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ORIGINAL PAPER

Consistent performance of invasive plant species within and among islands of the Mediterranean basin

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Abstract Since the success of an invasive species depends not only upon its intrinsic traits but also on particular characteristics of the recipient habitat, assessing the performance of an invader across habitats provides a more realistic analysis of risk. Such an analysis will not only provide insights into the traits related to invasiveness, but also the habitat characteristics that underpin vulnerability to invasion that, taken together, will facilitate the selection of management strategies to mitigate the invader's effect. In the present study, we considered the Mediterranean basin islands as an excellent study region to test how the same invasive species perform in different habitats within a single island, and to scale up differences among islands with similar climate. We tested how the performance of three widespread plant invaders with clonal growth but contrasting life-history traits, a deciduous tree *Ailanthus altissima*, a succulent subshrub *Carpobrotus* spp., and an annual geophyte *Oxalis pes-caprae*, varied depending upon the species identity, habitat, and invaded island. The environmental parameters considered were habitat type, elevation, species diversity in the invaded plot, and several soil traits (% C, % N, C/N, pH, and relative humidity). The study documents that the performance of these three important and widespread plant invaders is dependent mainly on species identity, and less upon the invaded island's general features. Likewise, differences in performance among habitats were only significant in the case of *Ailanthus*, whereas *Carpobrotus* and *Oxalis* appear to perform

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equally well in different environments. *Ailanthus* thus appears to have a broader spectrum of invasiveness, being able to invade a larger number of habitat types. On the contrary, *Carpobrotus* spp. have not yet invaded habitats different from those where the species have been originally introduced and where they are still commonly spread by humans. *Oxalis* distribution is mainly related to agricultural activities and disturbed sites, and the total area infested by this geophyte may be more reflection of the extent of suitable habitats than of invasiveness or ecological impact. Our results confirm the potential for these species to significantly alter the functioning of ecosystems in the Mediterranean islands and highlight the risk to other islands not yet invaded.

Keywords Alien plants · *Ailanthus altissima* · *Carpobrotus* spp. · Habitat variation · Mediterranean ecosystems · *Oxalis pes-caprae* · Plant invaders

Introduction

Global biodiversity scenarios predict that Mediterranean ecosystems may experience proportionally more dramatic increases in biological invasions than other ecosystems (Sala et al. 2000). Mediterranean islands, in particular, are especially vulnerable to such invasions mainly because of the intrinsic traits of many island biotas (Hulme et al. 2007 and references therein). As a consequence, the relatively high proportion of alien species, especially plants, compared to neighboring mainland areas undoubtedly place additional pressures upon the threatened status of many island endemics (Hulme 2004). Nevertheless, there are still few detailed studies assessing the risk that plant invaders represent to these unique ecosystems (but see Lloret et al. 2004; Gritti et al. 2006; Lambdon and Hulme 2006a; Vilà et al. 2006a; Hulme et al. 2007). In addition, invasions are not independent of the other drivers of change in Mediterranean ecosystems which include land use change (particularly the expansion of urban areas and associated infrastructures), rising CO_2 levels, warmer temperatures, greater nitrogen deposition, altered disturbance regimes, and increased habitat fragmentation (Dukes and Mooney 1999; Sala et al. 2000; Hulme 2006). Such drivers can interact and potentially enhance biological invasions (Vilà et al. 2006b and references therein). Recent models actually predict that, under the worst-case scenario, almost all Mediterranean habitats may become vulnerable to alien plants (Gritti et al. 2006).

The success of an invasive species is in part dependent on particular characteristics of the recipient region or invaded habitat types (Emery and Gross 2007; Funk and Vitousek 2007). Moreover, characteristics important in the invasion of one habitat can be irrelevant in another (Pyšek et al. 1995; Lloret et al. 2005; Lambdon and Hulme 2006b; Thomsen and D'Antonio 2007). Therefore, any realistic assessment of risk of invasion, invader performance, impact, and management options should be based on information gathered within its broad distributional range and the different habitats susceptible of invasion. Such an analysis will not only provide insights into the traits related to invasiveness but also into the habitat characteristics that underpin vulnerability to invasion that, taken together, will facilitate the selection of management strategies to mitigate the invader's effect (Hulme 2006). Assessing these trends at both local and regional spatial scales will help identify whether general management strategies are adequate or if a case-by-case approach is needed (Hulme 2003; Lloret et al. 2004; Pauchard and Shea 2006).

In the present study, we focused on three widespread plant invaders considered as serious pests in Mediterranean regions of the world, which are widely distributed throughout the Mediterranean Basin (Quézel et al. 1990; Hulme 2004; Vilà et al. 2004). We examined both the performance of the species and the attributes of the invaded habitat to disentangle the relationship between invasiveness and invasibility. To ensure our results were robust, we considered a range of islands across the Mediterranean basin in order to scale up from local island effects to regional performance. To our knowledge this is the first study to attempt such an approach for any global region. The study is a companion paper to Vilà et al. (2006a), the objective of which was to evaluate the impact, rather than the performance, of plant invaders on vegetation structure and soil properties. Our specific questions were: (1) Do focal species perform similarly across the Mediterranean region covered by the study islands? (2) Does species' local performance depend upon the habitats in which they grow?, and (3) What environmental variables influence species performance at regional and local scales?

Material and methods

Study taxa

In the Mediterranean invaded range, the three studied focal species have a remarkable prevalence of clonal growth but contrasting life-history traits: a deciduous tree *Ailanthus altissima*, a succulent subshrub *Carpobrotus* spp., and an annual geophyte *Oxalis pes-caprae*. Only *Ailanthus* and *Carpobrotus* are capable of sexual reproduction and propagation by seeds in the Mediterranean invaded range (Vilà et al. 2006a), yet all three focal species exhibit marked capacity for local vegetative spread. Therefore, in the following text, the populations of these three invaders will be described as clones, representing single genets. Generally speaking, clonality is widespread in plants. In the temperate zone, 65–70% of the vascular plants species are clonal (Svensson et al. 2005; Honnay and Bossuy 2005). Clonality may also be a relevant trait, especially for population maintenance, for a few cosmopolitan or other invasive taxa (Pyšek and Richardson 2007; Richardson et al. 2007).

Ailanthus altissima (P. Miller) Swingle (Simaroubaceae) is a fast-growing deciduous tree 8–10 m high, native to China and North Vietnam but widely planted in Europe as an ornamental since the 18th century. It was introduced earlier in the continental Europe and later on the islands, e.g., in Menorca in 1901, Sardinia in 1908, Crete in 1910, and Corsica in 1931. It is currently an invasive species in all continents except Antarctica. It has wind-dispersed seeds (samaras) and it also strongly resprouts, developing root networks that form dense clonal stands (Kowarik 1995; Kowarik and Säumel 2007). In its introduced range, it is best known for its fast occupation of highly disturbed sites (Call and Nilsen 2003), but is also capable of invading natural vegetation (Hadjikyriakou and Hadjisterkotis 2002), especially flood plain vegetation, rocky outcrops or other similarly open habitats.

Carpobrotus spp. L. (Aizoaceae) are robust, scrambling, mat-forming succulents native to the Cape Region (South Africa) which invade coastal areas around the world (D'Antonio et al. 1993; Hulme et al. 2007, and references therein). *Carpobrotus* was introduced to Europe around 1680 and has since been planted as an ornamental and used to stabilize dunes and slopes. In Menorca it was introduced before 1824. In Corsica, this taxon has been present since at least 1877. *Carpobrotus* fruits are readily eaten by small mammals, and the seeds dispersed by endozoochory (Bourgeois et al. 2005). The fleshy, thick leaves allow this taxon to robustly resist drought and saline conditions. Small branches can also be dispersed to short distances and subsequently root and produce new individuals. The high stolon elongation rate (c. 40 cm/year) and branching rate allow the species to rapidly occupy the space (Sintes et al. 2007). This, together with the advantage of performing well in different light environments (Traveset et al. 2008), make *Carpobrotus* one of the most aggressive invaders in the Mediterranean area.

Oxalis pes-caprae L. (Oxalidaceae), also a native of the Cape Region and currently widespread throughout the Mediterranean Basin and North Africa, is a functionally sterile though genetically diverse, tender geophyte (Rottenberg and Parker 2004), up to 30 cm in height that rarely produces seeds. Instead, it reproduces via the production of small (2 mm to 2 cm in diameter) underground bulbs dispersed up to 47 cm by subterranean contractile roots (Pütz 1994). Further dispersal often occurs by ploughing, adhesion to vehicle tires or livestock hooves, and any other means of soil movement such as earthworks and road construction (Gimeno et al. 2006). This agricultural invader, especially abundant in cultivated or abandoned fields and in roadsides, arrived in Europe during the 19th century. We know that it was present in Corsica by 1833, and that it was introduced to Crete in 1880 and to Menorca in 1904. It produces oxalates that are toxic to livestock in large quantities (Libert and Franceschi 1987). A high spatial concordance between recruitment stages and a high propagule pressure due to human and livestock bulb dispersal appears to determine the success of this invader, at least in some areas (Vilà et al. 2006c).

These three taxa are hereafter collectively referred to as the invader, or individually referred to by genus.

Study islands and field survey

The performance of the three invaders was assessed on eight islands, which were chosen as representative in terms of range of island size, isolation, and geographic distribution along an east-west gradient: Crete and Lesbos in the Aegean archipelago of Greece, Sardinia in Italy, Corsica and the Hyères Archipelago (i.e., Bagaud and Porquerolles) in France, as well as Mallorca and Menorca in Spain (Fig. 1). Selection of these islands was also based on researcher affiliation and expertise. Basic geographic parameters of the study islands as well as the number of plots monitored per invader in each island are given in Table 1.

Assessments took place between 2001 and 2003 on all islands. For each of the three invaders, we randomly selected plots (clones) encompassing representative habitats where they are usually established. In the case of *Ailanthus*, the habitats were: roadsides, orchards/vineyards/olive groves, oldfields, shrublands/forests, and temporary streams. As remarked above, *Ailanthus* is also commonly found in urban and urbanized environments throughout its European invaded range (see Kowarik and Säumel 2007) including Mediterranean islands (Hulme et al. 2007). Nevertheless, we did not take these habitat types into account, and instead focused on natural or seminatural habitat types, with the exception of roadsides, which were considered as important networks promoting invasion and therefore worth monitoring. For *Carpobrotus*, we compared plots in sand dunes with those on the rocky shore. Lastly, for *Oxalis*, we compared: roadsides, vineyards/olive groves, oldfields, and shrublands/forests. Plots were separated by at least 1 km, although they were usually much further apart. Most of these plots correspond to the 'invaded' plots that were compared with nearby non-invaded plots in the related impact study (Vilà et al. 2006a). Although the initial purpose was to monitor 30 plots per island and species, this was not possible as many plots were destroyed during the course of the study, or simply because finding suitable sites for assessments was not possible for other logistical reasons. For instance, *Carpobrotus* is only a casual taxon in Lesbos, whereas *Ailanthus* is nearly absent in Porquerolles and in Bagaud, and thus these species were not studied in those islands.

For each chosen plot in each island, we recorded performance variables related to clone size, clone density, fecundity, shoot growth rate (in *Ailanthus* and *Carpobrotus*), flower density (*Carpobrotus*), and bulb density (*Oxalis*; Table 2). To record shoot growth rate (cm/month), we marked five shoots in each *Ailanthus* clone and one branch in each *Carpobrotus* clone during Spring–Summer 2002 and measured their elongation during the following year. From each plot, we recorded the following environmental parameters: habitat type, elevation, % organic C and % N in soil, C/N, soil pH, and species richness. Soil samples were collected at random from three different subplots within each clone and subsequently pooled for each clone. Soil analyses were carried out following the methods described in Vilà et al. (2006a). Species richness was obtained by recording the number of plant species in 2 × 2 m plots centred on the clones of each invader (see also details on vegetation surveys in Vilà et al. 2006a).

We used Gini's coefficient as a measure of dissimilarity of frequencies of stems in different size categories. We categorized the diameter at breast height (DBH), i.e., measured at approximately 130 cm above the ground (see, e.g., Avery and Burkhart 2002) of each stem in each of the following groups: <5 cm, 5–10 cm, 10–15 cm, and so on up to >50 cm.

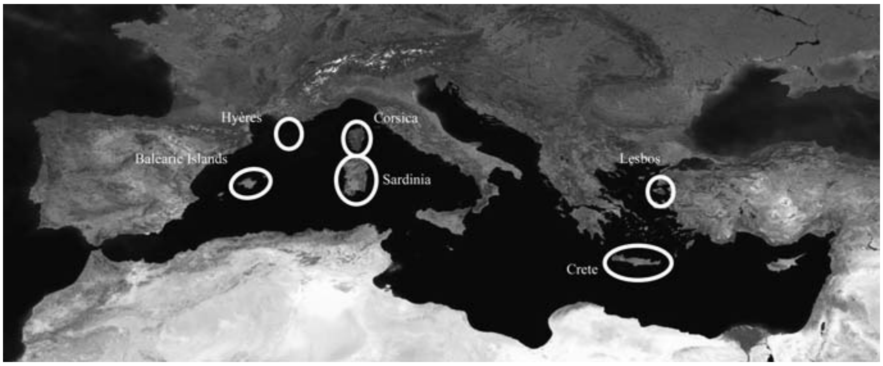

Fig. 1 Map of the Mediterranean basin showing the islands in which the study was carried out

Table 1 Basic geographical and climatological parameters of the different Mediterranean islands studied and the number of study plots (clones) of each species examined in each

Island (country)	Area (km^2)	Distance from nearest mainland (km)	Longitude	Latitude	Annual rainfall (mm)	Mean *T*, January (°C)	Mean *T*, July (°C)	*Carpobrotus*	*Ailanthus*	*Oxalis*
Mallorca (Spain)	3656	170	2°54′	39°35′	304.3	10.2	24.6	25	28	30
Menorca (Spain)	702	200	4°13′	39°51′	457.2	11.9	25.3	23	19	24
Bagaud (France)	6	8	6°21′	43°00′	521.5	8.0	24.4	13	0	0
Porquerolles (France)	12	2	6°13′	43°00′	521.5	8.0	24.4	20	0	24
Corsica (France)	8682	82	9°15′	42°25′	606.7	9.2	22.3	0	29	0
Sardinia (Italy)	24,090	230	9°35′	40°54′	600–800[a]	10.1	25.3	30	30	30
Crete (Greece)	8700	100	26°25′	30°15′	647.0	12.2	26.1	14	14	10
Lesbos (Greece)	1632	18	26°35′	39°15′	289.1	8.7	27.7	0	41[b]	30

Note that not all three species were studied on all islands

[a] From 430 to 1400 mm/year from the coast to inner mountainous area, so this is an average indicative value

[b] Environmental variables could not be obtained in this island, so these clones were not included in the generalized linear mixed models (GLMM), although they were used in some of the correlation analyses

Table 2 List of performance variables measured for each invader species

Variable	*Ailanthus*	*Carpobrotus*	*Oxalis*
Size	Clone area[a]	Clone area[a]	Clone area[a]
Density	No. of clones in a 25 m radius (clone density)	No. of clones in a 25 m radius (clone density)	*Oxalis* plant cover in a 4 m^2 quadrat (estimated to the closest 5%)
Growth	Total no. of stems	Annual horizontal growth rate of adventive shoots[b]	No. of emerging plants in a 40 cm^2 quadrat
Growth	DBH of largest stem		
Growth	Sprout annual vertical growth rate[c]		
Reproduction	Seed production of largest stem in clone		
Reproduction	No. of fruiting stems	No. of flowers in a 4 m^2 quadrat	No. of viable bulbs in a 40 cm^2 quadrat

[a] For each clone, we obtained the maximum distance from the center to the edge as well as the perpendicular distance from the center, adjusting the area to an ellipse

[b] One adventive shoot was randomly chosen and marked from each clone and measured after 12–15 months

[c] Averaged from five sprouts per clone, measured at the time of marking and after 12–14 months

DBH, diameter at breast height

Statistical analysis

For each focal species, we used generalized linear mixed models (GLMMs) to test for differences across islands and among habitats in the performance variables. While habitat was included as a fixed effect, island was considered a random factor in all analyses. In this sense, we attempted to say something about a wider set of Mediterranean islands, beyond the particular sample of islands considered in the study. The island × habitat interaction was not included in the models as habitat varied within islands (see results). The predictor variables included in the models (a separate one for each plant species) were habitat type, elevation, species richness, pH, and % organic C and % N in soil. The response variables, considered as indicators of local invasive success, were: clone area, clone density, shoot growth rate (in the case of *Ailanthus* and *Carpobrotus*), density of flowers (*Carpobrotus*), and density of emerging plants (*Oxalis*). The GLMMs were performed by using the GLIMMIX macro of the MIX procedure in SAS (v. 9.0) statistical package (Littell et al. 1996) whereas all other analyses were carried out with STATISTICA (v. 6.0). Means are accompanied by their standard errors unless otherwise stated.

Results

Ailanthus performance

The size of *Ailanthus* clones did not differ among islands (Table 3). However, a significant effect of habitat type was found, with temporary streams having a smaller average clone size than those in oldfields and roadsides (Fig. 2a). Also, clones were significantly larger at lower elevations, and larger clones were positively associated with higher N contents in the soil, though only marginally (Table 3). In a separate analysis, we found that islands did not differ significantly either in elevation or % soil N ($Z = 1.30$, $P = 0.10$, and $Z = 1.19$, $P = 0.12$, respectively) and that there was no interaction between these two factors ($Z = 0.81$, $P = 0.21$). Likewise, these two response variables did not differ among habitats ($F_{4,6} = 1.49$, $P = 0.32$ and $F_{4,7} = 2.30$, $P = 0.16$, respectively), and their interaction was again nonsignificant ($Z = 0.52$, $P = 0.30$); these variables are therefore not responsible for differences in clone size among habitats. Clone area was shown to be independent of pH, % organic C in soil, and species richness (Table 3). When we included C/N ratio in the model instead of % organic C and N, the results did not change (data not given).

The density of *Ailanthus* clones in any one habitat was also similar among islands, but differences among habitats were significant (Table 3; Fig. 2b); clones in shrublands/forests are usually less dense than in the other habitats. Clone density does not appear to be associated with either elevation, species richness, or any of the measured soil properties (Table 3).

The growth rate of *Ailanthus* shoots was similar in the three islands where comparisons were possible (Table 3), but also was dependent upon habitat where the clone grows, being higher in temporary streams than elsewhere (Fig. 2c). Shoot growth rate was positively associated, though nonsignificantly, with N contents in soil whereas it was independent of elevation, soil pH, % organic C, C/N ratio or species richness in the clone (Table 3).

Larger clones tended to bear thicker stems, as would be expected if clone area is related to clone age ($r = 0.35$, $P < 0.0001$, $N = 159$; Fig. 3a). Nevertheless, the thickest stems (DBH >50 cm) were found in Crete despite this island not having the largest *Ailanthus* clones (Fig. 2a). Larger clones also had more heterogeneous stem size distributions, as shown by the positive correlation between Gini's coefficient and total number of stems per clone ($r_s = 0.20$, $P = 0.02$, $N = 137$). Clones with fruiting stems (i.e., with fertile female flowers) and nonfertile clones (presumably with male flowers or hermaphrodite sterile flowers, as they did not produce any seed during the two monitoring years) were similar in size ($F_{1,130} = 2.36$, $P = 0.13$), but the former were significantly denser that the latter (2.43 ± 0.20, $N = 65$ versus 1.76 ± 0.14, $N = 71$, respectively; $F_{1,131} = 14.5$, $P = 0.0002$). Stems with higher DBH (presumably older) tend to produce higher seed crops, although the correlation is not strong ($r = 0.33$, $P = 0.01$, $N = 58$ females); moreover, the most fecund stems are not always found in the largest clones ($r = 0.14$, $P = 0.28$, $N = 58$; Fig. 3b). Up to 350,000 seeds were recorded for an individual *Ailanthus* stem.

Table 3 Results of the GLIMMIX models used to test for the effect of the different predictor variables for each focal species

Species	Predictor variable	Clone area			Clone density (Ai and Ca)			Shoot growth rate (Ai and Ca)			Flower density (Ca)		
					Plant cover (Ox)			N emerging plants (Ox)			N viable bulbs (Ox)		
		df	*Z* or *F* value	*P*	df	*Z* or *F* value	*P*	df	*Z* or *F* value	*P*	df	*Z* or *F* value	*P*
Ailanthus	Island	4, 70	1.24	0.108	4, 70	0.97	0.166	2, 20	0.55	0.293	–	–	–
	Habitat	4, 70	3.05	*0.022*	4, 70	3.23	*0.017*	2, 20	4.68	*0.022*	–	–	–
	Altitude	1, 70	8.73	*0.004*	1, 70	2.7	0.105	1, 20	0.28	0.603	–	–	–
	Soil pH	1, 70	0.82	0.369	1, 70	0.34	0.561	1, 20	1.54	0.229	–	–	–
	% organic C	1, 70	1.63	0.206	1, 70	0.02	0.893	1, 20	0.55	0.466	–	–	–
	[N] in soil	1, 70	3.75	*0.057*	1, 70	0.07	0.787	1, 20	3.66	*0.07*	–	–	–
	Species richness	1, 70	0.14	0.714	1, 70	1.98	0.163	1, 20	0.08	0.783	–	–	–
Carpobrotus	Island	3, 66	0.79	0.214	3, 66	1.12	0.132	3, 35	0.75	0.225	3, 54	0.22	0.412
	Habitat	1, 66	0.39	0.535	1, 66	0.95	0.333	1, 35	2.44	0.127	1, 54	2.35	0.131
	Altitude	1, 66	2.24	0.14	1, 66	0.5	0.482	1, 35	0.03	0.86	1, 54	0.75	0.39
	Soil pH	1, 66	0.86	0.356	1, 66	1.84	0.18	1, 35	0.96	0.334	1, 54	9.9	*0.003*
	% organic C	1, 66	1.06	0.307	1, 66	1.98	0.164	1, 35	0.59	0.448	1, 54	3.51	*0.067*
	[N] in soil	1, 66	0.5	0.483	1, 66	7.37	*0.009*	1, 35	0.27	0.606	1, 54	4.72	*0.034*
	Species richness	1, 66	3.78	*0.056*	1, 66	1.24	0.269	1, 35	0.17	0.68	1, 54	0.46	0.503
Oxalis	Island	4, 82	1.3	0.097	4, 83	0.54	0.294	4, 76	0.93	0.175	–	–	–
	Habitat	3, 82	0.33	0.801	3, 83	1.77	0.158	3, 76	0.62	0.603	3, 44	0.39	0.76
	Altitude	1, 82	1.4	0.24	1, 83	0.14	0.707	1, 76	0.54	0.465	1, 44	1.2	0.278
	Soil pH	1, 82	3.96	*0.05*	1, 83	0.21	0.647	1, 76	0.03	0.857	1, 44	2.59	0.115
	% organic C	1, 82	0.58	0.45	1, 83	0.19	0.663	1, 76	7.72	*0.007*	1, 44	0.81	0.372
	[N] in soil	1, 82	0.49	0.487	1, 83	1.91	0.171	1, 76	7.08	*0.01*	1, 44	0.33	0.57
	Species richness	1, 82	8.38	*0.005*	1, 83	7.67	0.007	1, 76	5.41	*0.023*	1, 44	0.97	0.33

Significant or marginally significant *P* values are shown in *italics*. Ai: *Ailanthus*, Ca: *Carpobrotus*, Ox: *Oxalis*

Carpobrotus performance

As for *Ailanthus*, clones of *Carpobrotus* did not differ in size either among islands or between the two habitats where they are usually found (Table 3; Fig. 4a). There was no significant association between clone area and any of the environmental variables measured, although larger clones showed marginally lower species richness (Table 3). When we included the ratio C/N in the model instead of % C and N, results were not significantly altered. Although mean density of clones was higher in the French islands Bagaud and Porquerolles (Fig. 4b), the high intra-island variation in these islands masked differences with the rest of islands (Table 3). Likewise, density of clones was similar in dunes as in rocky shores, and was positively associated to N levels in the soil (Table 3). The ratio C/N, however, had a nonsignificant effect on clone density (all $P \gg 0.05$).

Consistent with results for clone area, growth rate of *Carpobrotus* adventive shoots did not differ either among islands or habitats (Table 3; Fig. 4c). Shoot growth rate was not associated with any other variable measured. The density of flowers per clone was also similar among islands and among habitats (Table 3), although significant correlations with environmental parameters were found. Specifically, flower density was negatively associated with soil pH, positively associated with N levels and C/N ratio ($F_{1,54} = 4.33$, $P = 0.04$), and only marginally, with organic C levels (Table 3).

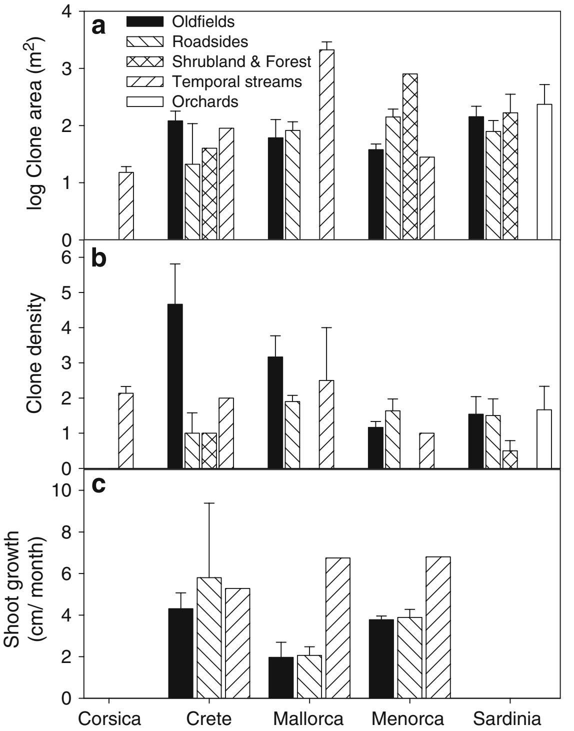

Fig. 2 Mean and standard error of *Ailanthus* (**a**) clone area, (**b**) clone density (number of clones within a 25 m radius), and (**c**) mean growth rate of five randomly chosen sprouts per clone, measured in different habitats of the study islands. Lesbos is not included in the graph as the variable habitat was not considered in this island. In each island, *Ailanthus* plots were monitored only from those habitats in which this species was frequent

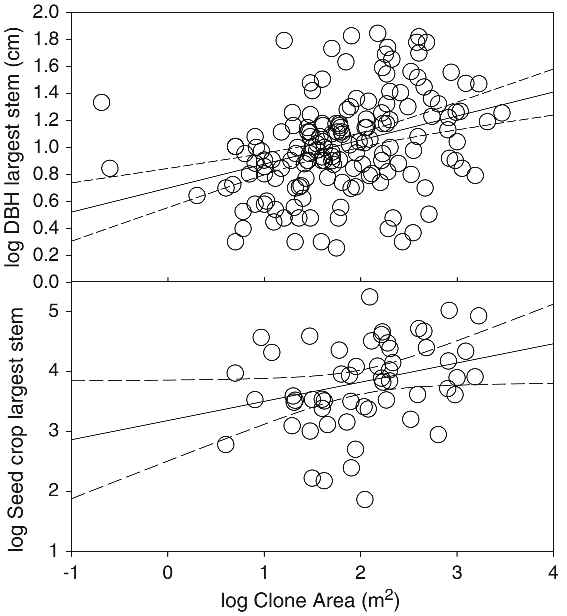

Fig. 3 Relationship between *Ailanthus* clone area and (**a**) DBH of the largest stem and (**b**) seed crop of the largest stem across all habitats and islands studied

Oxalis performance

Clone size of *Oxalis* was similar across islands (Table 3), although those on Crete tended to be the largest. In this island, some clones (or populations of clones, as for this species it was sometimes hard to know the limits of a single clone) extend for several kilometers (Fig. 5). No effect of habitat was detected, and the only soil property associated with clone size was pH (Table 3), larger clones occurring on more acidic soils. Clone size was highly and negatively associated with species richness (Table 3). Regarding plant cover and density of emerging plants, neither of these variables differed among islands. Both were negatively associated with species richness (Table 3). Density of emerging plants was positively associated with soil organic C and N contents (Table 3), although not with the C/N ratio, ($F_{1,78} = 0.59$, $P = 0.44$). Neither soil organic C nor N contents differed among islands ($Z = 0.54$, $P = 0.29$ and $Z = 0.93$, $P = 0.17$, respectively) or among habitats ($F_{3,83} = 1.77$, $P = 0.16$ and $F_{3,76} = 0.62$, $P = 0.60$, respectively). Finally, the number of viable bulbs (in 40 cm^2) was not associated to any of the predictor variables included in the model (Table 3).

Discussion

Invasive performance of the three studied invaders, measured in terms of clone size and clone density, is similar across islands, although *Oxalis* clones are often much larger in Crete. This suggests that the different Mediterranean islands are similarly susceptible to the invasion by the three species, and that the establishment success within each island is more likely to depend upon the frequency and availability of suitable habitats for each invader. This low variability in performance might indeed be an important feature of invasive species in general, although further studies are needed to confirm this. Our findings reveal that habitat is a relevant predictor of clone size for at least one species, *Ailanthus*. Despite showing a higher resprout growth rate in temporary streams (possibly due to higher water

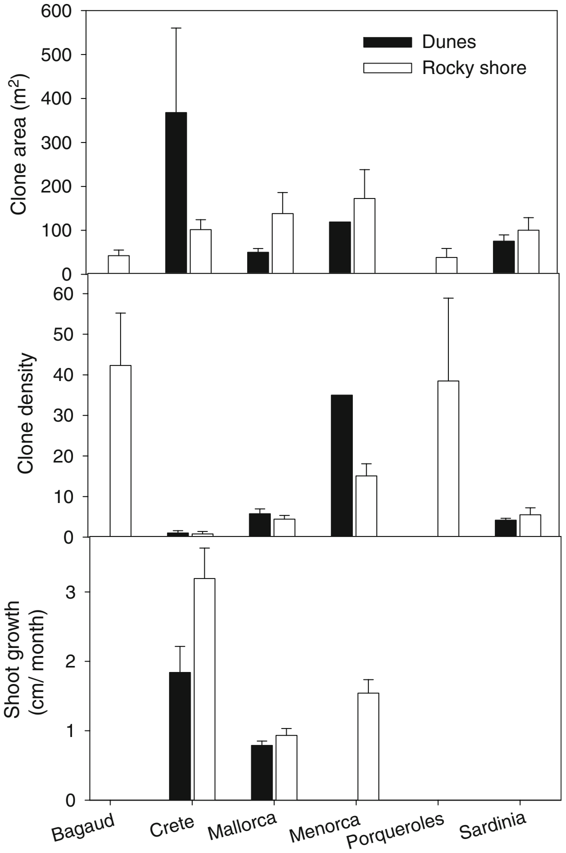

Fig. 4 Mean and standard error of *Carpobrotus* (**a**) clone area, (**b**) clone density (number of clones within a 25 m^2 radius), and (**c**) growth rate of a randomly chosen adventive shoot per clone, measured in the two habitats where this species is usually found in the study islands. Neither Bagaud nor Porquerolles (in the Hyères Archipelago) have dune systems, which is why *Carpobrotus* is only found in the rocky coast habitat in these two islands

availability), clones are smaller in this habitat than in others where the species is usually found, such as roadsides or oldfields. Possible explanations for these results might be: (1) a more recent colonization of these natural areas, (2) a more frequent disturbance events, and/or (3) greater interspecific competition with other plants (trees) that live in these habitats. In fact, riparian habitats and temporary stream vegetation communities in Mediterranean islands are often characterized by a significant exotic plant community, including many neophytes and archeophytes, such as *Arundo donax*. Density of *Ailanthus* clones is lower in shrublands/forests than in more disturbed areas, which suggests a greater resistance of the later seral stages of plant succession to invasion (Meiners et al. 2002). Kowarik (1995) reported a much slower ramet growth rate of this species within the forest than in the open. In the Mediterranean islands, clones of *Ailanthus* appear to be larger at lower elevations, suggesting that lower winter temperatures might constrain their expansion. At the same time, they could expand even more under the current conditions of increasingly warmer temperatures (Gritti et al. 2006). In parts of central Europe, warm climates have already been shown to favor the spread of *Ailanthus* (Kowarik and Samuel 2007). Although many of these reported patterns are correlative, and thus caution has to be applied when attributing cause and effect, it seems likely that the positive relationship between clone size and N levels in the soil could reflect a role of eutrophication on plant performance rather than an impact of this species on soil chemistry (Vilà et al. 2006a).

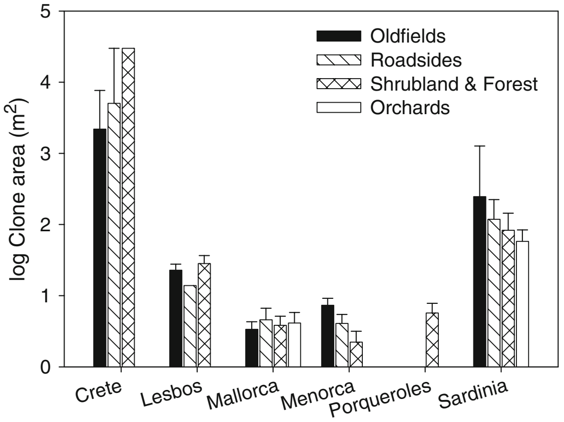

Fig. 5 Mean and standard error of the area of *Oxalis* clones in different habitats of the study islands

Fertile *Ailanthus* clones (with samara-bearing stems) were as large as nonfertile trees but the former were denser that the latter, which is probably related to the capacity of fertile clones to promote the establishment of new clones in the nearby area, for instance, along roadsides. A single *Ailanthus* tree can produce several hundred thousand seeds. Such high fertility combined with a high germination rate (unpublished data), an extensive vegetative spread, and the production of numerous suckers from the roots can certainly account for this species' marked invasiveness (Hulme 2004; Kowarik and Samuel 2007).

As in the case of *Ailanthus*, *Carpobrotus* clones did not vary in size at the regional (across islands) scale, and were found to perform similarly in dune systems and rocky shores. This result is consistent with the findings of a study on *Carpobrotus* growth patterns (Traveset et al. 2008); in such study, the growth rate of shoots, which can reach up to 40 cm/year, was found to be more dependent on microsite type than on habitat type. Density of *Carpobrotus* clones was also similar across islands, although those in the Hyères Archipelago were slightly denser than in the other islands, often extending to several kilometers similarly to the case of *Oxalis* in Crete. We do not know with certainty the reason for this but it might well be related to the high seed dispersal of this taxon in these islands by abundant rabbits and rats (Bourgeois et al. 2005).

The density of *Carpobrotus* flowers was highly associated with soil pH, being higher in more acidic soils. There is evidence that the decomposition of *Carpobrotus* litter strongly influences soil chemistry, particularly pH and soil organic C and N (Vilà et al. 2006a). The performance results suggest that where plant performance was high (e.g., flower density), soil impacts were also greatest.

The largest *Oxalis* clones were found in Crete, although there is no evidence (to our knowledge) showing that the introduction of this geophyte in that island was any earlier than in the other studied islands. Despite the observed slight difference in clone sizes, no notable differences were detected either at the regional scale or in different habitats within islands in any of the response variables related to the performance of this invader. However, as in the case of *Carpobrotus*, larger clones were associated with lower species richness as well as to lower soil pH. Likewise, plant cover and density of emerging plants were also associated with a lower number of plant species in the clone. These findings are again consistent with those of Vilà et al. (2006a), who report a significantly more acidic soil and a decrease in species richness in invaded plots by *Oxalis*, although with some differences across islands. In contrast to the impact study, however, a parameter describing species performance, such as density of emerging plants, was found to be associated to high levels of organic C and N in the soil. We cannot conclude whether this is because of the presence of the invader or because the greater nutrient levels enhance seedling growth.

In summary, this study documents that the performance of three widespread invasive plants is dependent mainly on the identity of the species, but not upon the invaded islands' general features, which is in contrast to the findings relating to their impacts (Vilà et al. 2006a). Likewise, differences in the performance among habitats were only significant in the case of *Ailanthus*, whereas *Carpobrotus* and *Oxalis* appear to perform equally well in different environments. *Ailanthus* is the species showing the broadest spectrum of invasiveness, being able to invade a large number of habitat types. *Carpobrotus* spp., so far, has not shifted to invade habitats diverse from those where it was originally introduced and where it is still commonly spread by human intervention. *Oxalis* distribution is mainly related to agricultural activities and disturbed sites. These findings may actually support the hypothesis that the total area infested may be more a reflection of the extent of suitable habitats than of invasiveness or ecological impact (Campbell 1997). This is especially true when a considerable time has elapsed since the first introduction. Nevertheless, our results also confirm the potential for these species to significantly alter the functioning of ecosystems in the Mediterranean islands, probably including also those islands not yet invaded. The island set may be regarded as representative of the main land use types and land cover categories of all the Mediterranean basin islands, and the performance traits are therefore predictors of what might occur in those islands that have not yet been invaded (Hulme et al. 2007).

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