Species attributes and invasion success by alien plants on Mediterranean islands

FRANCISCO LLORET, FRÉDÉRIC MÉDAIL*, GIUSEPPE BRUNDU†, IGNAZIO CAMARDA†, EVA MORAGUES‡, JUAN RITA§, PHILIP LAMBDON¶ and PHILIP E. HULME¶

*Center for Ecological Research and Forestry Applications (CREAF) and U. Ecologia, Department Biologia Animal, Biologia Vegetal i Ecologia, Fac. Ciències, Universitat Autònoma Barcelona, 08193 Bellaterra, Barcelona, Spain, *Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP, CNRS UMR 6116), Université Paul Cézanne/Aix-Marseille III, Europôle Méditerranéen de l'Arbois, BP 80, 13545 Aix-en-Provence cedex 04, France, †Dipartimento di Botanica ed Ecologia vegetale, Università degli Studi di Sassari, Via F. Muroni 25, 07100 Sassari, Italy, ‡Institut Mediterrani d'Estudis Avançats (CSIC-UIB), c. Miquel Marqués 21, 07190 Esporles, Majorca, Spain, §Departamento de Biología, Universidad de las Islas Baleares, Ctra Valldemossa km 7, 5. 07071 Palma de Mallorca, Majorca, Spain, and¶NERC Centre for Ecology and Hydrology, Banchory, Aberdeenshire AB31 4BW, Great Britain*

Summary

1 Species attributes have been used to explain invasion patterns assuming the prevalence of biological mechanisms, although this approach often suffers several methodological and conceptual limitations, such as local idiosyncrasies, differences among habitats, phylogenetic constraints and insufficient sample size.

2 The relative importance of 15 species traits for explaining the abundance over 350 naturalized alien plant species was assessed across five Mediterranean islands (Corsica, Crete, Majorca, Malta and Sardinia). A comparative analysis accounting for phylogeny was used to examine variation in semi-quantitative estimates of species abundance in comparable habitats across the five island floras.

3 Species were divided into those with affinity for semi-natural, agricultural and ruderal habitats. Both vegetative and reproductive attributes were evaluated for individual islands and averaged across all islands.

4 Vegetative propagation, large leaf size, summer flowering, long flowering period and dispersal by wind or vertebrates were positively associated with average alien abundance across all five islands. Fewer significant trends were found in island-specific patterns.

5 The relative importance of a few reproductive traits is reflected in over-representation of Caryophyllales, Asterales and Poales (late flowering, large seed size and anemochory). Although significant covariation in traits was found there was no evidence for well-defined invasive syndromes.

6 Succulence was important in ruderal habitats, long flowering period in agricultural habitats and vertebrate seed dispersal in semi-natural habitats, suggesting that empty niches, avoidance of competitors and exploitation of mutualists, respectively, are important.

7 The study highlights the importance of estimating invasion success across a wide region, but analyses of specific invasion stages are also needed. Reproductive traits, which may be more relevant for long-distance colonization, and vegetative traits, which determine local dominance and persistence, were, nevertheless, both related to abundance within islands.

Key-words: alien plant species, biogeography, biological invasions, invasion syndrome, island ecology, Mediterranean Basin, naturalized species, species traits

Correspondence: F. Lloret (e-mail francisco.lloret@uab.es).

Introduction

The invasion of terrestrial ecosystems by non-native plants is a major component of global change, with considerable potential for significant impacts on the species composition and ecosystem function of native communities (Mack *et al.* 2000; Pimentel *et al.* 2001). A major goal in the study of biological invasions is the identification of potentially invasive species before they impact upon ecosystems (Hulme 2003), either by finding an 'invasive species syndrome' or by constructing decision trees that might screen species in terms of their potential invasion risk (Scott & Panetta 1993; Reichard & Hamilton 1997; Goodwin *et al.* 1999; Bennett 2001). Both approaches have used comparative analyses of species attributes in order to identify key traits associated with species invasiveness (Roy 1990; Thompson *et al.* 1995; Crawley *et al.* 1996; Williamson & Fitter 1996; Rejmánek 2000; Sutherland 2004), on the assumption that invasion primarily reflects species attributes rather than characteristics of the environment.

However, the analysis of the relationship between invasiveness and species attributes suffers from methodological and conceptual limitations. Analyses that compare native and alien species within a flora are questionable: native species do not actually constitute a reliable control group because the attributes of alien species may have been selected by human criteria, such as horticultural desirability (Thompson *et al.* 1995; Crawley *et al.* 1996). Historical and stochastic events, as well as geographical particularities, may determine idiosyncratic species responses in different geographical areas (Lloret *et al.* 2004) and analyses from a single flora may therefore be unable to distinguish between traits of generic rather than locally specific importance. Attributes often covary due to phylogenetic constraints, and, while comparison of closely related species reduces this problem (Rejmánek & Richardson 1996), resulting generalizations are limited in scope. The relationship between attributes and invasion success may also differ among habitats (Pysek *et al.* 1995) to the extent that traits important in the invasion of one habitat are unimportant in another. Finally, the sample size (number of species) and the availability of data on species traits may be insufficient to detect significant differences (Kolar & Lodge 2001).

This study attempts a comprehensive analysis of the relative importance of 15 species traits on the abundance of over 350 naturalized alien plant species invading five Mediterranean islands (Corsica, Crete, Majorca, Malta and Sardinia) in which these limitations are addressed. Mediterranean islands are particularly appropriate model systems for studying invasions due to the diversity of alien taxa, long history of species introductions and detailed floristic records (Hulme 2004). A comparative analysis accounting for phylogeny was used to examine variation in semi-quantitative estimates of species abundance in comparable habitats across the five island floras. This approach enabled the following questions to be addressed. (i) Are certain species traits related to the success of alien plant species in the invasion of Mediterranean islands? (ii) Do covarying suites of traits facilitate the identification of well–defined invasive syndromes? (iii) How specific are these relationships to the type of habitat invaded?

Although we examined the relationship between species abundance and individual traits, different traits are unlikely to be independent of each other, and we also investigated the success with which clustering into syndromes accounted for differences in species abundance.

Materials and methods

Data on the species composition, habitat affinities, status and species attributes of the naturalized alien flora of the five Mediterranean islands were drawn from the literature for the whole Mediterranean basin (Tutin *et al.* 1964–80; Tutin *et al.* 1993) and for each island (see Table 1 for a description of island characteristics): Corsica (Natali & Jeanmonod 1996; completed by Jeanmonod & Burdet 1997, 1998, 1999; Jeanmonod 2000; Jeanmonod & Schlüssel 2001), Crete (Jahn & Schönfelder 1995; Chilton & Turland 1997, 2002), Majorca (de Bolòs & Vigo 1984–2001), Malta (Haslam *et al.* 1977) and Sardinia (Pignatti 1982; Viegi 1993; Camarda 1998). These data were updated and validated by local botanists (E. Moragues and J. Rita for Majorca, I. Camarda and G. Brundu for Sardinia, and F. Médail for Corsica) based on their own field observations and collections.

Only naturalized species, that is, those sustaining populations without direct intervention by humans (Richardson *et al.* 2000a; Pysek *et al.* 2004), were included in the data base. Cultivated (but not naturalized ornamentals) and casual species (as defined by the sources) as well as hybrids, subspecies and taxa of unknown origin (overall, 500 taxa) were excluded from the data base. Cultivated taxa (even where naturalized) were

Table 1 Description of the five islands where the naturalized alien flora was analysed

Island	Location	Distance to mainland (km)	Area (km²)	Maximum altitude (m)	Population density (km⁻²)
Crete	35°10′ N, 25° E	120	8 700	2456	61.1
Malta	35°50′ N, 14°25′ E	230	246	240	1569.1
Corsica	42°10′ N, 9° E	90	8 682	2710	30.0
Sardinia	40° N, 9° E	200	24 090	1834	67.9
Majorca	39°15′ N, 2°55′ E	180	3 656	1346	201.5

Table 2 Description of the species attributes and the respective categories assessed to each species. Information for each species was obtained from the literature

Attributes	Categories
Vegetative traits	
Longevity	Annual, biennial, perennial
Vegetative propagation	Yes (bulbs, rhizomes, fragmentation), No
Leaf size	Very small (< 1 cm^2), Small (1–7 cm^2), Medium (7–20 cm^2), Large (20–50 cm^2), Very large (> 50 cm^2)
Spinescence	Yes, No
Succulence	Yes, No
Pubescence	Yes, No
Growth form (after Raunkiaer 1934)	Therophytes (annuals), geophytes (buds below ground), hydrophytes, hemicryptophytes (buds at ground level), chamaephytes (buds less than 0.5 m from the ground), nanophanerophytes (buds borne on aerial shoots, between 0.5 and 2 m from the ground), macrophanerophytes (buds borne on aerial shoots, more than 2 m from the ground)
Height	Stem height, when a range of values was reported, we used the mid-point of the range
Reproductive traits	
Reproduction type	Hermaphrodite, unisexual monoicous, dioicous, mixed
Pollination type	Wind, animal, mixed (wind and animal), water
Flowering phenology	Autumn-winter, spring, summer
Flowering span	Short (1–3 months), medium (4–6 months), long (> 6 months)
Fruit type	Capsule, legume and folicle, Achen and nucule, fleshy
Seed size	Very small (< 1 mm Φ), small (1–2 mm Φ), medium (2–5 mm Φ), large (5–10 mm Φ), very large (> 10 mm Φ)
Dispersal mode	Unspecialized, hydrochory, anemochory, zoochory

excluded because they are often of uncertain origin and taxonomic assignation, and have been deliberately spread over the territory. The final data base consisted of 354 species (162 species from Corsica, 88 species from Crete, 83 from Malta, 119 from Majorca and 105 from Sardinia).

Fifteen attributes were assessed for each species. They integrate a wide range of traits associated with both colonization and plant performance, and are thus potentially involved in invasion success (Table 2). As species are not independent units and phylogenetic constraints may influence species abundance patterns, each species was allocated to phylogenetic groups and the relationship between abundance and phylogenetic groups analysed (Whittaker *et al.* 2000). Taxonomic order was used as the grouping level, following a recent ordinal classification for angiosperms (APG 1998). Following Pysek *et al.* (2002), three broad habitat categories were used to classify species occurrence: (i) ruderal (human-made habitats, excluding arable land) (*n* = 242 species), (ii) agricultural (arable and traditional agricultural habitats) (*n* = 98 species), and (iii) semi-natural (i.e. relatively low impacted plant communities, including semi-natural forested and treeless habitats) (*n* = 218 species). Many species occurred in more than one habitat, so the sum for the three habitat categories is higher than the total number of species studied.

For each species, a semi-quantitative estimate of species abundance (ranging from 1 to 4) was derived from descriptions in the individual island floras (Table 3). Expert knowledge was used to compare these different estimates and derive a single average abundance score across all five islands.

The relationship between species abundance and attributes was analysed for univariate and multiterm effects, including their respective interactions, by generalized lineal models (GLM) using the gamma distribution for the error term, and the reciprocal link function (Crawley 1993), following the Statistica 5.1. package. In each case, models were considered adequate when the effect terms were significant at $P = 0.05$, and the change in explained deviance was significant in a χ^2 test with the difference in degrees of freedom between models. This approach was also used to evaluate the relationship between taxonomic group (order) and species abundance. Multivariate models including taxonomic group and species attributes were also used. In taxonomic groups where particular attribute categories were poorly represented and models could not therefore be calculated, we either merged attribute categories (e.g. dispersal, first flowering) or did not analyse the attribute (e.g. leaf size). Analyses were performed for the average abundance across all islands and for the abundance estimates for individual islands. Different models were developed for the whole set of species, and for subsets of species with affinities to ruderal, agricultural and semi-natural habitats.

To test the hypothesis that a suite of co-occurring plant attributes may represent an 'invasive syndrome', we performed a cluster analysis, considering only attributes that proved significant in the models described above. We used a k-means clustering procedure with three pre-established groups, following the criteria of using the minimal number of groups that produced significant differences for all variables ($P < 0.01$, after ANOVA).

Table 3 Species abundance classes considered for each island, according to the different authority sources

Island	Score	Description of classes	Authority
Crete	1	Occurring in one out of four provinces	Jahn & Schöndelder (1995)
	2	Occurring in two out of four provinces	
	3	Occurring in three out of four provinces	
	4	Occurring in four out of four provinces	
Malta	1	Rare or rather rare	Haslam *et al.* (1977)
	2	Locally frequent	
	3	Common or frequent elsewhere	
	4	Abundant or common everywhere	
Corsica	1	Rare	Jeanmonod & Burdet (1997)
	2	Locally common	F. Médail, personal observation
	3	Common	
	4	Very common	
Sardinia	1	Very rare and rare	Viegi (1993), Camarda (1998)
	2	Occasional	G. Brundu & I. Camarda, personal observation
	3	Rather common	
	4	Common	
Majorca	1	Rare	E. Moragas & J. Rita, personal observation
	2	Occasional	
	3	Frequent	
	4	Abundant or dominant	

After allocating each plant species to one cluster group, we performed an ANOVA with the average species abundance as the dependent variable, and cluster as the main factor. Significant differences in average species abundance between cluster groups would support particular syndromes being linked to invasion success, whereas their absence would suggest that invasion success would be better explored individually for each attribute, or for more simple combinations of attributes.

Results

Because multiterm models did not significantly increase the explained deviance when compared with univariate models, results are initially presented for each significant variable separately. Five attributes significantly explained variation in average species abundance: vegetative propagation ($\chi^2 = 4.60$, $P = 0.032$), leaf size ($\chi^2 = 11.88$, $P = 0.018$), flowering phenology ($\chi^2 = 22.06$, $P < 0.001$), length of the flowering period ($\chi^2 = 5.11$, $P = 0.024$) and dispersal mode ($\chi^2 = 8.22$, $P = 0.016$). Species that reproduced vegetatively, had large leaves, flowered in summer, had an extended flowering period or were dispersed by wind or animals had the highest average abundances across all five islands (Fig. 1).

The species attributes identified as significant varied among the three habitats. Among species occurring in ruderal habitat, vegetative propagation ($\chi^2 = 6.25$, $P = 0.012$), large leaf size ($\chi^2 = 10.19$, $P = 0.037$), succulence ($\chi^2 = 6.48$, $P = 0.011$) and summer flowering ($\chi^2 = 16.18$, $P < 0.001$) were related to higher abundance. For species in agricultural habitats, only summer flowering ($\chi^2 = 8.89$, $P = 0.012$) showed a significant effect. For species in semi-natural habitats, the attributes that showed significant effect (Fig. 1) were vegetative propagation ($\chi^2 = 7.75$, $P = 0.005$), large leaf size ($\chi^2 = 13.45$, $P = 0.009$), summer flowering ($\chi^2 = 157.48$, $P < 0.001$), wind and animal dispersal ($\chi^2 = 7.50$, $P = 0.024$), and presence of fleshy fruit ($\chi^2 = 6.14$, $P = 0.046$).

When analysing the relationship between species attributes and abundance in each island, significant effects were only found in two islands: Corsica and Majorca (Fig. 2). In Corsica, summer flowering ($\chi^2 = 6.15$, $P = 0.046$) and presence of achenes ($\chi^2 = 6.17$, $P = 0.046$) produced significant increase in the abundance of species growing in semi-natural habitats. Among ruderal habitats, annuals were more abundant than perennials ($\chi^2 = 6.02$, $P = 0.049$), while species producing dry fruits (achenes, capsules, etc.) were more successful than those having fleshy fruits ($\chi^2 = 7.17$, $P = 0.028$). In Majorca, succulence had a significant effect for all species ($\chi^2 = 6.37$, $P = 0.012$) and for species found in semi-natural habitats ($\chi^2 = 8.53$, $P = 0.003$); in both cases, succulent species were less successful. Finally, in this island, spinescence was associated with lower success in semi-natural habitats ($\chi^2 = 4.45$, $P = 0.035$).

Taxon (at order rank) explained a significant amount of variation in average species abundance ($\chi^2 = 48.49$, $P = 0.008$), but the deviance explained did not increase in multivariate models that include both taxonomic group and species attributes. Among orders with five or more species, Oxalidales, Sapindales, Caryophyllales, Malpighiales, Asterales and Poales were the most successful (Table 4). This pattern was also observed in species likely to be found in semi-natural habitats ($\chi^2 = 55.05$, $P = 0.001$), but not in ruderal and agricultural habitats. There were no substantial differences in the more successful orders of species living in semi-natural habitats, except for the increasing success of Solanales. No significant effects of taxonomic group were found when analysing the five islands separately.
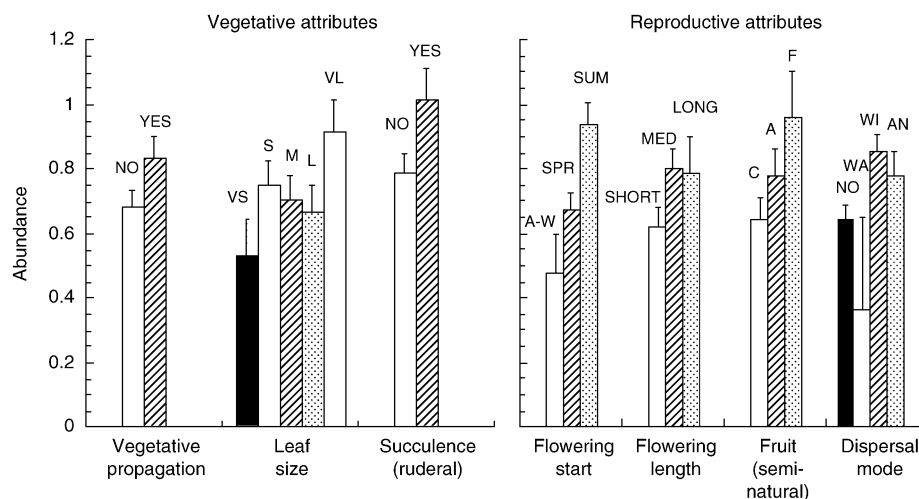
Fig. 1 Average abundance (error bars: SE) of species with different vegetative and reproductive attributes in five islands of the Mediterranean Basin. Only attributes with a significant effect on average abundance are shown and data on succulence therefore correspond only to ruderal species, and data for fruit type to species living in semi-natural habitats. Key to leaf size categories: VS = very small (less than 1 cm²); S = small (1–7 cm²); M = medium (7–20 cm²); L = large (20–50 cm²); VL = very large (more than 50 cm²). Flowering phenology: A-W = autumn to winter; SPR = spring; SUM = summer. Flowering length: SHORT = 1–3 months; MED = 4–6 months; LONG = more than 6 months. Fruit type: C = capsule; A = achenes; F = fleshy fruits. Dispersal mode: NO = none; WA = water; WI = wind; AN = animal. Presence or absence of vegetative propagation and succulence is indicated by YES or NO, respectively.
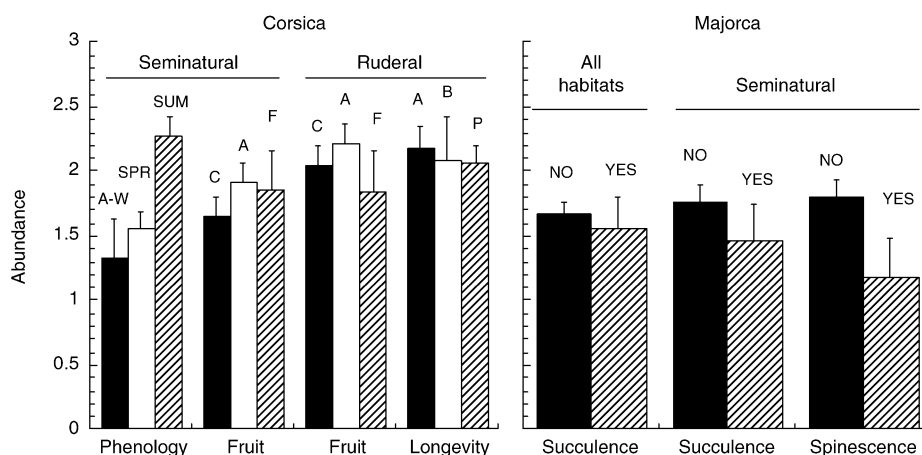

Fig. 2 Mean abundance (error bars: SE) of species with different attributes in Corsica and Majorca. In Corsica, data on flowering phenology correspond to species living in semi-natural habitats, data of fruit type were obtained from ruderal species and from species living in semi-natural habitats, and data on longevity from ruderal species. Only attributes with significant effects on the species abundance on an island are shown. Key to flowering phenology categories: A-W = autumn to winter; SPR = spring; SUM = summer. Fruit type: C = capsule; A = achenes; F = fleshy fruits. Longevity: A = annual; B = biennial; P = perennial. Presence or absence of succulence and spinescence is indicated by YES or NO, respectively.

Cluster analysis separated three groups of species with similar suites of attributes. Cluster 1 included species with vegetative propagation, small or very large leaves, short to medium flowering period in spring, and no specialized dispersal mechanisms. Typical species with these characteristics belong to Oxalidaceae (*Oxalis pes-caprae* L.), Convolvulaceae (*Ipomoea* sp. pl), Fabaceae (*Trifolium* sp. pl) and Onagraceae (*Oenothera rosea* L'Hér.). Most succulent species, such as *Opuntia* sp. pl., were also allocated to this cluster. Cluster 2 included species with medium size leaves, flowering in summer over more than 3 months, and producing wind-dispersed achenes. Typical species of this cluster include

Asteraceae (*Tagetes minuta* L., *Galinsoga paviflora* Cav., *Conyza* sp. pl), and Poaceae (*Panicum capillare* L., *Pennisetum villosum* R.Br.). Cluster 3 included species with very small leaves, but also species with medium- to large-size leaves, short and spring flowering, and capsular fruits; all three dispersal syndromes were represented but wind and animal dispersal were most common. This was the most heterogeneous cluster that included trees such as *Acacia dealbata* Link. and *Tamarix* sp. pl, hydrophytes such as *Elodea canadensis* Michaux and annuals such as *Tropaeolum majus* L.

There were significant differences in average abundance of the species belonging to each cluster (one way

Table 4 Average abundance of the species belonging to different taxonomic orders. See Table 3 for the description of abundance values (SE: standard error; Max: Maximum value; N: number of species)

All species					Species living in semi-natural habitats				
Order	Mean	SE	Max	N	Order	Mean	SE	Max	N
Laurales	1.50	–	1.5	1	Oxalidales	4.00	–	4.0	1
Oxalidales	1.34	0.70	4.0	5	Sapindales	1.93	1.18	3.6	2
Sapindales	1.11	0.64	3.6	5	Laurales	1.50	–	1.5	1
Proteales	1.00	–	1.0	1	Dipsacales	1.05	0.49	2.0	3
Caryophyllales	0.91	0.11	3.2	52	Proteales	1.00	–	1.0	1
Dipsacales	0.87	0.39	2.0	4	Caryophyllales	0.94	0.18	3.2	29
Malpighiales	0.85	0.22	2.6	10	Asterales	0.93	0.17	3.4	24
Asterales	0.83	0.11	3.4	40	Solanales	0.91	0.23	2.8	12
Poales	0.81	0.10	2.8	51	Poales	0.80	0.12	2.8	33
Lamiales	0.75	0.18	2.3	14	Alismatales	0.75	0.36	1.8	4
'Conifers'	0.70	0.10	1.0	6	Malpighiales	0.70	0.13	1.0	7
Alismatales	0.69	0.25	1.8	8	Liliales	0.66	0.28	2.8	9
Asparagales	0.68	0.25	2.0	7	Gentianales	0.65	0.21	1.0	4
Solanales	0.67	0.12	2.8	26	'Conifers'	0.64	0.09	1.0	5
Gentianales	0.65	0.21	1.0	4	Asparagales	0.59	0.16	1.0	4
Fabales	0.63	0.12	4.0	41	Fabales	0.58	0.10	2.4	30
Myrtales	0.62	0.20	1.7	7	Apiales	0.56	0.16	1.0	5
Arecales	0.60	0.20	0.6	2	Myrtales	0.53	0.18	0.8	3
Liliales	0.55	0.18	2.8	14	Lamiales	0.51	0.15	1.3	9
Ranunculales	0.53	0.11	1.0	4	Brassicales	0.48	0.16	1.4	8
Brassicales	0.48	0.12	2.0	17	Saxifragales	0.40	0.20	1.0	4
Apiales	0.43	0.25	1.0	8	Fagales	0.40	–	0.4	1
Rosales	0.42	0.10	1.2	10	Ranunculales	0.37	0.15	0.7	3
Fagales	0.40	–	0.4	1	Rosales	0.28	0.06	0.7	7
Saxifragales	0.37	0.16	1.0	5	Malvales	0.24	0.04	0.4	5
'Boraginales'	0.27	0.07	0.3	2	Ericales	0.23	0.02	0.2	2
Malvales	0.24	0.04	0.4	5	'Boraginales'	0.20	–	0.2	1
Ericales	0.23	0.02	0.2	2	Commelinales	0.20	–	0.2	1
Commelinales	0.20	0.50	0.0	2	Arecales	–	–	–	0

ANOVA, $F_{2,351} = 5.23$, $P = 0.006$). While no significant difference was found in the average abundance of species found in clusters 1 and 2, species in cluster 3 had significantly lower average abundances than the other two clusters (post-hoc Tukey-Kramer test, $P < 0.05$).

Discussion

Several biological attributes were found to explain differences in the abundance of alien species across five Mediterranean islands. The regional perspective was especially important as few attributes were observed to explain abundance patterns on individual islands. The absence of significant patterns for each island may be due to the lower number of species considered at this level, as well as the stochastic effects associated with a single geographical area (Kolar & Lodge 2001; Lloret *et al.* 2004).

Among the non-reproductive attributes, vegetative propagation has previously been found to correlate with invasiveness in woody plants (Reichard & Hamilton 1997; Daehler 1998). Although vegetative propagation does not guarantee long-distance spread, this trait may ensure an optimal establishment, and then a rapid expansion and maintenance within suitable habitats, enhancing competitive ability and more efficient use of resources (Pysek *et al.* 1995; Jakobs *et al.* 2004; Suehs *et al.* 2004). Some species, e.g. *Melia azedarach* L., an ornamental weedy tree that typically reproduces by seeds, may exhibit clonal growth following disturbance such as fire, herbivory or animal injury (Tourn *et al.* 1999). The relationship between leaf size and species abundance reflects extreme size classes: aliens with very large leaves are more likely to become abundant, while the opposite trend is observed for species with very small leaves. Crawley *et al.* (1996) proposed that aliens could colonize more easily at 'both ends' of any niche axis defined by native species, enhancing the existence of extreme values for some traits in alien floras. Large leaf size is often associated with higher competitive ability, particularly in nutrient-rich moderately disturbed habitats (Grime 1979), and has previously been found to differ between alien and native species in Australia (Lake & Leishman 2004). Other attributes related to plant size (e.g. growth form, height) or life cycle (e.g. longevity) failed to explain significant variation in species abundance. Thus long-lived trees and shrubs were neither more nor less likely to be successful invaders than short-lived herbaceous species. This contrasts with findings for the British Isles in which introduced species tended to be larger than native plants (Crawley *et al.* 1996). There was no evidence for

morphological attributes related to herbivore defence, such as pubescence or spinescence, as important determinants of species abundance.

Among the reproductive traits, time of flowering (e.g. phenology, length of flowering period), remained a significant attribute for all types of species. Although flowering period has not been identified as important in the alien invasion of temperate floras (Thompson *et al.* 1995; Reichard & Hamilton 1997) this may not be the case in Mediterranean biomes (e.g. Lake & Leishman 2004). Flowering in these regions is often bimodal, with peaks in spring and autumn (Santandreu & Lloret 1999), rather than the single summer peak seen in many temperate floras. Longer flowering periods may increase the likelihood of cross-pollination and reproductive success in circumstances where pollination is seasonal and/or competition for pollinators is high. Although mutualists may be important in invasion success (Richardson *et al.* 2000b), seed dispersal was a more significant correlate of species abundance than pollination mutualisms in this study. Both vertebrate and wind dispersal have been previously identified as important attributes of plant invaders (Rejmánek 1996; Lake & Leishman 2004). These reproductive traits explain the taxonomic heterogeneity in invasion success with an over-representation of Caryophyllales, Asterales and Poales, which tended to show late flowering, large seed size and anemochory. These taxa are often over-represented in alien floras (Binggeli 1996; Weber 1997; Daehler 1998; Vilà *et al.* 2001).

Overall, these findings support the hypothesis that different ecological strategies can trigger invasion success as a result of interactions with the native community. Competitive performance may be enhanced by the existence of some vegetative traits, such as vegetative propagation or large leaves. Niche differentiation may be favoured by characters that are rare or extreme in the native community (small or large leaves, summer flowering) and the associated avoidance of competitors may be reinforced by the exploitation of mutualists, such as pollinators. As expected, the importance of particular biological attributes for these interactions is often habitat dependent (Thompson *et al.* 1995; Pysek *et al.* 1995; Rejmánek 1999). For example, succulence was found to correlate with invasion success in ruderal habitats, largely due to the occurrence of *Opuntia* sp. pl and *Agave americana* L. near villages and farms. Succulence constitutes an efficient way to resist the seasonal water deficit of the Mediterranean climate; this trait is rare among native species from the Mediterranean Basin, but it is fairly common in other Mediterranean-type regions, such as California (with several species of *Opuntia* and *Agave*) and South Africa (where Mesembryanthemaceae are common).

Thus, our results support the hypothesis that invasion success may be triggered by functional traits qualitatively different from those occurring in the native flora, in which some life-forms may be more saturated than others (Crawley *et al.* 1996). Succulents appear to regenerate poorly in established vegetation where microsites may be limited (Vilà *et al.* 2003) and thus this trait appears not to be important in the invasion of semi-natural habitats. In agricultural habitats, summer flowering was the only significant trait related to invasion. In native grasslands, most species flower in spring or early summer (Bosch *et al.* 1997), and later flowering may allow release from pollinator competition. Alien species in Mediterranean Italy have also been shown to differ in the timing of flowering relative to natives (Celesti-Grapow *et al.* 2003). For species invading semi-natural habitats, dispersal mode was significant, especially the presence of fleshy fruit. Native fleshy-fruited species are also more common in undisturbed, late successional communities (e.g. Debussche & Isenmann 1994), where vertebrates could also be efficient vectors for alien shrubs or trees (e.g. *Pittosporum tobira* (Thunb.) W.T. Aiton, *Phytolacca dioica* L.). Animal dispersal may be particularly relevant for the colonization of semi-natural habitats, where propagule pressure is often lower than in anthropogenic habitats (Vilà *et al.* 2003). The finding that certain traits were significant across all habitats but not within a single habitat probably reflects the lower sample sizes when single habitats were examined.

Ecological trade-offs determine the covariation of species traits and, accordingly, some set of well-correlated attributes could explain successful invasion. Crawley *et al.* (1996) identified the existence of at least two groups of aliens, according to the classical r- and K-strategies, but with more contrasted characters than the native flora. While our study certainly identified species that could be grouped in relation to a suite of traits, these groups did not reflect successful invasive species syndromes. These results lend further support to the hypothesis that a universal pattern of attributes is unlikely to explain invasion success (Thompson *et al.* 1995; Pysek 1998; Rejmánek 2000). As the relevance of biological attributes may change during the processes of dispersal, colonization and invasion, analyses should also focus on specific invasion stages. For example, reproductive traits may be expected to be more relevant for long-distance colonization, while vegetative traits would prevail in achieving local dominance. Both types of traits were related to abundance within the studied Mediterranean islands, but more research is needed to test this hypothesis.

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