

Consistency in the habitat degree of invasion for three invasive plant species across Mediterranean islands

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Abstract Habitats are known to vary in their vulnerability to invasion by alien plants and different species often colonise distinct habitats. To assess the consistency in the degree of invasion of particular habitats, this study examined the frequency of occurrence and local abundance of three invasive plant taxa: *Ailanthus altissima*, *Carpobrotus* spp., and *Oxalis pes-caprae* across different habitat types on

four representative Mediterranean islands. We conducted systematic field surveys recording the presence-absence and cover of these taxa on the islands of Mallorca, Corsica, Sardinia and Crete. Drawing on the results of 5,285 sample points, the frequency of occurrence of the three invaders tends to be higher than expected in urban, ruderal and roadside habitats. In contrast, scrub habitats rarely contain any of the three invaders, indicating that they may be more resistant to invasion. The degree of invasion, determined by the local abundance of an invasive plant in any one habitat, varies according to the identity of the invader and the island. However, based on average abundance, *Oxalis pes-caprae* exhibits the highest degree of invasion, and *Carpobrotus* spp. the least. There is no indication that any one of the four islands is more prone to either higher frequencies or abundances of the three invaders. These patterns suggest that anthropogenic changes in Mediterranean islands will increase the vulnerability of certain habitats to invasion and increase the distribution of these three invasive taxa at any of the four islands.

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Introduction

Islands are often perceived as highly vulnerable to the invasions of alien mammals and plants (Elton 1958;

Loope and Mueller-Dombois 1989; MacDonald and Cooper 1995). In contrast to the high profile impacts of mammals on islands that include extinction of endemic species (Courchamp et al. 2003), the consequences of alien plant invasions have recently been portrayed as comparatively benign (Sax and Gaines 2008). Although the proportion of island floras comprising alien species can be high, e.g., ~50% (Hulme 2004), there is scant evidence that native species have been lost from islands as a result of competition from alien species. This may, in part, be a consequence that alien plant driven extinctions occur over a much longer time scale than alien animal driven extinctions and that the major impact of alien plants on island biodiversity has yet to be realised. Alternatively, alien plant species may be largely restricted to human dominated habitats of islands and their impact on native communities, and hence the threat to endemics, might be limited.

Anthropogenic habitats tend to exhibit the highest levels of plant invasion across continental Europe, as a result of both higher disturbance and propagule pressure (Chytrý et al. 2009; Pyšek et al. *in press*). This pattern is expected to hold true for islands as well, and it is supported by studies examining islands and neighbouring continental areas (Gimeno et al. 2006). However, while human dominated habitats are more frequently invaded on both islands and continents, the range of habitats occupied by alien plants on islands has been found to be broader (Gimeno et al. 2006). This may indicate a potentially greater threat of invasive plants on islands. To assess such a threat we need to know the range of habitats invaded on islands, the proportion of available habitats occupied by invaders, and the average abundance of the invader in specific habitats.

In this context, the Mediterranean Basin is a good example of an island-rich, historical refuge zone of high conservation value. Estimates of local or regional endemism vary from 37.4 to 50%, with many of these plants being island or mountain top endemics (Heywood 1995; Andrés and Ojeda 2002). Furthermore, the fragile island habitats in the Mediterranean Basin have been associated with human intervention for thousands of years (Cody 1986) and are increasingly disrupted by ever-expanding urban development, tourism, and transport infrastructures (Médail and Quézel 1997; Hulme 2004), as well as

invasive plants that invariably accompany this process (e.g., Lloret et al. 2004).

To determine the vulnerability of different Mediterranean habitats to invasion, we conducted an extensive field survey of three “high risk” invasive plants across different habitat types on four large islands spanning the Mediterranean Basin (Mallorca, Corsica, Sardinia and Crete). The species selected were three of the most widespread alien plants on Mediterranean islands (Hulme et al. 2008), known to have significant impacts on native plant diversity and soil structure (Vilà et al. 2006) and able to reach high local abundance (Traveset et al. 2008). These species were the fast-growing tree *Ailanthus altissima*, the scrambling succulent chamaephyte *Carpobrotus* spp., and the annual geophyte *Oxalis pes-caprae*. Our specific aims in this study are (1) to determine which habitats are more invaded by the three alien species and (2) to test if there are consistencies in habitat invasion among species and among islands.

Materials and methods

Invasive taxa

The three alien taxa (hereafter called “invaders”) were chosen for their wide distribution across most Mediterranean islands, their occurrence in a range of different habitats and, while all three are clonal, the diversity of life-forms they represent. All three are included in the one hundred of the most invasive species in Europe (DAISIE 2009).

Ailanthus altissima (P. Mill.) Swingle (Simaroubaceae) is a fast-growing tree native to China and North Vietnam (Basnou and Vilà 2009). It has been introduced to most continents as an ornamental tree and for the landscaping of roadsides. Seeds are wind- and water-dispersed (mean production of 300,000 seeds/individual/year), and the species exhibits strong resprouting and clonal growth of stems (Kowarik 1995). Exudates from all parts of the plant have been shown to be allelopathic (De Feo et al. 2003) and herbicidal (Heisey and Heisey 2003).

Carpobrotus spp. L. (Aizoaceae) are robust, scrambling, mat-forming succulents native to South Africa (Wisura and Glen 1993; Delipetrou 2009), have been introduced as ornamentals within public and private gardens, and to stabilise soils along coastal

dunes, rocky slopes, and cliffs (e.g., D'Antonio et al. 1993; Suehs et al. 2001). In the Mediterranean Basin, the presence of two hybridising taxa (*C. edulis* and *C. affine acinaciformis*) is well documented (Suehs et al. 2004a, b). These two strongly clonal taxa produce fleshy fruits (mean production of 1,000 seeds/fruit and 25 fruits/m²) and seeds are dispersed endozoochorously by small mammals (Bourgeois et al. 2005) or secondary myrmecochory. In addition, stem fragments are capable of rooting and establishing a new clone (Vilà and D'Antonio 1998).

Oxalis pes-caprae L. (Oxalidaceae) is a geophyte native to South Africa and in the Mediterranean is functionally sterile (Lambdon 2009). The species does not produce seeds but spreads asexually via the production of underground bulbs (Pütz 1994) that are often dispersed on agricultural machinery. It is primarily a colonist of disturbed ground and agricultural fields from the coast to around 600 m in elevation (Ross et al. 2008).

Study islands and field survey

Field surveys were undertaken on four Mediterranean Basin islands (Fig. 1): Mallorca (Spain), Corsica (France), Sardinia (Italy) and Crete (Greece). These islands are four of the largest in the Mediterranean, supporting a high human population density and encompass a strong East-West climatic gradient (Table 1). The basic geographic and climatic parameters of the islands are presented in Traveset et al. (2008).

Five randomly chosen 10 × 10 km UTM cells per invader were surveyed on each island. Sampling reflected the geographic distribution of taxa and

where all three taxa coincided geographically, sampling could be limited to the same five UTM cells (e.g., Crete, Sardinia) but, where greater geographic heterogeneity occurred, UTM samples were designed to target landscapes known to be invaded by particular taxa. In some cases, different UTM cells were surveyed separately for each invader (e.g., Mallorca) while the sampling strategy in Corsica used a mixture of unique and shared UTM cells for different taxa (Table 1). For all islands, there exist considerable montane areas in which invaders are absent, our sampling strategy thus targeted “invaded” landscapes, though the degree of invasion in each case was still relatively low.

To stratify the sampling, each UTM cell was divided into 100 1 × 1 km squares, within which one random point was selected and surveyed. At each point, the following data were recorded: (1) the UTM East and North coordinates (*East, North*), (2) the habitat types within a 50 m radius of the random point (i.e., agricultural, coastal, fen, forest, grassland, railroad, river, road, rocky, ruderal, scrub, or urban), (3) the presence/absence of each invader in each habitat found within the 50 m radius area, and (4) the abundance (% cover) of each invader in each habitat according to a DAFOR scale (Rich et al. 2005): Dominant (>75%), Abundant (50–75%), Frequent (25–50%), Occasional (5–25%) and Rare (<5%). For analysis, the DAFOR semi-quantitative categories (i.e., 1–5) were considered. Therefore, at each random point, we could obtain the frequency of occurrence and cover abundance values of the invader as well as the overall availability of each habitat. Variation in the number of sampling points per invader and island occurred due to the inaccessibility of certain

Fig. 1 Map of the Mediterranean Basin including the four sampled islands (Mallorca, Corsica, Sardinia and Crete) for the presence of the invaders *Ailanthus altissima*, *Carpobrotus* spp. and *Oxalis pes-caprae*



Table 1 The surface area, distance from the nearest mainland, population density, annual tourist density, number of UTM cells, and total number of points sampled in these UTM cells for each of the four study islands surveyed

Island	Surface area (km ²)	Distance (km)	Population density (persons/km ²)	Tourist density (persons/km ² /year)	UTM cells	Sample points
Mallorca (Spain)	3,656	170	174	1,712	15	1,078
Corsica (France)	8,682	82	30	709	11	1,306
Sardinia (Italy)	24,090	230	68	104	5	1,485
Crete (Greece)	8,700	100	72	241	5	1,416

points (e.g., cliffs, military areas, private property) resulting in a total of 5,285 sampling points (out of a maximum of 6,000) collected across the four islands (Table 1).

Degree of invasion

Four variables were derived to assess the degree of invasion at both the island and habitat scales: (1) proportion presence (PP), the proportion of sampling points (e.g., frequency of occurrence) in which an invader was found, (2) the mean invader abundance (DAFOR) scored across all sampling points where it was found (i.e., excluding zeros), (3) invasion saturation (IS); cf. Pyšek and Pyšek (1995), and (4) habitat apparency (HA). Invasion saturation (IS) compares the average abundance of a species across all sampling points where it was found (i.e., excluding zeros) to the average abundance across all sampling points that were sampled (i.e., including zeros). Values near 0 indicate that the invaded habitats in the region are far from saturated (e.g., many sampling points have no invader), whereas values approaching 1 indicate that the invaded habitats in the region are close to saturation and, therefore, most sampling points are occupied. IS was assessed for each taxon and for each habitat in which it was found, and then averaged across all habitats to obtain a score for each island:

$$IS = \left(\sum_{i=1}^{i=n} DAFOR_0 / DAFOR_i \right) / n \quad (1)$$

here, n indicates the number of different invaded habitats, $DAFOR_0$ is the mean DAFOR score for habitat i including zeros, and $DAFOR_i$ is the mean DAFOR score for habitat i excluding zeros. Invasion saturation could only be calculated for habitats that exhibited some occurrence of the invader and was

calculated for each habitat in which an invader occurred. After which an average was then derived across all the habitats for an individual island.

Habitat apparency (HA) which measures whether an invader tends to be abundant in rare or common habitats was also calculated:

$$HA = \sum_{i=1}^{i=h} (H_i / N) DAFOR_i \quad (2)$$

here, h is the total number of habitats, H_i the number of sampling points in which habitat i was recorded, N the total number of sampling points across all habitats and $DAFOR_i$ is the mean DAFOR score for habitat i excluding zeros. For each habitat on any one island, H_i and N are the constants and thus HA provides a relative measure of the apparency of an invader and whether it tends to be abundant in common or rare habitats. HA varies from 0 (i.e., no habitat is invaded) to 5 (i.e., the invaders can, on average, reach dominance in all habitats).

Statistical analysis

First, we tested the null hypothesis that the observed frequency of occurrence of each invader in a particular habitat reflected the availability of the habitat in the landscape. Statistical significance was calculated as the proportion of frequencies randomly generated from available-habitat data (based on 5,000 randomizations plus the one field observation) that were as extreme or more extreme (one tailed) than observed invaded frequencies (Manly 1997).

Second, we also tested if differences in the mean DAFOR scores across individual habitats and their among-habitat means resulted from a random allocation of the available DAFOR scores to the invaded habitats. Significance was calculated as the proportion of habitat means versus overall-mean differences

(based on 5,000 randomizations plus the one field observation) that were as extreme or more extreme (one-tailed) than field observations (Manly 1997).

Third, mean DAFOR scores were compared between islands and between invaders using two-group randomization tests due to extreme heteroscedasticity that was not resolved via data transformation. Significance was assessed by comparing the mean differences between two groups with the one-tailed distribution generated from 5,000 random samples without replacement of those two groups with Bonferroni adjustment (Manly 1997).

Finally, a two-way factorial Multivariate Analysis of Variance (MANOVA) was used to compare invader and island effects, as well as an island by invader interaction on invader occurrence (PP), invasion saturation (IS) and habitat apparency (HA). PP and IS values were Box-Cox transformed ($PP' = (PP^{0.39} - 1)/0.39$ and $IS' = (IS^{0.37} - 1)/0.37$) before analysis to eliminate heteroscedasticity (Sokal and Rohlf 1995). Post hoc Scheffé tests were then used to pinpoint pair-wise differences between islands and between invaders (Sokal and Rohlf 1995).

Statistical analyses were computed using the open source R software program, with the stats and ade4 packages (R Development Core Team 2008).

Results

Habitat degree of invasion

The percentage of habitats sampled per island is given in Table 2. For all invaders, urban, ruderal, and road habitats were all significantly ($P < 0.05$) over-represented on at least one island (Table 3). Coastal habitats were significantly over-represented only for *Carpobrotus* on all islands. In contrast, agricultural habitats were significantly over-represented only for *Oxalis* in Sardinia and Crete, while river habitats were significantly over-represented only for *Ailanthus* in Corsica. With the exception of *Ailanthus* in Mallorca, scrub habitats were consistently ($P < 0.05$) under-represented on all islands. Forests, grasslands and rocky habitats are either significantly under-represented, or non-significantly represented for any invader and island. Finally, fen habitats were always non-significantly under-represented.

Table 2 The percentage of habitats sampled per island

Island	Mallorca	Corsica	Sardinia	Crete
Agricultural	25,79	13,86	25,79	29,94
Coastal	5,75	6,20	0,07	0,99
Fen	0,00	1,61	0,00	0,21
Forest	13,91	7,73	6,20	5,58
Grassland	31,54	7,73	43,30	5,58
Railroad	0,00	0,77	0,00	0,00
River	1,67	6,20	0,07	4,03
Road	0,37	10,57	0,00	8,19
Rocky	0,00	3,60	0,40	3,60
Ruderal	6,12	3,60	1,14	6,64
Scrub	4,82	26,19	19,66	29,31
Urban	10,02	11,94	3,37	5,93

Comparisons between mean DAFOR scores for individual habitats and their overall habitat abundance reveal significant differences in the abundances of each invader (Fig. 2). Significantly ($P < 0.05$) higher-than-average abundances were detected for *Oxalis* in grassland habitats in Mallorca, agricultural habitats in Corsica and Crete, and forest habitats in Sardinia, whereas *Carpobrotus* was more abundant than expected in roadside habitats in Mallorca and coastal habitats in Corsica. Significantly lower-than-average abundances were found for *Oxalis* in ruderal habitats in Mallorca and Sardinia, roadside habitats in Corsica, and grassland, rocky and scrub habitats in Crete. Similarly, significantly lower-than average abundances were found for *Carpobrotus* in urban habitats in Corsica, as well as for *Ailanthus* in forest and ruderal habitats in Sardinia.

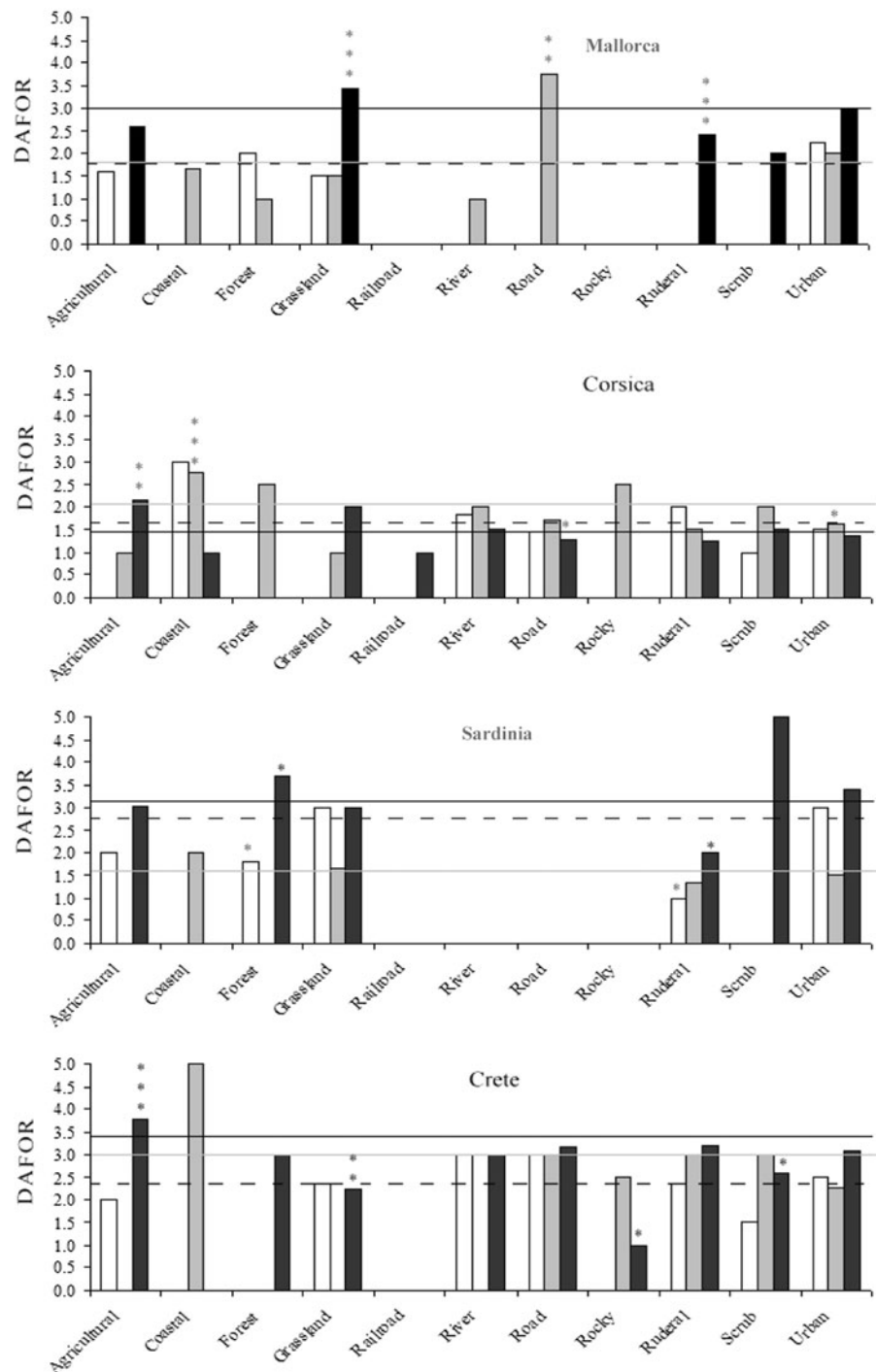
Invader and island differences

No significant differences between mean DAFOR scores were found between the invaders where they were present (Fig. 3). In contrast, all island pair-wise differences between mean DAFOR scores, except Mallorca vs. Sardinia, were significant. Corsica (mean DAFOR \pm SE = 1.67 ± 0.11) had significantly lower mean scores than Mallorca (DAFOR = 2.27 ± 0.16 ; $P < 0.01$), Sardinia (DAFOR = 2.31 ± 0.22 ; $P < 0.01$) and Crete (DAFOR = 3.09 ± 0.27 ; $P < 0.001$), while Crete had significantly higher mean abundance scores than Mallorca ($P < 0.01$) and Sardinia ($P < 0.05$).

Table 3 Comparison between available and occupied habitat frequencies for each invader and island

	Mallorca	Corsica	Sardinia	Crete
Significant ($P < 0.05$) over-represented				
<i>Ailanthus</i>	Urban	Urban River Road	Urban	Urban Ruderal
<i>Carpobrotus</i>	Urban Coastal Road	Urban Coastal	Urban Coastal Ruderal	Urban Coastal Ruderal
<i>Oxalis</i>		Urban Road Ruderal	Urban Agricultural	Agricultural Ruderal
Non-significant over-represented				
<i>Ailanthus</i>	Agricultural	Ruderal	Forest Grassland Ruderal	Grassland River Road
<i>Carpobrotus</i>		Ruderal		Road Rocky
<i>Oxalis</i>	Forest	Railroad	Forest Ruderal	Road Urban
Non-significant under-represented				
<i>Ailanthus</i>	Forest Grassland Scrub	Coastal Fen Forest Grassland Railroad Rocky	Rocky	Coastal Fen Forest Rocky
<i>Carpobrotus</i>	River	Forest Road Rocky Fen Railroad	Grassland Forest River Rocky	Fen Forest Grassland River
<i>Oxalis</i>	Grassland Rocky	Agricultural Coastal Grassland Fen	Grassland Rocky	Grassland River Coastal Fen
Significant ($P < 0.05$) under-represented				
<i>Ailanthus</i>		Agricultural Scrub	Agricultural Scrub	Agricultural Scrub
<i>Carpobrotus</i>	Agricultural Forest Grassland Scrub	Agricultural Grassland River Scrub	Agricultural Scrub	Agricultural Scrub
<i>Oxalis</i>	Forest Scrub	Forest River Rocky Scrub	Scrub	Scrub Forest Rocky

Fig. 2 Mean DAFOR scores for *Ailanthus altissima* (white), *Carpobrotus* spp. (grey) and *Oxalis pes-caprae* (black) in different habitats in Mallorca, Corsica, Sardinia and Crete. The mean DAFOR scores across habitats are indicated by horizontal lines (*Ailanthus altissima*: dotted lines; *Carpobrotus* spp.: grey; *Oxalis pes-caprae*: black). Asterisks indicate significant differences relative to the all-habitat means at the $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***) levels



The two-way factorial MANOVA on PP, IS and HA revealed significant island ($F = 5.56, df = 9, P < 0.001$) and invader ($F = 89.15, df = 6, P < 0.001$) effects, as well as a significant island \times invader interaction ($F = 6.72, df = 18, P < 0.001$), indicating

that habitat trends of invasion degree were not the same across islands.

Post hoc Scheffé tests pinpointed two significant island differences for PP, with Crete (mean \pm SE: PP = $0.27 \pm 0.05; P < 0.01$) and Mallorca

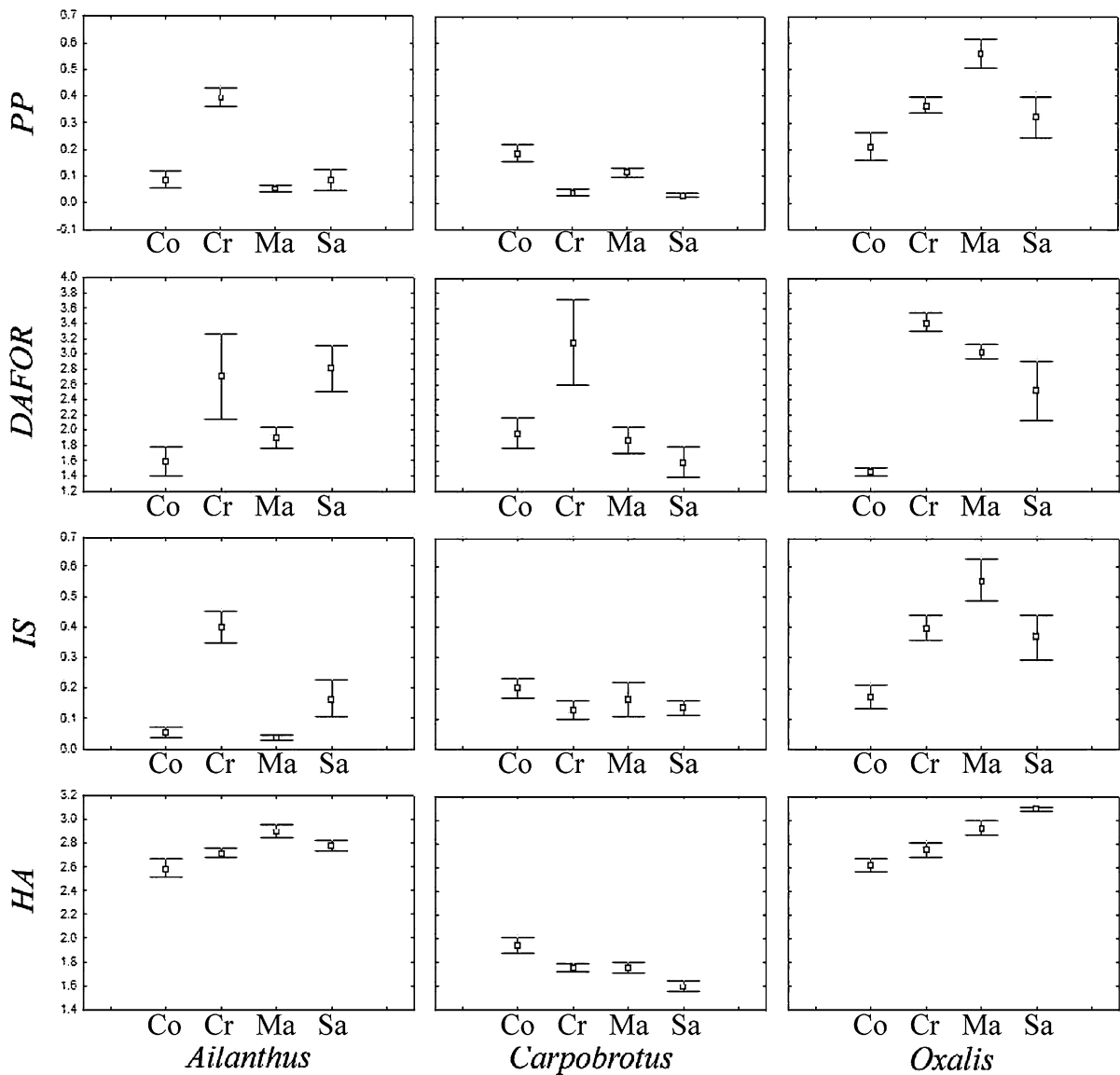


Fig. 3 Means (\pm standard errors) for the proportion presence (PP), mean DAFOR scores when present (DAFOR), invasion saturation (IS) and habitat apparency (HA) for the invaders

Ailanthus altissima, *Carpobrotus* spp. and *Oxalis pes-caprae* on the islands of Corsica (Co), Crete (Cr), Mallorca (Ma) and Sardinia (Sa)

(PP = 0.24 ± 0.06 ; $P < 0.05$) having significantly higher frequency of occurrence compared to Sardinia (PP = 0.15 ± 0.04). Corsica (IS = 0.14 ± 0.02 ; HA = 2.39 ± 0.09) had significantly lower invasion saturation than Crete (IS = 0.31 ± 0.04 ; $P < 0.001$, Fig. 3) and habitat apparency than Mallorca (HA = 2.53 ± 0.15 ; $P < 0.05$, Fig. 3).

Similarly, post hoc Scheffé tests highlighted two significant invader differences ($P < 0.001$) for PP, and IS means: *Oxalis* mean frequency of occurrence

and invasion saturation (PP = 0.36 ± 0.04 ; IS = 0.37 ± 0.04) were significantly higher than either *Carpobrotus* (PP = 0.09 ± 0.02 ; IS = 0.16 ± 0.02) or *Ailanthus* (PP = 0.16 ± 0.04 ; IS = 0.16 ± 0.04). All three invader comparisons were significant for habitat apparency with *Carpobrotus* (HA = 1.76 ± 0.04) having the lowest, *Oxalis* (HA = 2.85 ± 0.05) the highest, and *Ailanthus* (HA = 2.75 ± 0.04) an intermediate habitat apparency. All remaining post hoc Scheffé tests were non-significant.

Discussion

This study attempts, for the first time, to systematically and empirically assess general trends in the regional and local abundance of three widespread invader plants across four Mediterranean islands. Four different measures of the habitat degree of invasion were used to explore these trends and better characterise the risks these taxa pose to Mediterranean habitats. Habitat is considered a good predictor of the degree of plant invasion at the regional scale measured as alien species richness or percentage of aliens in the total flora (Chytrý et al. 2008a, b; Pyšek et al. *in press*). In our study, we found that the degree of invasion measured as the frequency of occurrence and local abundance of an invader was rather consistent across sites. Overall, the trends support the view that invaders are primarily a threat to anthropogenic habitats while less disturbed habitats appear resistant to invasion. Nevertheless, certain patterns were context dependent and differed among islands.

Anthropogenic habitats as hotspots of invasion

The frequency of occurrence of invaders in anthropogenic habitats (i.e., urban, ruderal, road and railroad) was either in proportion to significantly higher compared to their availability. Frequency of occurrence was never less than what might be expected given the availability of these habitats. The association of invasive species with human activities and ruderal areas has been widely demonstrated at different spatial scales (Cadotte and Lovett-Doust 2001; Vilà and Pujadas 2001; Deutschewitz et al. 2003; O'Farrell and Milton 2006; Hulme 2009a). However, our study highlights that although invaders frequently occur within anthropogenic habitats, they do not necessarily attain high abundance. This suggests that, while human activities may facilitate high frequency of invader occurrence in these habitats possibly due to higher propagule pressure, abundance may itself be limited by frequent disturbances and/or a lack of suitable conditions for population growth (Traveset et al. 2008; Vilà et al. 2008). Thus, while often perceived as potential sources for further invasion, such anthropogenic habitats may not necessarily act as important sources for spread to the wider environment (Botham et al.

2009) and longer human presence does not necessarily result in an increased degree of invasion (Planty-Tabacchi et al. 1996). Given the rapid anthropogenic transformation of the Mediterranean, a better understanding of the role of these habitats in the spread of alien species is required.

Mediterranean scrubs as invasion-resistant habitats

For certain habitats, the frequency of invader occurrence was consistently lower than expected from habitat availability, and invaders never reached higher than average abundance. This is particularly the case for Mediterranean scrublands that have previously been shown to have a low level of plant invasion (Pino et al. 2005; Vilà et al. 2007). Most alien species introduced to the Mediterranean tend not to be as tolerant as the native species to the xeric conditions typical of this habitat (Lambdon et al. 2008; Traveset et al. 2008; Vilà et al. 2008). This result is especially interesting in light of the fact that scrub habitats form a large fraction of typical Mediterranean island vegetation, including our study islands. Maintaining natural scrub habitats may thus serve as a significant barrier to invasive species spread (Marvier et al. 2004).

Context dependent trends in invasion

Most natural habitats exhibit patterns that are intermediate between anthropogenic and scrub habitats. The degree to which these habitats were consistently sampled across habitats varied and reflected the often different landscapes sampled across the Mediterranean. Riparian and rock outcrop/cliff habitats were encountered relatively infrequently and in general the frequency of invader occurrence was what might be expected given their availability in the landscape. Riparian areas are found to be particularly vulnerable to plant invasions (Pyšek et al. *in press*) but this may not be true for the taxa selected for our study. Other habitats did not reveal consistent trends when compared across the four islands, notably forest, grassland, and coastal habitats. None of these habitats revealed lower or higher than expected frequencies of invader occurrence, and they never presented consistently higher or lower than average local abundances. A more detailed analysis that examines the role of the

landscape matrix and the degree to which such habitats are fragmented or close to propagule sources is needed to fully assess such variability in habitat vulnerability to invasion (Ohlemüller et al. 2006).

Invader differences on the degree of invasion

There were no consistent trends across islands in the four measures of invasion we calculated for each taxon. However, both the frequency of occurrence and invasion saturation highlight that there were marked differences among islands in the degree of invasion for *Ailanthus* (particularly in Crete) and *Oxalis* (particularly in Mallorca) but no such inter-island variation for *Carpobrotus* spp. Nevertheless, the frequency of invader occurrence and invasion saturation was low for all invaders on all islands (with the exception of *Oxalis* in Mallorca), indicating that the invaders remain relatively rare. Given that the three invaders were introduced over 100 years ago (Traveset et al. 2008), average rates of spread across these islands do not appear to be particularly high since a significant proportion of suitable habitat remains available for colonisation. Other measures of the degree of invasion such as mean local abundance and habitat apparency present a different picture. Mean local abundance was consistently higher for all three invaders on Crete, but trends in abundance were more individualistic on the other islands. Habitat apparency varied least among islands but most among species, with *Carpobrotus* revealing particularly low habitat apparency. Furthermore, the degree of invasion of *Ailanthus* is highest on Crete and lowest on Corsica, whereas for *Carpobrotus* it is highest on Corsica and lowest on Sardinia, while for *Oxalis* it is highest on Mallorca and lowest on Corsica. Thus, at the level of an island, the degree of invasion is dependent on the invader. This indicates that island level attributes that are known to influence alien species richness such as area, human population size, GDP and/or level of trade (Hulme 2009b) may be less important in the degree of invasion of individual species. On the other hand, the comparison across species enables the three invaders to be ranked from highest to lowest degree of invasion as: *Oxalis* > *Ailanthus* > *Carpobrotus*. This mirrors the ranking generated by an invasion success index that combines both regional and local abundance (Hulme et al.

2008). Previous studies on these three invaders have already demonstrated that establishment and seedling survival were higher for *Oxalis* and lower for *Carpobrotus* and especially for *Ailanthus* in a broad range of different habitat types (Vilà et al. 2008). In contrast, clonal performance was higher for *Ailanthus* in a large number of habitat types, and *Carpobrotus* and *Oxalis* spread only in coastal and agricultural/disturbed habitats respectively (Traveset et al. 2008). However, species rankings can be also affected by propagule pressure (e.g., Ross et al. 2008), minimum residence time (e.g., Pyšek and Jarosík 2005), and not necessarily by population performance of each taxon.

Conclusions

This study sheds light into why islands tend to accumulate alien invaders without a concomitant loss of native species (Sax and Gaines 2008). First, alien species, even some of the worst invaders, are largely restricted to anthropogenic habitats where levels of native plant endemism are often low (Vilà and Muñoz 1999). Nevertheless, native ruderal annuals that evolved in the Mediterranean (Blondel and Aronson 1999) occur in varying associations in fields, pastures and on roadsides: habitats typically invaded by alien plant species. Many of these native colonisers have restricted distributions and could represent the elements of the Mediterranean flora most at risk from invasions (Hulme et al. 2008). Second, even where native habitats are colonised, saturation is low and patterns of abundance are highly variable indicating that native species may be threatened in some localities but not in all their area of distribution even if aliens are present. However, some caution is required when interpreting the current patterns of distribution and abundance of these three invaders, particularly due to the absence of historical data on the rate of spread. The relatively recent anthropogenic changes in Mediterranean islands (Hulme 2004) may accelerate the spread of these invaders, altering local abundance and saturation. Similarly, future climate change may lead to a wider range of habitats threatened by alien species (e.g., Gritti et al. 2006). Thus any statement of risk must also look towards future trends in the dynamics of these taxa.

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