Local and regional abundance of exotic plant species on Mediterranean islands: species traits or island attributes?

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ABSTRACT: Biological invasions by non-native or "exotic" plant species are widely recognised 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. A fundamental challenge posed by biological invasions has been the identification of characteristics associated with the invasion success of exotic species. We have examined these questions at different spatial scales. Firstly, the importance of life-history traits and biogeographic origin on the local (within island) and regional (between island) abundance of 396 exotic species was examined across a set of key, well-studied islands in the Mediterranean Basin. Secondly, a larger number of species were assessed across a wider range of islands, using less detailed published information. Naturalization rates (the number of islands on which they were recorded to be naturalized) were the least reliable indicators of true invasiveness, but a combined index from both spatial scales gave the best overall picture of invasion success. We found that life-history traits may play a lesser role than invasion history. However, local abundance was highly variable between islands and even between ecologically-similar species. The comparison of these approaches demonstrates that 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.

1 INTRODUCTION

Biological invasions by non-native or "exotic" plant species are considered one of the most important environmental problems resulting from human-caused global environmental change. The consequences of such invasions include losses to the economic value, biological diversity and function of the affected ecosystems (Mooney and Hobbs 2000, Mack et al. 2000, Pimentel et al. 2001). There are theoretical reasons to expect dramatic effects of plant invaders on isolated habitats, such as those on geographical islands (Lonsdale 1999). Particularly, their importance in Mediterranean-type ecosystems has been extensively documented (Di Castri et al. 1990, Vilà et al. 2001).

In order to develop screening procedures for potentially harmful species, it will be necessary to devise methods for assessing invasion risk: a function of both the consequences of invasion, and the likelihood of its occurrence. At present, the consequences are poorly-understood. In contrast, likelihood, in terms of known invasion success, can be evaluated from copious data on the extent and history of plant invasions. "Invasion success" is, in turn, a function of both the likelihood of

naturalization in a given territory, and the ability to spread across the territory once established (naturalized species are considered here as those able to reproduce consistently and to sustain populations (see Richardson et al. 2000). Furthermore, the analysis of the invasion process across both scales is essential, since generalizations from local surveys are often highly inconsistent (Weber 1997, Daehler 1998, Pyšek 1998) and are unlikely to provide insights into the main drivers of invasion patterns (Collingham et al. 2000). Therefore, our approach evaluates the phenomenon at different hierarchical levels: regional geographical distribution and local abundance.

Different criteria may be applied to analyze invasion success for a set of species: taxonomy, biological traits, biogeographic origin, and mode of introduction. These species traits are likely to interact with characteristics of the invaded area, such as the extent and type of habitat and the land-use types.

The use of species traits has been proposed to describe biological attributes of vegetation that are believed to reflect ecological processes, such as plant invasions (Roy 1990). Several studies have investigated sets of traits of invasive non-native plants (Rejmánek and Richardson 1996, Binggeli 1996, Crawley et al. 1996, Reichard and Hamilton 1997, Goodwin et al. 1999). These attempts have achieved varying success, highlighting the difficulties for screening potentially undesirable species (Scott and Panetta 1993, Mack et al. 2000, Mooney and Hobbs 2000). However, the relationship between biological attributes and invasion success, as estimated from abundance patterns in the invaded area, remain to be investigated (Thompson et al. 1995). Assemblages of non-native species with different biogeographic origins may show different colonization patterns, according to their mode of introduction and dispersal history.

We have explored the patterns of exotic plant occurrence on islands spanning the whole Mediterranean basin, considering the role of several taxonomic, biogeographic, and biological attributes on invasion success, as predicted by the abundance patterns of non-native plants at two different levels: i) "Regional", indicated by island naturalization rate, and ii) "Local", considered as a qualitative estimate of species abundance within a particular island

2   METHODS

Literature records were used to construct a detailed database of 376 exotic plant species. We excluded casual species (as quoted by the source reference), hybrids, subspecies, and taxa of unknown origin. We also excluded extensively cultivated taxa because they are often of uncertain origin and taxonomic assignation, and may have been massively propagated close to natural habitats. Regional abundance data were collated from 80 islands for which the floras were considered reliable and contemporary ($24 < 10$ km^2, $10 < 1$km^2 in area). The naturalization rate was considered as the proportion of islands where the species was considered to be present. For those species native to some part of the Mediterranean, islands where they were indigenous were excluded from the total. If this reduced the invisible island pool to less than 20, the species was omitted from further analyses. Local abundance data was collated across five Mediterranean islands: Crete, Malta, Sardinia, Corsica, and Majorca, and included the full set of exotic taxa. This information was updated for Majorca, Minorca, Sardinia, Corsica and Lesbos by local botanists.

Species were classified into five bioclimatic zones according to their native origin, and also as European/non-European. "European" species included those native to the European continent, Mediterranean Basin and cosmopolitan species, and "non-European" species whose native origin was from other continents. The bioclimatic zones comprised "Mediterranean" (from the Mediterranean basin sensu stricto), "Mediterranean exotic" (from other Mediterranean climate biomes in Australia, California, Chile or South Africa), "Boreal-temperate", "Tropical" and "Arid-subtropical" (from warm regions which are neither Mediterranean or truly tropical).

We selected fifteen biological attributes which are available from literature: growth form, stem height, longevity, vegetative propagation, leaf size, succulence, spinescence, reproduction type, pollination type, date of flowering start, length of flowering period, fruit type, seed size and dispersal type. Data was compiled from eight Mediterranean islands: Crete, Rhodes, Lesbos, Malta, Sar-

dinia, Corsica, Majorca and Minorca. Extrinsic factors taken into consideration included island area, date of introduction and frequency of introduction. Dates were obtained from literature records where available. Frequency of introduction was estimated by local botanists on the five key islands using a six point scale. Those species which were not considered to be deliberately introduced were allocated a score of 1 or 2, depending on whether they were likely to be rare or relatively frequent as accidental imports.

3   RESULTS AND DISCUSSION

3.1   *Assessing invasion success*

The local and regional components of invasion success were moderately well correlated (Fig. 1, r^2 = 0.56), thus species which are naturalized on many islands tend to be the most widespread on those islands. However, there remain important differences in the assessments generated by each approach. The highest ranked species are compared in Table 1. A subjective appraisal of these lists suggests that the Regional abundance method yields the least useful measure, ranking some species highly ("over-weighting") which few authorities (e.g. Di Castri et al. 1990) would regard as major invasive problems in the region (*Sorghum halepense*, *Punica granatum*, *Matricaria recutita*, *Ornithogalum arabicum*), and omitting other important names (e.g. *Ailanthus altissima*, *Ricinus communis*) from the top fifteen. The local abundance method seems to offer a more accurate reflection of the species, which generate most environmental concern. The product of the two indices may offer the best measure, as it is a mathematical reflection of "abundance per unit area" throughout the whole region (Table 1). However, this criterion generates a similar list to that produced by Local abundance. All methods rank *Oxalis pes-caprae* as by far the most successful invasive species in the Mediterranean region.

Table 1. The top 15 ranked successful invaders species according to Local and Regional abundance criteria, and to an Invasion success index, which is the product of these two measures

Most locally-abundant		Most regionally-abundant		Highest overall success	
Species	Mean score	Species	P(islands invaded)	Species	Su in
Oxalis pes-caprae	0.85	Oxalis *pes-caprae*	0.481	*Oxalis pes-caprae*	0.
Ailanthus altissima	0.75	*Arundo donax*	0.354	*Arundo donax*	0.
Opuntia ficus-indica	0.7	*Agave americana*	0.291	*Opuntia ficus-indica*	0.
Conyza bonariensis	0.7	*Opuntia ficus-indica*	0.278	*Agave americana*	0.
Xanthium spinosum	0.7	*Nicotiana glauca*	0.253	*Nicotiana glauca*	0.
Aster squamatus	0.7	*Amaranthus albus*	0.241	*Conyza bonariensis*	0.
Nicotiana glauca	0.65	*Conyza canadensis*	0.241	*Ailanthus altissima*	0.
Carpobrotus edulis	0.65	*Sorghum halepense*	0.229	*Xanthium spinosum*	0.
Agave americana	0.6	*Amaranthus retroflexus*	0.228	*Carpobrotus edulis*	0.
Chenopodium ambrosioides	0.6	*Conyza bonariensis*	0.215	*Amaranthus albus*	0.
Ricinus communis	0.6	*Punica granatum*	0.203	*Aster squamatus*	0.
Medicago sativa	0.6	*Matricaria recutita*	0.2	*Phytolacca americana*	0.0
Arundo donax	0.55	*Ornithogalum arabicum*	0.190	*Conyza canadensis*	0.0
Phytolacca americana	0.55	*Xanthium spinosum*	0.190	*Sorghum halepense*	0.0
Mirabilis jalapa	0.55	*Carpobrotus edulis*	0.190	*Amaranthus retroflexus*	0.0
Medicago sativa	0.386	*Punica granatum*	-0.200	*Chenopodium ambrosioides*	0.

One possible explanation for the discrepancy in the regional abundance list is that the over-weighted species (those which were ranked at least 15 places lower in the local abundance list) could represent incipient threats, which have only recently begun to colonize. However, the mean

date of introduction of the ten highest-ranked of these is in fact earlier than that of the ten highest other species (1705 ± 117 years s.e.m. vs. 1862 ± 22 years s.e.m.). Another possibility is that many over-weighted species may be widely cultivated (introduced to many islands but naturalizing only rarely). This hypothesis is also not generally supported: the correlation between success index and frequency of introduction scores is very weak, either when restricted to the over-weighted group (r^2 = 0.055) or even when all species are included (r^2 = 0.003). Thus, propagule pressure has very little influence on invasiveness. "Over-weighted" species tend to be native to parts of the Mediterranean, and the fact that they have never naturally colonized the entire area may indicate that they are not vigorous colonizers. It seems more likely that these species, although capable of surviving in a naturalized state, are not effective dispersers. Dispersal ability may thus be an important determinant of invasiveness.

Although Local abundance offers a useful measure of invasion success, this is only true when assessed across several different islands. The five included in this study differed widely in their scores for each species, and the correlation between any pair of islands was always very weak (r^2 < 0.1). This indicates a high degree of local variation in colonization success. At the regional scale, island identity explained 38.8% of the deviance in a multinomial ordinal logit model of naturalization rate (p < 0.0001). Island area is an important contributory factor to this (p < 0.0001), explaining 58.5% of the island term.
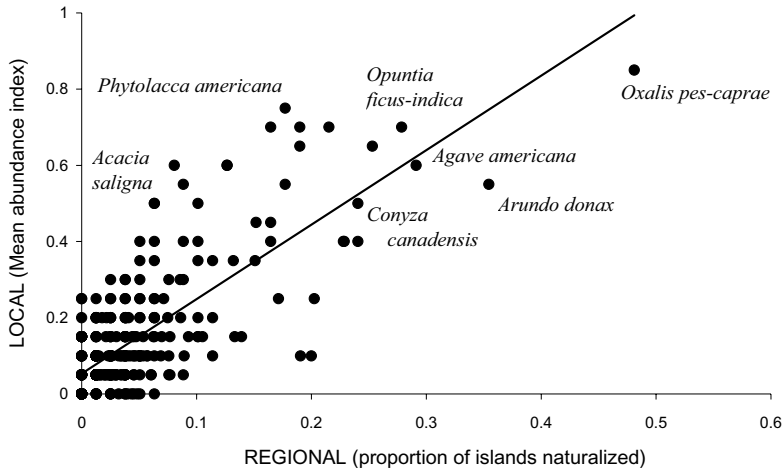

Figure 1. Relationship between regional and local abundance indices for 376 species of exotic plants, with some key species indicated

3.2 *Biogeographic origin*

The correlation between local and regional abundance was stronger for species of non-European origin, which were also more widespread than European species (Lloret et al. 2004). Although explaining only a small proportion of deviance in a log-linear model of the success index (2.5%) the bioclimatic groupings also reinforced these findings. Mediterranean native species had a lower mean success index than other groups (0.0044, n = 105 species vs. overall mean of 0.0063, n = 239 species; p = 0.041), but none of the other groupings were significantly different (p > 0.05). This suggests that climatic adaptation to the Mediterranean regime is not particularly important. Although this conclusion is counter-intuitive, few temperate species are introduced to the region unless they have at least a degree of resilience to the Mediterranean environment, thus effectively undergoing a partial screening. The poorer performance of Mediterranean natives is less easily explained. However, some reproductive traits, such as flowering phenology and growth form types,

allow discrimination between the European/non-European groups (Stepforward Multivariate Discriminant Analysis, Wilk's Lambda = 0.908, $F_{7,324}$ = 4.69, p < 0.0001), which may indicate that confounding adaptive factors are involved. In addition, Darwin's naturalization hypothesis suggests that species with novel taxonomic origins may experience fewer obstacles (e.g. competition, herbivory etc.) to establishment than species closely related to natives (Daehler 2001, Duncan and Williams 2002).

3.3 *Taxonomy*

Previous authors have found that certain taxa have a predisposition towards invasion success (*e.g.* Pyšek 1998, Lockwood 1998), although this may reflect either the inheritance of characteristics truly associated with invasiveness or an increased frequency of introduction. Analysis of taxonomic trends has proved difficult in the past because many taxa contain very few individuals, leading to highly unbalanced data sets: especially at the lower taxonomic levels where evolution of these traits is most likely to occur (Daehler 1998). This analysis is restricted to the ranks of Order and Family. In a nested log-linear analysis of the invasion success indices, neither was found to be significant (p = 0.13 and 0.25 respectively), although the terms explained 11.5% and 14.8% of the model deviance. However, even at these levels, many families and orders contain just one naturalized member. This in itself is an indication that invasiveness is highly unpredictable across lineages. Although large families often contain more invasive members (*e.g.* Weber 1997), their mean invasibility is not detectably higher (Fig. 2).
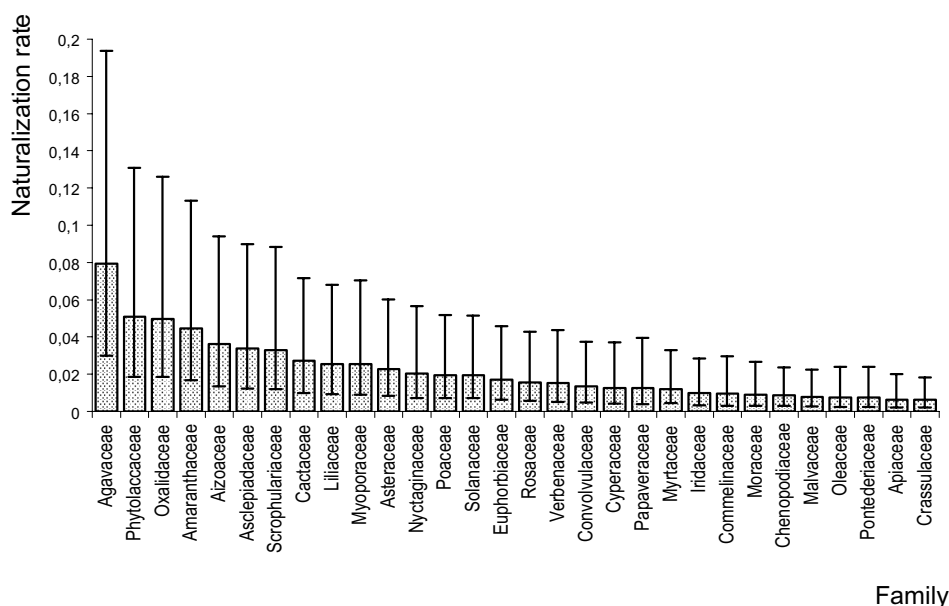

Figure 2. The 30 exotic plant families with the highest mean naturalization rates, excluding those with less than two species. Error bars represent standard errors of the mean. None of the families were significantly different (p > 0.05, multinomial logit model).

3.4 *Date of introduction*

Date of introduction may determine patterns of invasion success. More recently introduced species may show a restricted distribution because they have not yet occupied their full potential range, according to the Willis "age-and-area" hypothesis (Gaston 1994). This hypothesis could explain the lower abundance of non-European than European species, as observed. However, analysis of local

abundance data from islands where the first record of exotic occurrence is well documented (such as Corsica), did not show a clear relationship (Lloret et al. 2004). Neither were there significant differences in a comparison between archaeophytes (introduced before ca. 1500 AD) and neophytes for all eight islands (Crete, Rhodes, Lesbos, Malta, Sardinia, Corsica, Majorca and Minorca) (ordinal multinomial logit model, Wald = 2,50, p = 0.114). In this latter analysis, the same pattern was observed in Corsica, Sardinia, Majorca, and Crete, but in Malta archaeophytes were indeed more abundant. At the regional scale, there was also no relationship between date of introduction and abundance (p > 0.3 for each of five date classes, n = 353 species), explaining only 3.4% of the deviance between species in an ordinal multinomial logit model of naturalization rate. However, analysis of the combined invasion success index did yield a significant pattern, (12.5% of the deviance explained in an ordinal log-linear model; p = 0.004; Fig. 3). Neophytes were decreasingly successful as invaders with more recent introduction dates (but only the 1950+ date class was significantly different to 1600-1800). Archeophytes were less successful than long-established neophytes, although this pattern (and the lower mean invasion success of Mediterranean native species) may be an artifact of historical perception: older (principally intra-regional) introductions are more difficult to identify, as the species are often very well established. Also, the total area infested may be more a reflection of the extent of suitable habitats than of invasiveness or ecological impact; this is especially true when considerable time has elapsed since the first introduction (Campbell 1997). Whilst the "age-and-area" effect may be difficult to detect in the Mediterranean invasive flora, many of the most invasive species (*Ailanthus altissima, Oxalis pes-caprae, Carpobrotus edulis*) have certainly been introduced in the last two centuries.

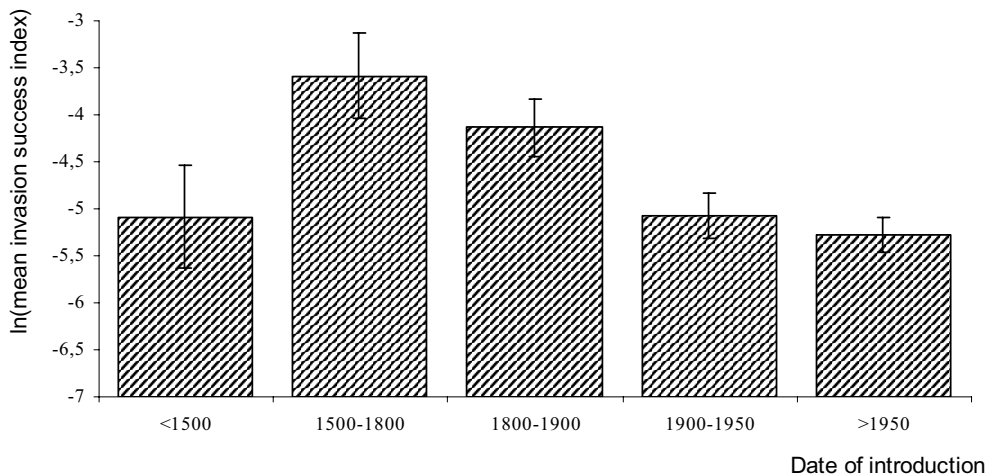Figure 3. Relationship between invasion success index and date of introduction (n >= 16 for all date classes). Error bars represent standard errors of the mean. Only the 1500-1800 and >1950 classes were significantly different (p < 0.05, log-linear model).

3.5 *Biological traits*

The regional success of non-native species can be significantly explained by biological traits (Step-forward Multivariate Discriminant Analysis, $F_{9, 213}$ = 4.98, p < 0.0001), although the discriminant power of the model is low (Wilk's Lambda = 0.826). Dispersal mode, length of the flowering period and succulence are the main attributes contributing to this result. The proportion of species with wind and animal dispersed seeds is higher in the group of successful non-natives than in the non-successful group. The proportion of species with expanded flowering period is also higher

among the widespread non-natives. Succulent species are also more common among the more successful non-natives.

The discriminatory power of species traits on invasion success increases at island level (Majorca, Wilk's Lambda = 0.593; Corsica, Wilk's Lambda = 0.744; Sardinia, Wilk's Lambda = 0.583; Malta, Wilk's Lambda = 0.581; Crete, Wilk's Lambda = 0.763). However, the specific attributes contributing to this discriminations differs between islands: pollination type and plant height in Majorca, time of first flowering and growth form in Corsica, time of first flowering and pubescence in Sardinia, fruit type and growth form in Malta, and leaf size in Crete.

The role of biological attributes on the invasion success by non-natives is a major concern for conservation management (Reichard and Hamilton 1997, Goodwin et al. 1998, Daehler 1998). Reproductive traits (dispersal mode, phenology) emerge as particularly important in this analysis. Dispersal processes may be relevant for long-distance spread (Binggeli 1996). However, their significance for local abundance is island dependent, and they also correlate to biogeographic origin (Lloret et al. 2004). Other traits related to growth form also appear to be relevant, particularly in some islands. However, the significance of these vegetative traits should better understood through analyzing the patterns of invasion success at different habitats (Roy 1990).

4 CONCLUSIONS

The analysis of invasion success must accommodate different geographical scales. Many exotics occur in a small part of their full potential range, emphasizing the importance of chance events, historical circumstances and local idiosyncrasies. Thus, although at the regional level the same common exotic species dominate the invasive flora, our key finding is the variable nature of local non-native species assemblages between islands of the Mediterranean Basin. The ability to discriminate factors, such as biological traits, that determine invasion risk increases when focused down to finer scales. Although there is not a single combination of biological attributes that predict invasion success, some reproductive traits, such as dispersal syndrome, often appear to be useful associated factors. Furthermore, life-history traits may play a lesser role in invasion success than the introduction history of the exotic species. The extent of a deterministic interpretation of invasion success is limited by this stochasticity, especially when islands are studied in isolation.

The application of screening procedures requires a comprehensive understanding of invasion risk. In this study, we have focused on those species, which are known to naturalize in the Mediterranean, examining which characteristics indicate invasiveness. This is valid, because highly invasive species account for only a small percentage of all naturalized plants. In future however, it may be revealing to examine a wider set of introduced species, identifying not only highly invasive from moderately adapted species, but a wider suite of invasion-related traits from the total species pool.

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