversity are not immune to species loss.

### Changes in species composition

Even in the absence of a significant effect on richness and diversity within an island, species composition could change markedly. Therophytes were particularly vulnerable to each of the three invaders. However, the effects of invasion on other life forms were weaker, and were not detected in all islands. *Oxalis* was the invader with the least effect on life-form representation.

The therophyte decrease is of concern because a large proportion of endemic species in the Mediterranean Basin are annuals (Heywood, 1995). High rates of extinction in therophytes (90%) have already been documented in Mediterranean Basin ecosystems, especially at low altitudes (Verlaque *et al.*, 2001). Therophyte recruitment depends on seed banks for population survival, and as they have a short life cycle they are more responsive to environmental and biotic changes than other life forms. The RI on the decrease of therophytes was especially high in plots invaded by *Ailanthus*, possibly as a consequence of allelopathic substances reducing establishment by inhibiting seed germination (Heisey, 1990; De Feo *et al.*, 2003). In plots invaded by *Carpobrotus*, the dense mat of overlapping stems and considerable litter layer would be a substantial obstacle to the germination and establishment of therophytes. In contrast, *Oxalis* had a non-significant effect on the percentage of therophytes across islands. This may be because the early and short-season phenology of this species (rosette production in late autumn and senescence in early spring) limits competition with annuals, which have a peak in abundance slightly delayed in time.

### Limited impact on soil properties

Although invader-driven changes in diversity and composition of species may consequently lead to changes in soil properties, the interspecific differences in invader impacts on vegetation were not concordant with changes in the soil. Furthermore, changes in soil properties were less evident than changes in vegetation structure. *Ailanthus* had the broadest impact on soil properties. *Ailanthus*, which produces herbicidal litter, appeared to have the capacity to alter soil C and N cycling, which resulted in a reduction of the C/N ratio.

The increased organic C, as well as the more acid soils associated with *Carpobrotus*, is consistent with the considerable litter produced by this species. However, the low but contrasted percentage C effects of *Carpobrotus* according to island indicate that this species has variable effects on C cycling, probably related to taxonomic identity, habitat, mat age and thickness. In addition, *Carpobrotus* leaves also have high contents of tannin and antibacterial compounds (Van der Watt & Pretorius, 2001), which may reduce the rate of litter decomposition.

Finally, *Oxalis* had no marked effect on N and C cycling. The lower impact of this species compared with *Ailanthus* and *Carpobrotus* might be related to their lower biomass and shorter temporal soil occupancy. *Oxalis* is a small plant, rosettes of which decompose rapidly each year, and has higher mineralization rates compared with other co-existing annual



species (Petsikos *et al.*, 2004), which suggests that this species is poor in lignin. This may explain why no change was observed in soil properties, except for the increased acidification of the soil as a result of exudation and/or release of oxalic acid, one of the strongest organic acids from plant tissues (Lane, 1984).

## CONCLUSIONS

Contrary to the assumption of strong biotic resistance to the impacts of invasion in the Mediterranean Basin (Di Castri, 1990; Quézel *et al.*, 1990), this study highlights significant impacts on native plants and soil properties arising from invasive plants. At a 2 × 2-m plot scale, species loss averaged 23%, but varied greatly depending on the identity of the invader and the island. No distinct biogeographical impact pattern in species loss was found, indicating that all islands are similarly susceptible. Of particular concern was the fact that the higher the species richness, the larger the RI in species loss. Therophytes appear to be a life-form group especially susceptible to plant invasion.

Species loss was highest in areas invaded by *Carpobrotus* and lowest in areas invaded by *Oxalis*. The habitats invaded by *Carpobrotus*, such as dunes, rocky cliffs and coastal garrigues, encompass a high number of endemic, rare or vulnerable species (Médail & Verlaque, 1997; Verlaque *et al.*, 2001), thus the consequence of *Carpobrotus* spp. spread on native species is of particular concern. *Ailanthus* and *Oxalis* occur in anthropogenic and ruderal habitats, and it has been suggested that in such habitats impacts of invasion are low due to the lesser role of competition in community structure (Williamson & Fitter, 1996; Meiners *et al.*, 2001). Although, in general, ruderal communities are not perceived as having high conservation value, a unique element of Mediterranean biodiversity is represented in ruderal and disturbed habitats. Many endemic and vulnerable segetal plants occur in these habitats, and could represent the elements of the Mediterranean flora most at risk from invasions (Heywood, 1995; Verlaque *et al.*, 2001).

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## REFERENCES

- Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, **85**, 2682–2686.
- Daniel, W.W. (1990) *Applied non-parametric statistics*. PWS-KENT, Boston.
- D'Antonio, C.M. & Mahall, B.E. (1991) Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany*, **78**, 885–894.
- De Feo, V., De Martino, L., Quaranta, E. & Pizza, C. (2003) Isolation of phytotoxic compounds from Tree-of-Heaven (*Ailanthus altissima* Swingle). *Journal of Agriculture, Food and Chemistry*, **51**, 1177–1180.
- 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, Dordrecht.
- Draper, D., Rosselló-Graell, A., Garcia, C., Tauleigne-Gomes, C. & Sérgio, C. (2003) Application of GIS in plant conservation programmes in Portugal. *Biological Conservation*, **113**, 337–349.
- Ehrenfeld, J.G. (2003) Effect of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.
- Elton, C.S. (1958) *The ecology of invasions*. Methuen, London.
- Galil, J. (1968) Vegetative dispersal in *Oxalis pes-caprae*. *American Journal of Botany*, **55**, 68–73.
- Gilbert, B. & Lechowicz, M.J. (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology*, **86**, 1848–1855.
- Goldberg, D.E., Rajaniemi, J., Gurevich, J. & Stewart-Oaten, A. (1999) Empirical approach to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.
- Harper, J.L. (1977) *Population biology of plants*. Academic Press, London.
- Heisey, R.M. (1990) Allelopathic and herbicidal effects of extracts from tree of heaven (*Ailanthus altissima*). *American Journal of Botany*, **77**, 662–670.
- Heywood, V.H. (1995) The Mediterranean flora in the context of world biodiversity. *Ecologia Mediterranea*, **21**, 11–18.
- Hu, S.Y. (1979) *Ailanthus*. *Arnoldia*, **39**, 29–50.
- Hulme, P. (2004) Islands, invasions and impacts: a Mediterranean perspective. *Island ecology* (ed. by J.M. Fernández-Palacios and C. Morici), pp. 359–384. Asociación Española de Ecología Terrestre and Excmo. Cabildo Insular de la Palma, Tenerife.
- Klute, A. (ed.) (1986) *Agronomy. Methods of soil analysis*. American Society of Agronomy, Soil Science Society of America, Madison.
- Kowarik, I. (1995) Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *Journal of Vegetation Science*, **6**, 853–856.
- Lane, K. (1984) Factors affecting the development of populations of *Oxalis pes-caprae* L. *Weed Research*, **24**, 219–225.



- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavelle, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London B*, **270**, 775–781.
- Libert, B. & Franceschi, V.R. (1987) Oxalate in crop plants. *Journal of Agriculture, Food and Chemistry*, **35**, 926–938.
- 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 & Biogeography*, **13**, 37–45.
- Médail, F. & Verlaque, R. (1997) Ecological characteristics and rarity of endemic plants from southeast France and Corsica: implications for biodiversity conservation. *Biological Conservation*, **80**, 269–281.
- Meiners, S.J., Steward, T., Pickett, A. & Cadenasso, M.L. (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography*, **24**, 633–644.
- Pauchard, A., Cavieres, L.A. & Bustamante, R.O. (2004) Comparing alien plant invasions among regions with similar climates: where to from here? *Diversity and Distributions*, **10**, 371–375.
- Peirce, J.R. (1997) The biology of Australian weeds: 31. *Oxalis pes-caprae* L. *Plant Protection Quarterly*, **12**, 110–119.
- Petsikos, C., Dalias, P. & Troumbis, A. (2004) Effects of *Oxalis pes-caprae* L. invasion on diversity and carbon cycle in the grassland understory of a Mediterranean olive grove. *Proceedings of the 10th International Conference on Mediterranean Climate Ecosystems (MEDECOS X)* (ed. by M. Ananoutsou and V. Papanatis), p. 144. Millpress Publications, The Netherlands.
- Quézel, P., Barbero, M., Bonin, G. & Loisel, R. (1990) Recent plant invasions in the Circum-Mediterranean region. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. Di Castri, A.J. Hansen and M. Debussche), pp. 51–60. Kluwer Academic, Dordrecht.
- Raunkiaer, C. (1934) *The life-forms of plants and statistical plant geography*. Clarendon Press, Oxford.
- Rottenberg, A. & Parker, J.S. (2004) Asexual populations of the invasive weed *Oxalis pes-caprae* are genetically variable. *Proceedings of the Royal Society of London B*, **271**, S206–S208.
- Sala, O.E., Chapin, F.S.I., Arnesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- SAS (2001) *PROC GLM in SAS*. SAS Institute, Cary, NC, USA.
- 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.
- 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 Monographs*, **69**, 25–46.
- Suehs, C.M., Affre, L. & Médail, F. (2004a) Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. *Heredity*, **92**, 31–40.
- Suehs, C.M., Affre, L. & Médail, F. (2004b) Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: II. Reproductive strategies. *Heredity*, **92**, 550–556.
- Van der Watt, E. & Pretorius, J.C. (2001) Purification and identification of active antibacterial components in *Carpobrotus edulis* L. *Journal of Ethnopharmacology*, **76**, 87–91.
- Verlaque, R., Médail, F. & Aboucaya, A. (2001) Valeur prédictive des types biologiques pour la conservation de la flore méditerranéenne. *Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Vie*, **324**, 1157–1165.
- Vilà, M. & D'Antonio, C.M. (1998) Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in coastal California. *Ecological Applications*, **8**, 1196–1205.
- Wearne, L.J. & Morgan, J.W. (2004) Community-level changes in Australian subalpine vegetation following invasion by the non-native shrub *Cytisus scoparius*. *Journal of Vegetation Science*, **15**, 595–604.
- Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.
- Wisura, W. & Glen, H.F. (1993) The South African species of *Carpobrotus* (Mesembryanthema – Aizoaceae). *Contributions to the Bolus Herbarium*, **15**, 76–107.
- Woods, K.D. (1993) Effects of invasion by *Lonicera tatanica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist*, **130**, 62–74.
- Zar, H. (1984) *Biostatistical analysis*. Prentice Hall, New York.

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