RESEARCH PAPER

Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important?

Francisco Lloret*, Fréderic Médail†, Giuseppe Brundu‡ and
Philip E. Hulme§

*Center for Ecological Research and Forestry Applications (CREAF), Fac. Ciències, Universitat Autònoma Barcelona, 08193 Bellaterra, Barcelona, Spain; †Institut Méditerranéen d'Ecologie et de Paléoécologie (C.N.R.S., U.M.R. 6116), Université d'Aix-Marseille III, Faculté des Sciences et Techniques de Saint-Jérôme, Case 461. F-13397 Marseille cedex 20, France; ‡Dipartimento di Botanica ed Ecologia Vegetale, Università degli Studi di Sassari, Via F. Muroni 25, 07100 Sassari, Italy; and §NERC Centre for Ecology & Hydrology, Banchory, Aberdeenshire AB31 4BW, UK

ABSTRACT

Aim We assess the importance of three relevant and readily obtainable life-history traits (dispersal syndrome, stem height and growth form) and biogeographical origin (European vs. non-European) on the local and regional abundance of over 400 exotic plant species across eight Mediterranean islands.

Location The Mediterranean islands of Lesbos, Rhodes, Crete, Malta, Corsica, Sardinia, Majorca and Minorca.

Methods We adopt two abundance criteria for each exotic species: the proportion of islands in which the species occurs (regional abundance), and a qualitative estimate of species abundance within each of five islands (local abundance). Subsequently, we assess the relationship between local and regional abundance, as well as the role of key life-history traits on both regional and local abundance. These analyses were undertaken separately for the European exotics and the non-European exotics.

Results Only 10.9% of the species occur on more than four islands, and only four species are present on all eight islands. Both local and regional abundances were higher for the non-European than the European species. Local and regional abundances were positively correlated, particularly for exotics with non-European origins. Wind-dispersed species tended to have higher regional abundance than species dispersed by other means but this trend only occurred for local abundance on two islands — Corsica and Majorca. Neither a species' growth form nor its stem height explained trends in regional or local abundance.

Conclusions Although wind-dispersed exotics are more widespread in the Mediterranean, plant life-history traits appear to play a lesser role in invasion success than area of biogeographical origin. In general, exotic species of non-European origin were more abundant at both local and regional scales. Invasion patterns should be interpreted at both local and regional scales, but the stochastic nature of biological invasions may limit deterministic interpretations of invasion patterns, especially if islands are studied in isolation.

Keywords

Alien species, biogeography, dispersal syndrome, island ecology, life-history traits, macroecology, Mediterranean Basin.

Correspondence: F. Lloret, CREAF, Fac. Ciències, Universitat Autònoma Barcelona, 08193 Bellaterra, Barcelona, Spain. E-mail: francisco.lloret@uab.es

INTRODUCTION

Biological invasion by non-native or 'exotic' plant species is widely recognized as an important component of human-caused global environmental change, often resulting in a significant loss in the economic value, biological diversity and function of invaded ecosystems (Mack *et al.*, 2000; Mooney & Hobbs, 2000; Pimentel *et al.*, 2001). For our purpose, we consider exotic species to be those 'that have been transported into a region by humans across a barrier that has apparently prevented natural dispersal' (Alpert *et al.*, 2000), whilst we would define the invasion process as the spread of these species into areas away from sites of

introduction (Richardson *et al.*, 2000). A fundamental challenge posed by biological invasions has been to identify life-history traits associated with the invasiveness of exotic species. Attempts to contrast the life-history traits of native and exotic plants have met with varying success and cast doubt over the utility of this approach for screening potentially invasive species (Scott & Panetta, 1993; Mack *et al.*, 2000; Mooney & Hobbs, 2000). For example, surprisingly little agreement was found in the relative importance of different life-history traits assessed in three analyses of the exotic flora of the British Isles (Thompson *et al.*, 1995; Crawley *et al.*, 1996; Williamson & Fitter, 1996). In addition, it is questionable whether native/exotic trait comparisons provide insights into species invasiveness or simply identify trends in horticultural fashion (Thompson *et al.*, 1995; Crawley *et al.*, 1996). Comparative studies of the relative success of different exotic species may provide a better measure of the traits relating to invasion (Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997). However, assessments of the naturalization rate in Hawaii and New Zealand provide conflicting views as to the relative success of exotic species belonging to native and non-native genera (Daehler, 2001; Duncan & Williams, 2002).

The problem is further compounded by the inconsistent success of exotic taxa among comparable geographical regions (Weber, 1997; Daehler, 1998; Pyšek, 1998) suggesting that generalizations from analyses of national checklists may not hold at regional scales. Studies at a single spatial scale are unlikely to discern the drivers of invasion patterns (Collingham *et al.*, 2000), which can be operating at different levels, from local biotic interactions and disturbances (Lambrinos, 2002) to landscape heterogeneity (Higgins *et al.*, 1996), and changes in the regional climate (Walther, 2000). Progress towards robust insights into species invasiveness must therefore take into account both local and regional invasion success, especially as these may be correlated (Gaston, 1994; Koleff & Gaston, 2002).

This study assesses the importance of three relevant and readily obtainable life-history traits on the local and regional abundance of over 400 exotic species across eight islands of the Mediterranean Basin, where the importance of invasive exotics has been extensively documented (e.g. Di Castri *et al.*, 1990; Quézel *et al.*, 1990; Vilà *et al.*, 2001). For each exotic species, we adopt two abundance criteria: the proportion of islands on which the species is found (regional abundance), and a qualitative estimate of species abundance within a particular island (local abundance). This extensive dataset presents a unique opportunity to test key macroecological ideas at the heart of invasions research. A positive relationship has often been found between local and regional abundance for a variety of organisms within their native range (Gaston, 1998), yet whether this relationship also holds for exotic species is unknown. Although several life-history traits, including dispersal syndrome, plant height and growth form, are thought to be important in the relative abundance of exotic species, this has never, to our knowledge, been examined at more than one spatial scale. In addition, it is generally expected that exotics with dissimilar geographical origins will exhibit different levels of invasion success as a result of variation in their ability to overcome biotic and abiotic

obstacles within the native community (Daehler, 2001; Duncan & Williams, 2002). It is with this background that we specifically address the following questions:
• Does a positive relationship exist between the local and regional abundances of exotic species in the Mediterranean Basin?
• Are exotic species with particular growth forms or dispersal syndromes generally more abundant and if so, do such trends hold for both local and regional abundance?
• Is the origin of exotic species, as defined by the proximity of their native range to the Mediterranean, important in determining either regional and/or local abundance?

MATERIALS AND METHODS

Data from the literature were used to construct a detailed database of exotic plant species on eight Mediterranean islands: Crete, Rhodes, Lesbos, Malta, Sardinia, Corsica, Majorca and Minorca (Tutin *et al.*, 1964–80; Tutin, 1993 for the whole Mediterranean Basin; Bolòs *et al.*, 1984–2001 for Majorca and Minorca; Natali & Jeanmonod, 1996, completed by Jeanmonod, 2000; Jeanmonod & Schlüssel, 2001; Jeanmonod & Burdet, 1997, 1998, 1999 for Corsica; Pignatti, 1982, Viegi, 1993; Camarda, 1998 for Sardinia; Haslam *et al.*, 1977 for Malta; Jahn & Schönfelder, 1995; Chilton & Turland, 1997, 2002 for Crete and Rhodes). This information was updated by local botanists using data from their own field observations and collections (M. Mus and J. Rita for Majorca and Minorca, I. Camarda and G. Brundu for Sardinia, F. Médail for Corsica, and I. Brezetou for Lesbos). The information from Malta, Crete and Rhodes was exclusively obtained from the most recent literature as reported above.

We excluded cultivated (but included naturalized ornamentals) or casual species (as defined by the sources), hybrids, subspecies, and taxa of unknown origin (> 500 taxa) from the database. We excluded cultivated taxa because they are often of uncertain origin and taxonomic assignation, and they have been deliberately spread over the territory and occur almost exclusively in agricultural habitats and field margins. Although the category of casual species may differ among sources, they usually correspond to species without self-replacing populations (Richardson *et al.*, 2000; Pyšek *et al.*, 2002). All other naturalized species, that is sustaining populations without direct intervention by humans (Richardson *et al.*, 2000), were included in the database.

Species were classified according to their native origin: 'European' species included those native to the European continent, Mediterranean Basin and cosmopolitan species (*n* = 205); and 'non-European' species were those whose native origin was from other continents or regions, including Macaronesia, North and South America, Central and Western Asia, Southern Saharan and South African species (*n* = 211). We did not split the non-European group into smaller biogeographical regions in order to maintain similar species numbers in the major origin classes, and because the main criteria for this classification was the geographical distance to Mediterranean islands.

We selected three important life-history traits that are commonly available from the literature (e.g. Pignatti, 1982; Tutin

et al., 1964, 80; Bolòs *et al.*, 1984–2001): dispersal type, growth form, and stem height. They integrate a wide range of attributes associated with both colonization and plant performance, and as such they are potentially involved in invasion success. The dispersal syndrome (anemochory, hereafter wind; zoochory, hereafter animal; and unspecialized) was determined according to the presence of structures on seeds, fruits or inflorescences that can facilitate dispersal. Growth form categories followed the Raunkiaer (1934) classification (Therophytes: annuals; Geophytes: buds below ground; Hemicryptophytes: buds at ground level, all above-ground parts dying back in response to unfavourable conditions; Chamaephytes: buds close to the ground; Phanerophytes: buds borne on aerial shoots), but we additionally distinguished a Succulent growth form. For stem height, when a range of values was reported, we used the midpoint of the range.

For each species, we used two measures of abundance: the proportion of islands on which it is found (regional abundance), and a qualitative estimate of species abundance within a particular island (local abundance). Broad estimates of local abundance were obtained from the literature and field observations for five islands (Crete, Sardinia, Corsica, Majorca and Malta) where literature or field observations provided this information. We established several categories that roughly correspond to the frequency of each species in the suitable habitats within the island (i.e. from occurrence in one or two available sites to occurrence in most of them). This criterion fits the traditional description of species abundance/frequency in the local floras of the region. These estimates were ranked in four (Crete, Malta, Sardinia), or five categories (Corsica, Majorca) depending on the literature sources and personal knowledge. For Crete, local abundance was assigned based on the number of regions ($n = 4$) in which the species was recorded within the island (Jahn & Schneider, 1995). For Malta, these categories correspond to the descriptions provided by Haslam *et al.* (1977): 1-rare or rather rare; 2-locally frequent or sometimes naturalized; 3-common or frequent elsewhere; 4-abundant or common everywhere. For Sardinia, the four categories were rare, locally common, common, and very common, according to local studies (Viegi, 1993; Camarda, 1998), and updated by G. Brundu and I. Camarda. For Corsica, the five categories correspond to those proposed by Jeanmonod & Burdet (1997, 99) and updated by F. Médail, i.e. very rare, rare, occasional, fairly common, and

common. For Majorca the five categories correspond to those proposed by Bolòs & Vigo (1984–2001) and updated by M. Mus, i.e. very rare, less rare, less common, rather common, and very common. Expert knowledge was used to compare the criteria for local abundance in the different islands, although the sources did not guarantee a complete degree of direct comparability. The problem of comparability was minimized by analysing each of the islands separately. Species native to one island but exotic to another were excluded from the analysis of regional abundance (112 species excluded), but they were included in the analysis of local abundance for the islands where each is considered as exotic (see Table 1 for the 'n' for each island).

We performed Spearman rank correlation tests to establish the relationship between the local abundance for each island (Crete, Malta, Sardinia, Corsica and Majorca) and the regional abundance in the Mediterranean Basin. This analysis was undertaken on the total exotic flora, and for the European and the non-European groups of exotics for each island separately. Frequency distributions were compared by χ^2 tests.

Comparisons between regional abundance and species traits were performed separately for each trait variable using nonparametric Kruskal–Wallis tests (dispersal syndrome and growth form) and Spearman rank correlations (stem height). Sequential Bonferroni tests ($\alpha = 0.1$) were applied when several variables were analysed on groups of species with the same values of abundance. The relationship between local abundance and species traits (dispersal type, growth form and stem height) was analysed using ordinal logistic regression models (JMP 3.1.5, SAS Institute, 1984–94). We used different tests for regional (nonparametric correlations) and local (ordinal logistic regression) abundance because in the first case abundance can be considered a continuous variable, while regional abundance is an ordinal discrete variable. These analyses were undertaken on the total exotic flora, and for the European and the non-European groups of exotics. Differences between species traits in relation to their biogeographical origin were analysed using χ^2 tests. For these analyses, the significance level was established at $P < 0.1$ due to the abundance of marginal effects with $0.05 < P < 0.1$.

Since species are not independent units and phylogenetic constraints may influence species abundance patterns, we allocated each species to phylogenetic groups and we analysed the relationship between abundance (regional and local) and phylogenetic

Table 1 Spearman rank correlation coefficients (*r*) for the relationship between regional abundance and local abundance for five islands of the Mediterranean Basin. All exotic species (independent of origin), exotics of European origin, and exotics of non-European origin have been presented separately

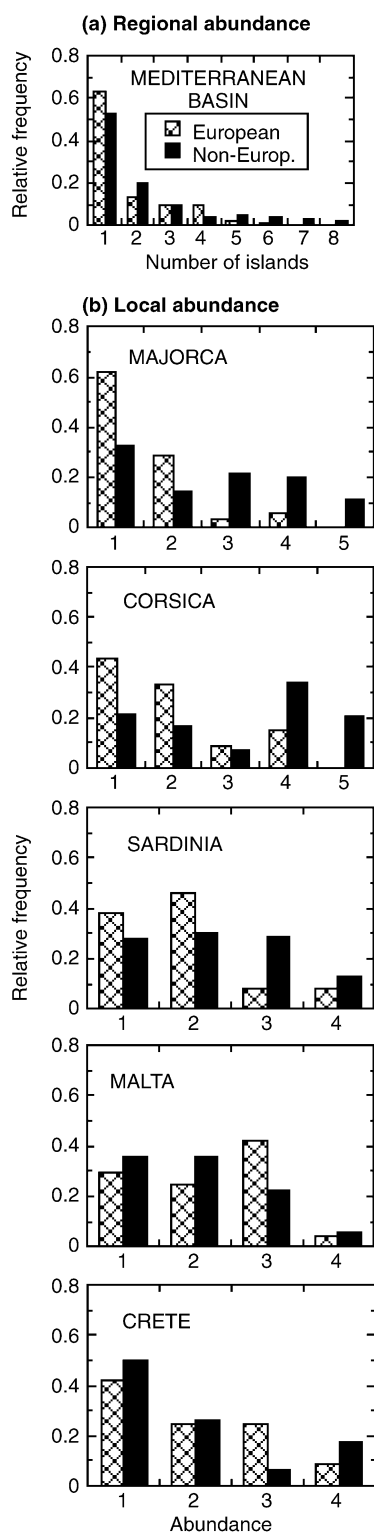|	Total			European			Non-European		
	r	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*
Crete	0.572	< 0.001	82	0.375	0.102	20	0.572	< 0.001	62
Malta	0.412	0.009	66	0.821	0.004	13	0.302	0.029	53
Corsica	0.527	< 0.001	126	0.043	0.779	43	0.509	< 0.001	83
Sardinia	0.516	< 0.001	99	0.804	0.049	7	0.498	< 0.001	92
Majorca	0.541	< 0.001	83	0.218	0.317	22	0.595	< 0.001	61

Figure 1 Frequency distributions of (a) regional (estimated as the proportion of islands *n* = 8) and (b) local abundance of exotics on islands in the Mediterranean Basin. Local abundance values are semiquantitative estimates from local floras and expert knowledge of species abundance within each island. Note that the abundance range may be different according to the information sources. Frequencies are presented separately for species of European and non-European origin.

groups (following Whittaker *et al.*, 2000) using the same tests as described above (nonparametric Kruskal–Wallis and Spearman rank correlations for regional abundance, and ordinal logistic regression for local abundance). We used two grouping levels, following the latest ordinal classification for angiosperms (APG, 1998): order level (32 categories), and a higher level classification that included five categories (conifers, monocots, rosids, asterids, and other eudicots).

RESULTS

No significant effects of phylogenetic groups on regional or local abundance were obtained for the two taxonomic grouping levels. Therefore, for further analyses the dataset can reasonably be considered to be independent of taxonomic artefacts.

There is a positive correlation between local and regional abundance. Exotics that are abundant within an island are also more widespread across the Mediterranean islands. However, this pattern mainly applies to species of non-European origin (Table 1). The distribution of exotics across islands is right skewed (Fig. 1). Only 10.9% of the species are present in more than half of the islands, and only four species (the tree *Ailanthus altissima* (Mill.) Swingle, the annuals *Amaranthus albus* L., *Amaranthus retroflexus* L. and the geophyte *Oxalis pes-caprae* L.) are present in all eight islands. Seven additional species are present on seven islands: *Agave americana* L., *Aster squamatus* (Sprengel) Hieron., *Carpobrotus edulis* (L.) N. E. Br., *Chenopodium ambrosioides* L., *Conyza bonariensis* (L.) Cronq., *Robinia pseudoacacia* L., and *Xanthium spinosum* L. Over half of all exotic species (55.6%) are present on only one island. The right-skewed pattern is also found for the local abundance distribution in Majorca, but not in Malta, Crete, Sardinia or Corsica (Fig. 1).

These general trends differ for species of European and non-European origin (Fig. 1). The frequency distribution of regional abundance significantly differs between these two groups ($\chi^2 = 14.51$, $P = 0.043$). The non-European exotics are more widespread than the European species, with only 3.2% of the European exotics found on more than half of the islands. The local abundance of the non-European species was also higher than the European species on Majorca ($\chi^2 = 25.81$, $P < 0.001$), Corsica ($\chi^2 = 33.03$, $P < 0.001$) and Crete ($\chi^2 = 6.77$, $P = 0.079$), while not significantly different on the two remaining islands (Sardinia, $\chi^2 = 3.56$, $P = 0.312$; Malta, $\chi^2 = 2.98$, $P = 0.395$; Fig. 1).

The most abundant exotics tend to have specific mechanisms for dispersal, particularly by wind (Fig. 2). There was a significant effect of the dispersal syndrome on regional abundance (Table 2), with wind-dispersed species being more abundant than either animal or unspecialized dispersal syndromes (nonparametric Tukey-type multiple comparisons test, $P < 0.05$). This pattern was also observed for local abundance on Majorca and Corsica, but not for Sardinia, Malta or Crete (Table 2).

The significant variation in regional abundance for species with different dispersal syndromes was attributable to the trend among the non-European species rather than the European species (Table 3). The same pattern was observed for local
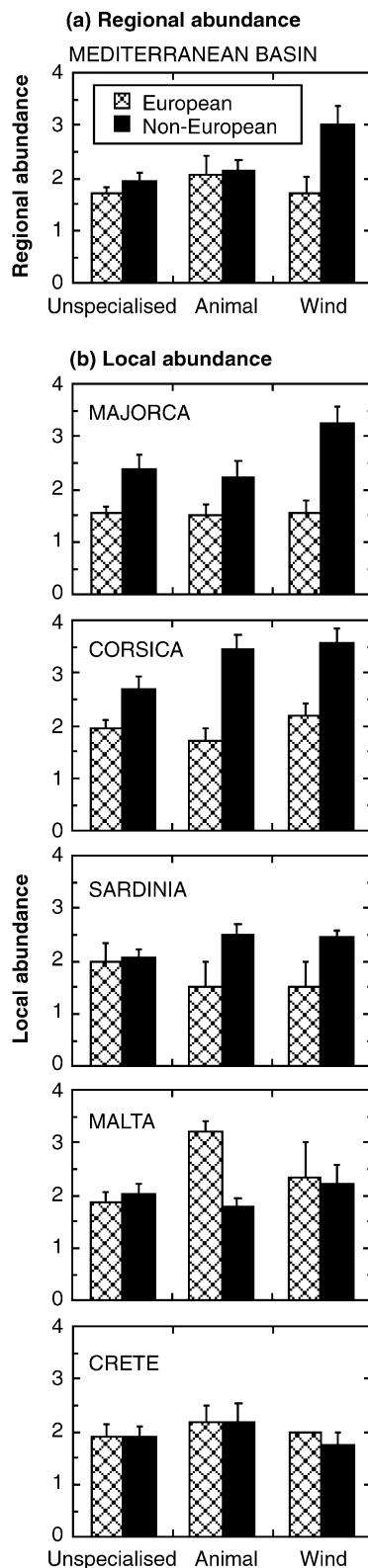
(a) Regional abundance

Figure 2 Trends in exotic abundance in the Mediterranean Basin in relation to three different dispersal syndromes: (a) Mean regional abundance (estimated as the proportion of islands, n = 8), and (b) mean local abundance for five islands. Means are presented separately for species of European and non European origin. Bars indicate one standard error.

abundance on Majorca and Sardinia. Species possessing wind and animal dispersal syndromes were more prevalent among the non-European exotics than among the European exotics ($\chi^2 = 9.39$, $P = 0.009$; Table 3). The same pattern was observed for Majorca ($\chi^2 = 9.04$, $P = 0.011$), Corsica ($\chi^2 = 5.74$, $P = 0.057$), and Crete ($\chi^2 = 9.94$, $P = 0.007$), but not for Malta ($\chi^2 = 3.12$, $P = 0.210$) or Sardinia ($\chi^2 = 1.99$, $P = 0.320$).

The species growth form did not significantly explain patterns of regional abundance (Table 2), or local abundance on any individual island. There were no differences in these relationships when the European and the non-European species were compared separately, except for Sardinia, where growth form had a significant effect on local abundance in the non-European group due to the abundance of succulents. Overall, differences between the European and the non-European species for growth form were not significant ($\chi^2 = 8.93$, $P = 0.063$), but the percentage of therophytes, phanerophytes and succulents was higher in the non-European than the European group, while the opposite trend was observed for hemicryptophytes and chamaephytes (Table 3). The distribution of different growth forms varied between the European and the non-European species in Malta ($\chi^2 = 16.95$, $P = 0.005$), but was not significant for Crete ($\chi^2 = 10.18$, $P = 0.070$), Sardinia ($\chi^2 = 5.17$, $P = 0.395$), Corsica ($\chi^2 = 8.98$, $P = 0.110$) or Majorca ($\chi^2 = 5.62$, $P = 0.345$).

Taller plants did not appear to have greater regional abundance than smaller plants (Table 2), but this trend was found to explain variation in local abundance on Majorca and Corsica. Taking into account species origin did not modify this trend for regional abundance. For the case of Majorca, a significant positive correlation was found between stem height and local abundance of the European, but not of the non-European exotics, while the converse was observed in Sardinia. In Corsica, no significant effect of stem height was observed in either of the two biogeographical groups. No significant differences in mean stem height were found between the European and the non-European exotic species over all islands (ANOVA, $F_{1,296} = 2.75$, $P = 0.098$) or for individual islands (Malta, $F_{1,75} = 2.38$, $P = 0.127$; Crete, $F_{1,93} = 0.69$, $P = 0.408$; Sardinia, $F_{1,110} = 1.23$, $P = 0.27$; Corsica, $F_{1,159} = 0.004$, $P = 0.953$; Majorca, $F_{1,114} = 0.36$, $P = 0.548$).

DISCUSSION

Exotic plant species on selected islands of the Mediterranean Basin exhibit unimodal, right-skewed abundance distributions at a regional scale. This pattern also occurs in the distribution of exotic plant taxa among the European territories described in *Flora Europaea* (Weber, 1997). Although found for a variety of organisms (Gaston, 1998), and probably reflecting that species with restricted distributions tend to be locally rare, this pattern is consistent with the relatively low success rate of non-native species introductions (Crawley *et al.*, 1996; Williamson & Fitter, 1996). According to the Willis 'age-and-area' hypothesis (Gaston, 1994), this pattern would result if the range of a species relates to its date of introduction. Since most exotics have been introduced relatively recently it may be that there has been insufficient time for them to occupy their full range. However, data from Corsica,

Table 2 Significance values for the relationship between species traits and both regional and local abundance for the total set of species and for species of European and non-European origin. Local abundance was analysed by ordinal regression models including dispersal syndrome, growth form and stem height as explanatory variables. Regional abundance was analysed by Kruskal–Wallis (dispersal syndrome and growth form) and Spearman rank correlations (stem height). Sequential Bonferroni tests ($\alpha = 0.1$) were applied to the tests for each biogeographical group. Significant values ($P < 0.1$) are highlighted in bold

	Regional abundance all eight islands	Local abundance				
		Majorca	Corsica	Sardinia	Malta	**Crete**
Total species						
Dispersal mode	0.021	0.005	0.030	**0.148**	**0.598**	**0.482**
Growth form	**0.225**	**0.258**	**0.166**	**0.410**	**0.324**	**0.679**
Stem height	**0.879**	0.084	0.072	**0.100**	**0.920**	**0.383**
European						
Dispersal mode	**0.457**	**0.796**	**0.662**	**0.998**	**0.896**	**0.875**
Growth form	**0.681**	**0.585**	**0.323**	**0.896**	**0.675**	**0.569**
Stem height	**0.476**	0.030	**0.198**	**0.146**	**0.789**	**0.790**
Non-European						
Dispersal mode	0.008	0.021	**0.147**	0.074	**0.204**	**0.773**
Growth form	**0.174**	**0.572**	**0.863**	0.085	**0.569**	**0.813**
Stem height	**0.556**	**0.823**	**0.422**	0.094	**0.721**	**0.246**

Table 3 Number of species belonging to each dispersal mode, growth form category, and stem height class in relation to their origin (Euro: European, Non-Euro: Non-European) for all eight islands, and separately for Majorca, Corsica, Sardinia, Malta and Crete. Asterisks indicate significant differences between the European and the Non-European groups (ns: no significant, *$P < 0.1$, **$P < 0.05$, ***$P < 0.01$)

	All eight islands		Majorca		Corsica		Sardinia		Malta		Crete	
	Euro	Non-Euro	Euro	Non-Euro	Euro	Non-Euro	Euro	Non-Euro	Euro	Non-Euro	Euro	Non-Euro
Dispersal mode												
Wind	14	44	9	20	15	26	2	25	3	9	1	19
Animal	17	66	10	18	18	22	2	23	5	20	12	15
Unspecialized	62	101	36	23	48	34	9	45	16	24	20	28
	***		**		*		ns		ns		***	
Growth form												
Therophytes	24	76	21	28	25	31	6	31	11	17	13	32
Geophytes	11	23	5	6	10	12	1	9	3	4	5	5
Hemicryptophytes	22	28	12	6	24	16	3	12	1	7	5	9
Chamaephytes	13	8	4	5	5	3	0	5	4	1	4	0
Phanerophytes	19	60	12	11	15	11	1	29	3	19	5	11
Succulents	3	14	1	5	1	8	2	7	1	5	1	5
	*		ns		ns		ns		***		*	
Stem height(cm)												
< 50	40	75	20	31	34	32	6	19	13	17	14	24
50–100	31	49	23	13	30	26	6	30	8	10	12	15
100–200	9	26	8	7	6	10	0	10	1	8	3	11
200–500	6	23	1	6	4	8	0	11	1	6	1	7
> 500	7	37	3	4	7	4	0	20	1	12	2	5
	ns		ns		ns		ns		ns		ns	

where the first record of exotic occurrence is well documented (Natali & Jeanmonod, 1996), reveals no significant correlation between local abundance and date of the first record (Spearman rank correlation, $r = -0.09$, $P = 0.251$, $n = 164$).

The positive correlation between local and regional species abundance suggests that factors determining the rate of invasion at a large spatial scale, such as propagule pressure, dispersal ability, or ability to compete successfully for resources, can also operate at smaller scales. Similarly, this pattern may arise from a positive relationship between a species' abundance and its ability to use a wide range of resources and conditions (Brown, 1984). Novotny (1991) notes that this positive correlation is particularly frequent in disturbed habitats where exotics species, many of which are ruderals, are often well established (Vilà & Muñoz, 1999). In the Mediterranean, as elsewhere, high local abundance may increase the probability of accidental or deliberate transport of species from one island to another. However, in the absence of evidence of a mechanism it should be borne in mind that the pattern could also be a result of undersampling of locally rare species (Gaston *et al.*, 1997).

Our study reveals the importance of considering a species' origin when exploring patterns in the abundance of exotic species. Weber (1997) also found different abundance distributions among European territories for the European and the non-European exotic species. Overall, the non-European species are more abundant in the Mediterranean islands than the European exotics. This pattern occurs both at local and regional scales. Such a result may be an artefact if exotic taxa of European origin had successfully colonized islands prior to any systematic botanical recording. Such an artefact would bias the data towards finding fewer successful exotics of European origin, a common problem in analyses of invasion (Crawley *et al.*, 1996). Alternatively, Darwin's naturalization hypothesis suggests that species with distinct taxonomic histories (including origin) may face fewer obstacles (e.g. competition, herbivory, etc.) to establishment than species taxonomically close to natives (Daehler, 2001; Duncan & Williams, 2002). To minimize this bias, we excluded from the analysis of regional abundance those European exotics that are considered native in some of the islands. Differences between species traits, particularly dispersal attributes, of the European and the non-European taxa support Darwin's naturalization hypothesis, but further analysis of a more complete set of traits and comparisons with the native flora are needed to shed light on the meaning of the different success rates of these groups.

The identity of species attributes that might lead some exotics to be more successful than others is an important conservation issue (Reichard & Hamilton, 1997; Daehler, 1998; Goodwin *et al.*, 1999). Species traits, especially dispersal attributes, emerge as important correlates of invasion success. Seed dispersal is related to colonization ability and has previously been linked to species invasiveness, particularly in species dispersed by vertebrates (Binggeli, 1996; Rejmánek, 1996; Rejmánek & Richardson, 1996). Our results highlight that while dispersal is of importance in the regional distribution, its significance for local abundance is island dependent. In the Mediterranean islands, the importance

of seed dispersal depends on species origin. Wind-dispersed species were more common in the non-European than the European group. It remains to be tested if this pattern is a consequence of differences in the proportion of wind-dispersed plants in the entire European and non-European flora from which exotic species are drawn. The higher regional abundance of wind-dispersed species may attest to the potential importance of long-distance dispersal in the colonization of Mediterranean islands and/or the ease with which wind-dispersed seeds are accidentally transported among islands. Both of these possibilities are consistent with the finding that dispersal syndrome is not correlated with invasion success in exotics of European origin.

Growth form and stem height are attributes related to resource exploitation and stress tolerance. Although occasionally correlated with invasion success (Binggeli, 1996; Thébaud & Simberloff, 2001), the importance of these traits may relate to habitat type and the community of species within which the exotic occurs (Roy, 1990; Rejmánek, 2000). That is, the contribution of these parameters to the invasion success should be better understood through the analysis of species growing in the same habitat. In our study on Mediterranean islands, growth form and stem height do not play a major role in regional abundance and they are of variable importance in local abundance. Although woody species and geophytes are over-represented in the exotic flora of the British Isles and exotics tend to be taller than their native counterparts, this may be a consequence of horticultural fashion rather than invasion success (Crawley *et al.*, 1996) or the result of the genetic attributes of the original founder population.

In summary, our study has highlighted the importance of analysing invasion success at both local and regional scales. Studies at a single spatial scale are unlikely to discern the drivers of invasion patterns. Furthermore, life-history traits may play a lesser role in invasion success than the biogeographical origin of the exotic species. Only dispersal syndrome appeared to be strongly related to invasion success yet its direct role in both local and regional abundance requires further study. While it is likely that studies of additional life-history traits (e.g. palatability, seed bank, drought tolerance, fire tolerance, fecundity, etc.) may discern further determinants of invasion success, a key finding is the stochastic nature of exotic species assemblages on the islands. Most exotics occurred on only one island and are likely to arise from chance events, historical circumstances and idiosyncratic invasions. These processes will undoubtedly limit our ability to model and predict invasion success, especially if islands are studied in isolation.

REFERENCES

Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 52–66.

APG (Angiosperm Phylogeny Group) (1998) An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden*, **85**, 531–553.

Binggeli, P. (1996) A taxonomic, biogeographical and ecological overview of invasive woody species. *Journal of Vegetation Science*, **7**, 121–124.

Bolòs, O. de & Vigo, J. (1984–2001) *Flora dels Països Catalans*. Volumes. 1–4. Barcino, Barcelona.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Camarda, I. (1998) Considerazioni su alcune specie di antica e recente introduzione in Sardegna e la loro dinamica di diffusione. *Biocosme Mésogéen*, **15**, 89–108.

Chilton. L. & Turland, N.J. (1997) *Flora of Crete: a supplement*. Marengo Publications, Retford.

Chilton. L. & Turland, N.J. (2002) *Flora of Crete: supplement II*, Additions 1997–2002. http://www.marengo.supanet.com/text/fcs.htm.

Collingham, Y.C., Wadsworth, R.A., Willis, S.G., Huntley, B. & Hulme, P.E. (2000) Predicting the spatial distribution of alien riparian species: issues of spatial scale and extent. *Journal of Applied Ecology*, **37** (Suppl. 1), 13–27.

Crawley, M.J., Harvey, P.H. & Purvis, A. (1996) Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London B*, **351**, 1251–1259.

Daehler, C.C. (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation*, **84**, 167–180.

Daehler, C.C. (2001) Darwin's naturalization hypothesis revisited. *American Naturalist*, **158**, 324–330.

Di Castri, F., Hansen, A.J. & Debussche, M. (1990) *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht.

Duncan, R.P. & Williams, P.A. (2002) Darwin's naturalization hypothesis challenged. *Nature*, **417**, 608–609.

Gaston, K.J. (1994) *Rarity*. Chapman & Hall, London.

Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London B*, **353**, 219–230.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance — range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.

Goodwin, B.J., McAllister, A.J. & Fahring, L. (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology*, **13**, 422–426.

Haslam, S.M., Sell, P.D. & Wolseley, P.A. (1977) *A flora of the Maltese Islands*. Malta University Press, Malta.

Higgins, S.I., Richardson, D.M. & Cowling, R.M. (1996) Modeling invasive plant spread: the role of plant–environment interactions and model structure. *Ecology*, **77**, 2043–2054.

Jahn, R. & Schönfelder, P. (1995) *Exkursionsflora für Kreta*. Ulmer, Stuttgart.

Jeanmonod, D., ed. (2000) Notes et contributions à la flore de Corse, XVI. *Candollea*, **55**, 41–74.

Jeanmonod, D. & Burdet, H.M., eds (1997) Notes et contributions à la flore de Corse, XIII. *Candollea*, **52**, 239–279.

Jeanmonod, D. & Burdet, H.M., eds (1998) Notes et contributions à la flore de Corse, XIV. *Candollea*, **53**, 171–210.

Jeanmonod, D. & Burdet, H.M., eds (1999) Notes et contributions à la flore de Corse, XV. *Candollea*, **54**, 385–416.

Jeanmonod, D. & Schlüssel, A., eds. (2001) Notes et contributions à la flore de Corse, XVII. *Candollea*, **56**, 139–170.

Koleff, P. & Gaston, K.J. (2002) The relationship between local and regional species richness and spatial turnover. *Global Ecology and Biogeography*, **11**, 363–375.

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

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

Mooney, H.A. & Hobbs, R.J. (2000) *Invasive species in a changing World*. Island Press, Washington DC.

Natali, A. & Jeanmonod, D. (1996) Flore analytique des plantes introduites en Corse. *Compléments au prodrome de la flore Corse* (ed. by D. Jeanmonod and H.M. Burdet), pp. 1–211. Conservatoire et Jardin botaniques de Genève, Geneve.

Novotny, V. (1991) Effect of habitat persistence on the relationship between geographic distribution and local abundance. *Oikos*, **61**, 431–433.

Pignatti, S. (1982) *Flora d'Italia*, Vol. 1–3. Edagricole, Bologna.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment*, **84**, 1–20.

Pyšek, P. (1998) Is there a taxonomic pattern to plant invasions? *Oikos*, **82**, 282–294.

Pyšek, P., Sadlo, J. & Mandak, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.

Quézel, P., Barbero, M., Bonin, G. & Loisel, R. (1990) Recent plant invasions in the circum-mediterranean region. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. Di Castri, A.J. Hansen and M. Debussche), pp. 51–60. Kluwer Academic Publishers, Dordrecht.

Raunkiaer, C. (1934) *The life form of plants*. Oxford University Press, Oxford.

Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced in North America. *Conservation Biology*, **11**, 193–203.

Rejmánek, M. (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171–181.

Rejmánek, M. (2000) Invasive plants: approaches and predictions. *Austral Ecology*, **25**, 497–506.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Roy, J. (1990) In search of the characteristics of plant invaders. *Biological invasions in Europe and the Mediterranean Basin* (ed. by F. Di Castri, A.J. Hansen and M. Debussche), pp. 335–352. Kluwer Academic Publishers, Dordrecht.

SAS (1984–94) *JMP 3.1.5*. SAS Institute Inc, Cary, NC, USA.

Scott, J.K. & Panetta, F.D. (1993) Predicting the Australian weed status of southern African plants. *Journal of Biogeography*, **20**, 87–93.

Thébaud, C. & Simberloff, D. (2001) Are plants really larger in their introduced ranges? *American Naturalist*, **157**, 231–236.

Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995) Native and alien invasive plants: more of the same? *Ecography*, **18**, 390–402.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A., eds (1964–80) *Flora Europaea*, Vol. 1–5. Cambridge University Press, Cambridge.

Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A., eds (1993) *Flora Europaea*, Vol. 1, 2nd edn. Cambridge University Press, Cambridge.

Viegi, L. (1993) Contributo alla conoscenza della biologia delle infestanti delle colture della Sardegna nord-occidentale. I. Censimento delle specie esotiche della Sardegna. *Bollettino Della Societa Sarda Di Scienze Naturali*, **29**, 131–234.

Vilà, M., García-Berthou, E., Sol, D. & Pino, J. (2001) Survey of the naturalised plants and vertebrates in peninsular Spain. *Ecologia Mediterranea*, **27**, 55–67.

Vilà, M. & Muñoz, I. (1999) Patterns and correlates of exotic and endemic plant taxa in the Balearic islands. *Ecologia Mediterranea*, **25**, 153–161.

Walther, G.R. (2000) Climatic forcing on the dispersal of exotic species. *Phytocoenologia*, **30**, 409–430.

Weber, E. (1997) The alien flora of Europe: a taxonomic and biogeographic review. *Journal of Vegetation Science*, **8**, 565–572.

Whittaker, R.J., Field, R. & Partomihardjo, T. (2000) How to go extinct: lessons from the lost plants of Krakatau. *Journal of Biogeography*, **27**, 1049–1064.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **76**, 1666–1670.

BIOSKETCHES

Francisco Lloret has research interests in the study of plant community dynamics and patterns of plant functional types in relation to anthropogenic sources of perturbation, such as exotic plant invasion, fire regime, land use changes, and climate change.

Frederic Médail has research interests in conservation biology, plant invasion and biogeography, specifically on Mediterranean islands. He is currently devoted to the conservation of plant diversity hotspots at several geographical scales in the Mediterranean Basin. He is member of several National scientific committees and of the Mediterranean Island Plants Specialist Group (IUCN).

Giuseppe Brudu, agronomist, deals primarily with geomatics applied to nature conservation, vegetation monitoring and mapping in Mediterranean environments, with special concern to protected areas. He is a member of the Italian Remote Sensing and G.I.S. Association (A.I.T.).

Philip Hulme is Head of the Community Ecology Section at the NERC Centre for Ecology and Hydrology. He currently manages several large-scale projects on plant invasions in the Arctic tundra, Scottish Glens, Mediterranean islands and the semi-arid tropics. He is secretary of the British Ecological Society's Invasive Species Specialist Group and is a member of the UK Government's Advisory Committee on the Releases to the Environment.