Assessing the risks to Mediterranean islands ecosystems from alien plant introductions

Philip E. Hulme[1,2], Giuseppe Brundu[3], Ignazio Camarda[3], Panos Dalias[4], Phil Lambdon[1], Francisco Lloret[5], Frederic Medail[6], Eva Moragues[7], Carey Suehs[6], Anna Traveset[7], Andreas Troumbis[4] and Montserrat Vilà[5]
1. NERC Centre for Ecology and Hydrology, Banchory, UK
2. National Center for Advanced Bio-Protection Technologies, PO Box 84, Lincoln University, Canterbury, New Zealand; e-mail: hulmep@lincoln.ac.nz
3. Dipartimento di Botanica ed Ecologia Vegetale, Università degli Studi di Sassari, Italy
4. Department of Environmental Studies, University of the Aegean, Mytilene, Greece
5. Centre for Ecological Research and Forestry Applications, Universitat Autònoma de Barcelona, Spain
6. Institut Méditerranéen d'Ecologie et de Paléoécologie (IMEP), Université d'Aix-Marseille III, France
7. Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Esporles, Mallorca, Spain

Abstract
The islands of the Mediterranean Basin probably represent some of the ecosystems globally most at risk from invasive species. Compared to neighbouring mainland areas, island floras have a significantly higher proportion of alien plant species. Yet the circumstances that have led to this situation and the subsequent consequences of plant invasions remain poorly understood. This knowledge deficit is addressed in this paper through a comprehensive review of recent research findings. Most alien plants occurring on Mediterranean islands have been introduced intentionally for economic purposes although there still exists a sizeable proportion that arrives by accident. A wide range of alien plant functional types have colonized Mediterranean islands. While certain traits appear important, e.g. reproductive strategies, species characteristics are closely allied to the habitats invaded. Large-scale biogeographic studies have highlighted a strong correlation between local and regional abundance suggesting a common driver of both small and large-scale invasion. Species with non-European origins appeared more successful at both spatial scales. These findings highlight the importance of estimating invasion success across a wide region thus minimizing local idiosyncrasies. Since the importance of different biological attributes may change along the dispersal, colonization and establishment phases of invasion, analyses of what makes a species invasive 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. Detailed mapping of species distribution highlighted that all habitats are to some extent at risk, though human disturbed areas proportionally more so. Impacts were examined for three focal species *Ailanthus altissima*, *Carpobrotus* spp. and *Oxalis pes-caprae*. Correlative analysis on six islands highlighted that impacts on biodiversity and soil properties are a function of both species and island with *Ailanthus* in general having the least impact while *Carpobrotus* reduced native plant diversity significantly. Although impossible to extrapolate to all invasive species, these results do highlight that significant losses in local species richness as well as ecosystem structure and func-

Plant Invasions: Human perception, ecological impacts and management, pp. 39-56
Edited by B. Tokarska-Guzik, J.H. Brock, G. Brundu, L. Child, C.C. Daehler & P. Pyšek

tion is likely to be occurring in the Mediterranean. To address this threat, mechanisms should be put in place to limit the further spread of known problem species across the Mediterranean through awareness-raising activities and better regulation of the import and disposal of alien plant material.

Introduction

Biological invasions by alien plant species are regarded as one of the most important drivers of environmental change in Mediterranean ecosystems (Sala *et al.* 2000). Yet until recently, the Mediterranean ecosystems of Europe have been perceived as less vulnerable to invasion than similar ecosystems on other continents due to the long interaction between humans and their environment (di Castri 1989, Fox 1990, Quezel *et al.* 1990, Blondel & Aronson 1999) and the fact that intentional species introductions were undertaken far more frequently by European settlers colonizing other continents than on their return to Europe (Crosby 1986). However, this perception needs significant revision since recent rapid economic development has heralded an order of magnitude change in the scale of human impacts on the environment and the increased globalization of trade has accelerated the rate of species introductions into the Mediterranean Basin (Hulme 2004).

The Mediterranean Basin is richer in islands than anywhere else outside of the tropics, and is in significant contrast to the continental nature of other regions with Mediterranean climates (e.g. California, Chile, South Africa, Australia). The ecology of islands is intimately associated with biological invasions and both the species composition and community structure of islands are recognized to be a function of colonization rates (Hubbell 2001). It follows that where colonization rates have been accelerated by human activity such ecosystems will be particularly at risk from biological invasions. Thus whereas the proportion of the flora of the Mediterranean Basin composed of aliens has been estimated to be only 1% (Quezel *et al.* 1990) values are substantially higher for Mediterranean islands e.g. Sardinia 9% (Viegi 1993), Balearics 16% (Moragues & Rita 2005), Corsica 17% (Jeanmonod 1998). Furthermore, island communities are widely believed to be more vulnerable to the impacts of alien taxa. The higher vulnerability of islands relative to comparable continental areas has been attributed to proportionally lower native diversity, the existence of unsaturated communities and as a result greater disharmony in species composition arising from the absence of key plant functional groups, lower competitive ability of native species and the higher susceptibility of insular species to the ecological impacts of invaders (Hulme 2004). Thus the islands of the Mediterranean Basin probably represent some of the ecosystems globally most at risk from invasive species. This is a result of both the relatively high percentage of alien species in the island floras and the threatened status of many endemic plant species (Hulme 2004). Yet, compared to the various monographs addressing plant invasions on oceanic islands e.g. Galapagos (Mauchamp 1997); Tiwi (Fensham & Cowie 1998); Guam (Fritts & Rodda 1998); Mauritius (Strahm 1999) there exist few detailed regional assessments of the threat from alien invasive plant species in Mediterranean islands.

To address this deficit, this paper presents a quantitative assessment of the abundance, distribution, traits and impacts of invasive alien plant species in Mediterranean islands. In addition, the islands also represent an outstanding opportunity to assess the relative magnitude of invasive species impacts within a single biome and to scale-up from local impacts up to regional implications (Pauchard *et al.* 2004). This information is crucial in the development and implementation of strategies to manage the risks posed by alien plants in the Mediterranean.

Due to the high costs often associated with the control and eradication of alien weeds (Pimentel *et al.* 2001), prevention is widely regarded as the most effective strategy in the management of biological invasions (McNeeley *et al.* 2001, Wittenberg & Cock 2001). Formulation of both general and ecosystem specific rules for the assessment of invasiveness of species and ecosystem invasibility are therefore two of the most important goals in the strategic management of plant invasions (Rejmánek 1999). Ecosystem invasibility has often been viewed exclusively as a habitat attribute (e.g. Crawley 1987, Rejmánek 1999) however, it is becoming clear that biogeographic and socio-economic drivers play an increasingly important role in invasion risk (Lonsdale 1999). Invasion risk reflects the likelihood of invasion and its subsequent consequences on native ecosystem function and species richness. Thus a comprehensive treatment for the islands of the Mediterranean Basin requires an assessment of (a) the number and strength of invasion pathways; (b) the ecosystem attributes responsible for vulnerability to invasion; (c) the species characteristics underpinning invasion success and (d) the impact of alien plants on recipient communities.

Routes of the alien problem: invasion pathways

The Global Invasive Species Program (GISP) toolkit (Wittenberg & Cock 2001) recommends examination of pathways as a more comprehensive approach to prevention. The International Plant Protection Council (IPPC) defines a pathway as "any means that allows the entry or spread of a pest" (IPPC, 2004). Despite the importance of this tool, few countries have a clear understanding of what pathways exist for introductions to their territory (Wittenberg & Cock 2001). Due to the distances involved, the spread of invasive plants among Mediterranean islands undoubtedly points towards human-mediated dispersal. Mediterranean islands are a major market for the import and export of international trade and humans have facilitated the spread of alien species into and within the Mediterranean Basin through a diversity of means. These include deliberate planting in the wild e.g. the use of *Opuntia* and *Agave* spp. as "green" fences (Le Houerou 1996), escapes from managed systems e.g. feral crops (Guillerm *et al.* 1990), as well as unintentional introductions as a by-product of trade either as contaminants e.g. weed seed in commercial grain supplies, or accidental "hitchhikers" attached to vehicles, machinery or textiles. The use of alien species in farming, forestry and for recreational purposes has increased in much of Mediterranean since the middle of the 20th century. Alien species may be imported because they grow faster than natives and thus offer increased economic returns (e.g. *Eucalyptus* spp. for forestry), satisfy demand for exotic horticultural produce (e.g. pomegranates), or simply because people like them (e.g. many ornamental plants). However, almost one third of alien plants naturalized on Mediterranean islands arrive by accident (Fig. 1).

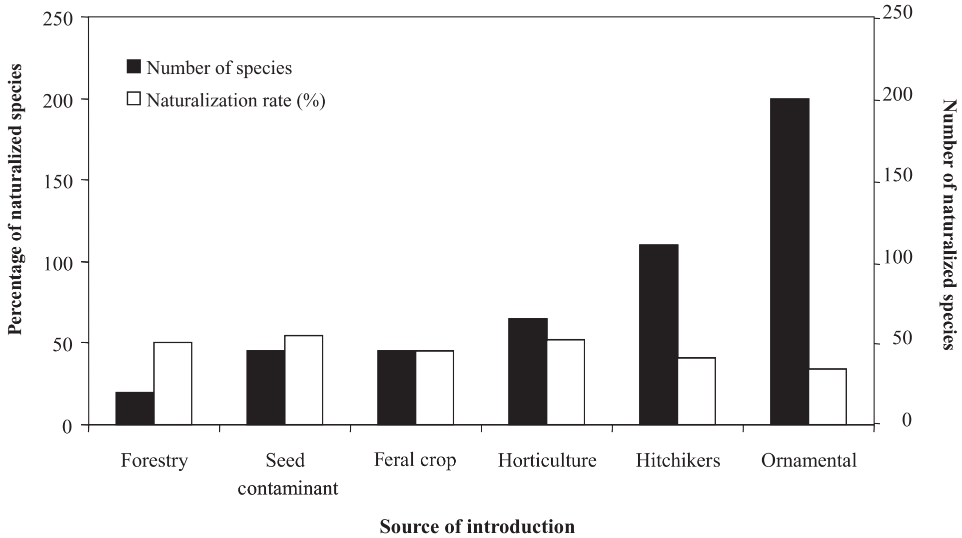


Fig. 1. Major pathways of introduction for alien plants occurring on Mediterranean islands. Both the number of species introduced and the percentage of species successfully naturalizing are presented for each of six invasion pathways.

Compared to equivalent mainland areas, Mediterranean islands often have a higher human population density, a more dense road network, more ports/harbours and airports per capita (or per area), greater dependence on imports and a higher flux of humans across their borders, especially through tourism (Island Commission 2000). These attributes strongly facilitate the introduction of alien species as contaminants of trade and/or hitchhikers on transport vectors. Yet even with the increased opportunities for accidental introductions, the majority of naturalized species arise from intentional introductions that have subsequently escaped from gardens, agriculture or forestry (Lambdon & Hulme 2006a). This pattern is surprisingly similar to that found for other biomes (Hulme 2005). Escapes of ornamental plants represent the largest single source of naturalized alien species. Almost half of all plant introductions to Mediterranean islands stem from the increasing popularity of gardens and landscaping associated with tourist developments. It therefore follows that this is likely to be a major source of naturalized species. However, the percentage of species that become naturalized is dependent on the source of the introduction and is negatively related to the number of species introduced for each type of source (r_s= -0.88, df 4, $p < 0.05$, Fig. 1). This may reflect that while fewer species may be introduced as forestry or agriculture crops such species and varieties tend to be selected to match closely the recipient environment and, in addition, are often planted on a large scale. In contrast, ornamentals may often require water and/or nutrient additions for survival and thus be less likely to naturalize outside a managed environment. Nevertheless, since the 1960s the vogue of "Mediterranean gardening" has encouraged the nursery industry to introduce a large number of taxa native to other Mediterranean countries. Thus an understanding of invasion pathways is pivotal in the interpretation of past invasions and may be the key to predicting future scenarios.

Invasion success: integrating trends in both local and regional abundance

The impact of alien species on ecosystem structure and function will be a product of species local abundance, regional distribution and effects on the recipient community (Parker *et al.* 1999). Insufficient knowledge exists as to how most alien plants affect native ecosystems and thus most rankings of impact rely on estimates of how widespread species occur. However, for Mediterranean islands, species abundance can be assessed both at the individual island scale as well as across the entire region. Thus "invasion success" is a function of both the likelihood of naturalization and spread within a given island as well as the number of islands the species has been able to colonize. 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, species should be evaluated at different hierarchical levels: regional distribution and local abundance.

The local and regional components of invasion success of 376 alien plant species found on Mediterranean islands are moderately well correlated (Fig. 2). Species that are naturalized on many islands tend to be the most widespread on those islands. The most widespread and locally abundant species is *Oxalis pes-caprae* L., a hitchhiker in soil attached to agricultural machinery or as a contaminant of the horticultural trade. Deliberate introductions such as *Agave americana* L. and *Opuntia ficus-indica* (L.) Mill. are both widespread and locally abundant in semi-natural habitats. Seed contaminants (*Conyza canadensis* (L.) Cronq., *Amaranthus albus* L.) are similarly widely distributed. These patterns indicate a clear role of introduction pathways on the distribution of alien plants. However, there remain important differences in the assessments generated at each spatial scale. A subjective appraisal suggests that the regional distribution yields the least useful estimate of potential impact, ranking some species highly which few authorities (e.g. di Castri *et al*. 1990, Hulme 2004) would regard as major invasive problems in the region. For example, feral crops (*Sorghum halepense* (L.) Pers., *Punica granatum* L., and *Ornithogalum arabicum* L. are found on most islands but rarely invade semi-natural habitats whilst horticultural species (*Solanum elaeagnifolium* Cav., *Ricinus communis* L.) are found on only a small proportion of islands, but can reach high local abundance. The local abundance assessment offers a more accurate reflection of the species that generate most environmental concern (Table 1). 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.

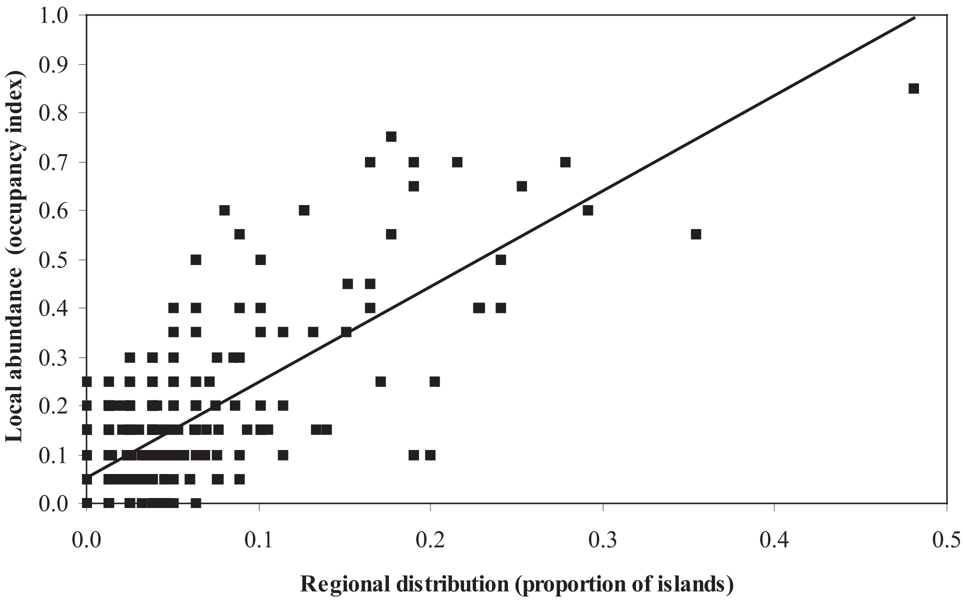


Fig. 2. Positive relationship between the local abundance (mean occupancy index) and the regional distribution (proportion of islands where the species occurred) for over 370 alien plant species in the Mediterranean basin ($y = 1.9543x + 0.0534$, $R^2 = 0.578$, $p < 0.001$).

Table 1. The top 10 alien species on Mediterranean islands ranked according to their local or regional abundance and in relation to the invasion success index, which is the product of these two measures.

Local abundance index		**Regional abundance index**		**Invasion success index**	
Oxalis pes-caprae	*0.85*	*Oxalis pes-caprae*	*0.48*	*Oxalis pes-caprae*	*0.41*
Ailanthus altissima	*0.75*	*Arundo donax*	*0.35*	*Arundo donax*	*0.20*
Opuntia ficus-indica	*0.70*	*Agave americana*	*0.29*	*Opuntia ficus-indica*	*0.20*
Conyza bonariensis	*0.70*	*Opuntia ficus-indica*	*0.27*	*Agave americana*	*0.18*
Xanthium spinosum	*0.70*	*Nicotiana glauca*	*0.25*	*Nicotiana glauca*	*0.17*
Aster squamatus	*0.70*	*Amaranthus albus*	*0.24*	*Conyza bonariensis*	*0.15*
Nicotiana glauca	*0.65*	*Conyza canadensis*	*0.24*	*Ailanthus altissima*	*0.13*
Carpobrotus edulis	*0.65*	*Sorghum halepense*	*0.22*	*Xanthium spinosum*	*0.13*
Agave americana	*0.60*	*Amaranthus retroflexus*	*0.22*	*Carpobrotus edulis*	*0.12*
Chenopodium ambrosioides	*0.60*	*Conyza bonariensis*	*0.21*	*Amaranthus albus*	*0.12*

The role of species traits vs. chance, history and biogeography

Numerous studies have attempted to discern species traits responsible for invasion success (Rejmánek 1999), yet the predictive power of such approaches has often been poor (Hulme 2003). The frequent difficulty in distinguishing between native vs. alien plant traits (e.g. Thompson *et al.* 1995, Crawley *et al.* 1996) suggest the key comparison must be between species traits and the relative abundance of invasive plants. However, abundance can be assessed at two spatial scales: local and regional. Interspecific variation in plant reproductive traits is a significant determinant of relative abundance within an island (Lloret *et al.* 2005). However, mode of introduction and especially origin are important correlates of regional distribution and to a lesser extent local abundance (Lloret *et al.* 2004a, b). By using the relationship between local and regional abundance as a measure of invasion success (Fig. 2) more robust assessments may be made as to the relative importance of biogeography, taxonomy and life-history in the spread of invasive species.

Further analysis of the invasion success index (the product of local and regional abundance scores, Fig. 2) highlights that the correlation between local and regional abundance is stronger for species of non-European origin, which are also more widespread than alien species introduced from elsewhere in Europe (Lloret *et al.* 2004a, b). Bioclimatic groupings also reinforce these findings. Species of Mediterranean origin have the lowest mean success index and this suggests that climatic adaptation to the Mediterranean regime is not particularly important. Although this conclusion is counterintuitive, 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 (Lloret *et al.* 2004b).

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 & Williams 2002, Lambdon & Hulme 2006b). Previous authors have found that certain taxa (e.g. Chenopodiaceae, Amaranthaceae, Poaceae) have a predisposition towards invasion success (e.g. Pyšek 1998), although this may reflect either the inheritance of characteristics truly associated with invasiveness or an increased frequency of introduction. Analysis of the importance of phylogeny on invasion success 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). For the Mediterranean invasives, while large families often contain more invasive members (e.g. Weber 1997), their mean invasiveness is not detectably higher (Lambdon & Hulme 2006). This in itself is an indication that invasiveness is highly unpredictable across lineages.

The date of species introduction may also determine patterns of invasion success. More recently introduced species may show a restricted geographic distribution because they have not yet occupied their full potential range. However, analysis of local abundance data from islands where the first record of exotic occurrence is well documented (such as Corsica), does not show a clear relationship with date of introduction (Lloret *et al.* 2004b). Neither are there significant differences in a comparison between archaeophytes (introduced before ca. 1500 AD) and neophytes (introduced after ca. 1500 AD) for eight islands (Crete, Rhodes, Lesbos, Malta, Sardinia, Corsica, Majorca and Minorca). At the regional scale, there is also no relationship between date of introduction and abundance.

However, analysis of the invasion success index does yield a significant pattern. Neophytes are increasingly less successful as invaders the more recent their introduction date (Fig 3). This pattern may arise from at least three non-mutually exclusive reasons. First, it is likely that introductions prior to the 20th century were probably made for economic rather than aesthetic reasons and thus species were indirectly screened for their suitability to establish in Mediterranean environments with limited human assistance (e.g. feral crops) and thus their ability to naturalize would be relatively high. Second, as a result of increased trade in the 20th century, many recent introductions are likely to be accidental and the smaller propagule pressure may result in lower rates of naturalization. Third, it is well known that there is often a lag-phase between species introduction and naturalization that can be anything up to 100 years (Pyšek & Hulme 2005). It is conceivable that while introductions prior to the 20th century have progressed through this lag-phase, this may not be true of more recent introductions. Although archeophytes are less successful than long-established neophytes, this pattern may be an artifact since ancient introductions are difficult to identify, as the species are often very well established. Nevertheless, many of the most invasive species (*Ailanthus altissima, Oxalis pes-caprae, Carpobrotus* spp.) have certainly been introduced in the last few centuries.

While the frequency and mode of species introduction are important they do not explain all variation in local abundance. To further elucidate the role of species traits in both local and regional abundance, the relative importance of fifteen species traits on the abundance of over 350 naturalized alien plant species was assessed across five Mediterranean islands (Lloret *et al.* 2005). Analyses were also undertaken on three subsets of species defined by their association with semi-natural, agricultural or ruderal habitats. Five attributes are found to be positively associated with average alien abundance across all five islands: vegetative propagation, large leaf size, summer flowering, long flowering period, and dispersal by wind or vertebrates. Fewer significant attributes are associated with abundance when assessed for individual islands and trends were island-specific. Although significant

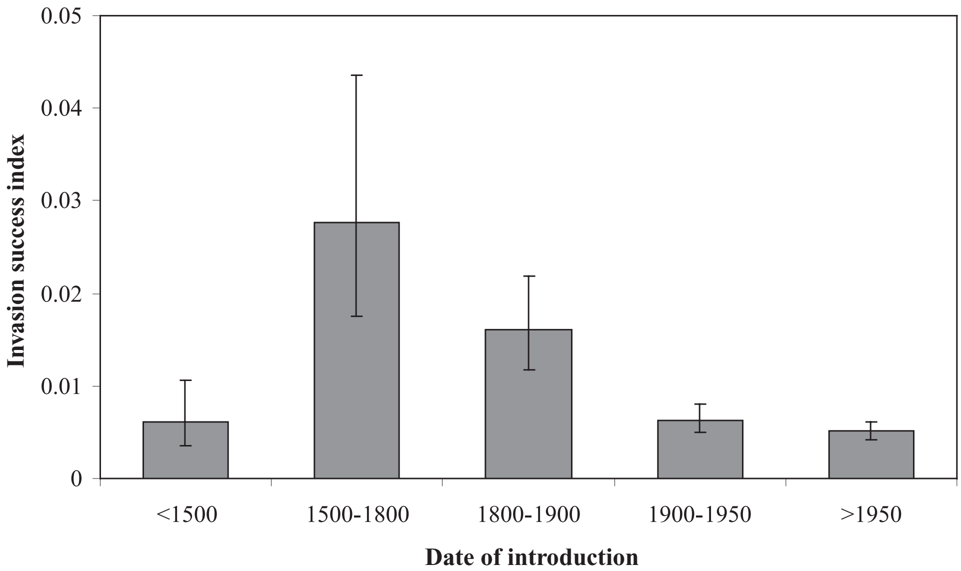


Fig. 3. Variation in the mean invasion success of alien plants on Mediterranean islands associated with different periods of species introduction.

covariation in traits is found, there is no evidence for well-defined and correlated sets of attributes constituting a global syndrome of invasion. Different attributes appear important in the three habitats: succulence in ruderal habitats, long flowering period in agricultural habitats and vertebrate seed dispersal in semi-natural habitats. These traits appear to reflect different strategies: empty niches, avoidance of competitors and exploitation of mutualists. Such findings highlight the importance of estimating invasion success across a wide region in order to minimise local idiosyncrasies. Since the importance of different biological attributes may shift along the dispersal, colonization and establishment phases of invasion, trait analyses should also focus on specific invasion stages e.g. reproductive traits may be expected to be more relevant for long-distance colonization.

Vulnerability of Mediterranean island ecosystems to invasion

A confounding factor in the analysis of local and regional abundance is that 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). However, a near ubiquitous finding in the search for clues to the differential habitat vulnerability is the high frequency of alien species in urban and agricultural environments (Crawley 1987, Cadotte & Lovett-Doust 2001). This appears as true for Mediterranean islands as it does for other ecosystems, and ruderal, wayside, urban as well as cultivated lands are host to a relatively large number of alien plant species (Fig. 4). Human population density is an important determinant of alien plant distributions in the Mediterranean Basin (Vilà *et al.* 2003, Pino *et al.* 2005). Human-dominated habitats are likely to have higher rates of species introductions (from gardens, transport networks, landscaping, crops etc.), a greater proportion of ruderal and disturbed areas, and higher nitrogen inputs from fertilizer, sewage and car exhausts all of which facilitate invasions (Pyšek 1998). The problems of invasive species are often viewed as those of disturbed and anthropogenic habitats rather than intact ecosystems (Fig. 4). However, a unique element of indigenous Mediterranean biodiversity is a distinct subflora of ruderal annuals that evolved in the Mediterranean (Blondel & Aronson 1999). These species occur in varying associations in fields, pastures and on roadsides: habitats typically invaded by alien plant species. Many of these local weeds have restricted distributions and could represent the elements of the Mediterranean flora most at risk from invasions.

The islands of the Mediterranean Basin have suffered a high degree of human interference and disturbance, a process that dates back over ten thousand years, and this has resulted in a marked transformation of the vegetation (Heywood 1995, Thompson 2005). In contrast to California and South Africa, where large areas of relatively intact vegetation remain, much of the Mediterranean Basin has been transformed from its native state (Mooney 1988). The result is the many secondary or subseral shrubland communities (maquis, garrigue, etc.) that form such a conspicuous part of Mediterranean landscapes. The consequences for biological invasions are that native species are likely to be good competitors under the strong selection regime imposed by humans on the Mediterranean flora and that the multiple stresses of fire, drought and grazing present a formidable challenge to prospective alien plant species. Again this trend is observed for Mediterranean islands and the secondary shrubland communities appear to have relatively few alien species (Fig. 4). But what are the trends in more pristine ecosystems? We see two contrasting groups: at the more vulnerable end of the spectrum are coastal, wetland and forest habitats while montane ecosystems have very few alien species at all. Clearly, certain pristine ecosystems of high conservation value are at risk from plant invasions and the idea of resistant communities is only likely to apply for secondary vegetation types and communities existing at environmental extremes (high salinity, aridity or low temperature).

In addition to higher propagule pressure increasing the probability of alien invasion, island communities are widely believed to be more vulnerable to the impacts of alien taxa (Hulme 2004). To test this hypothesis, a stratified field survey was undertaken to compare the regional and local abundance of *Oxalis pes-caprae* on islands and adjacent mainland areas. A wider regional distribution on islands may reflect large-scale differences in island and mainland areas. For example, islands often have a more benign environment (e.g. lower elevation, mild temperatures), higher degree of urbanization and development as well as a higher propagule influx through ports etc. (Hulme 2004). Meanwhile, a higher local abundance in comparable communities may reflect greater susceptibility to invasion due to lower native richness, unsaturated communities or less competitive native species on islands. Comparison between two Mediterranean islands (Majorca and Minorca) with adjacent regions on the Spanish mainland (València and Murcia) revealed trends in *O. pes-caprae* regional abundance to be consistent with the hypothesis with fewer sample sites invaded in the mainland regions (Gimeno *et al.* 2006). Moreover, as expected the regional distribution and local abundance of *O. pes-caprae* were correlated such that where the species is widely distributed it is also more abundant. The species has a wider distribution and higher abundance in agrarian localities or disturbed and ruderal habitats than in coastal localities, forests and shrublands. These findings suggest that local processes such as biotic resistance are less important than large-scale phenomena in the differential invasion of islands by *O. pes-caprae*. A variety of large-scale environmental drivers may play a role in the differences found but the most parsimonious explanations are that *O. pes-caprae* is still expanding its range, and it has occupied a larger proportion of available habitat on islands due to its strong dependence on human-mediated dispersal which is probably greater in the islands than in mainland areas (Vilà *et al.* 2006a).

A further factor influencing the higher invasibility of islands compared to mainland areas may result from differences in life-history of alien plants, either genetic or phenotypic. For example, comparison of the performance traits of *O. pes-caprae* between insular and mainland areas of Spain revealed that descendants from insular populations produced 20% more vegetative bulbs without reducing allocation to bulb size, above ground biomass or flowering than descendants from the mainland (Vilà & Gimeno 2005). Since *O. pes-caprae* reproduces exclusively via bulbs in the Mediterranean Basin, such differences in life-history could result in higher rates of invasion on islands. Similarly, seedlings of *Carpobrotus* spp. (*C. edulis*, *C.* aff. *acinaciformis* or hybrids) were consistently larger in insular than in mainland populations (Suehs *et al.* 2005).

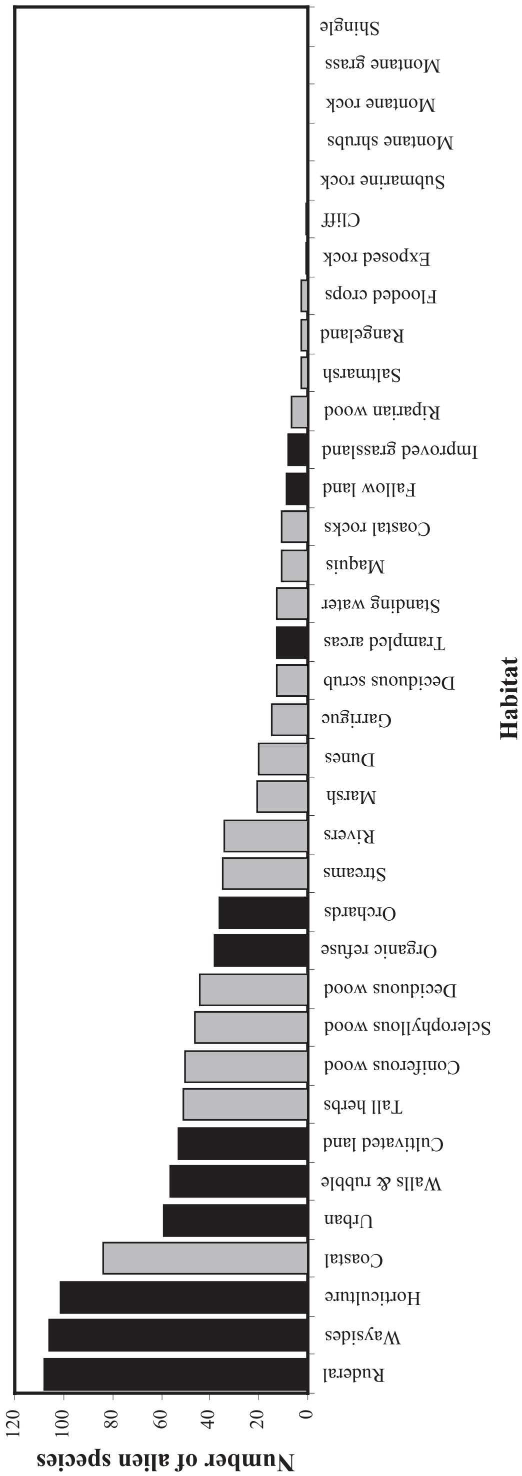


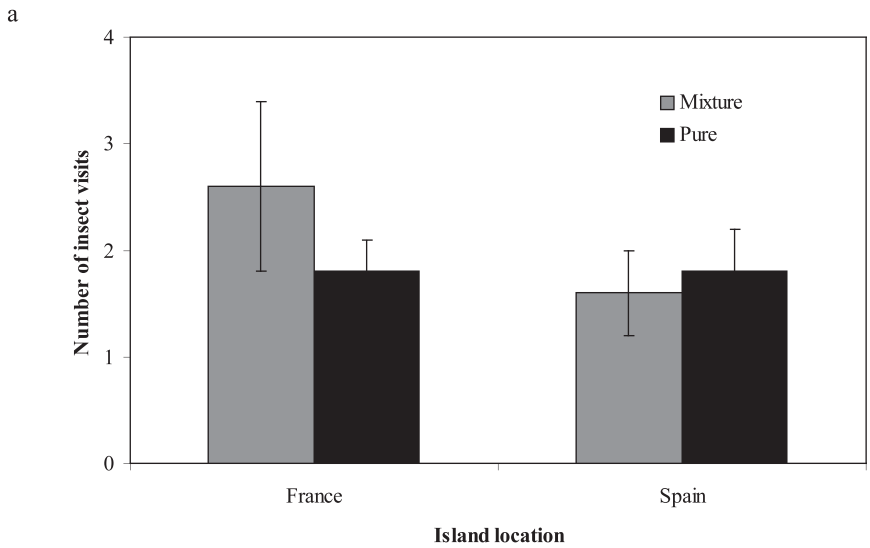
Fig. 4. Number of alien species occurring in different Mediterranean island habitats. Human-dominated habitats are highlighted by dark shading.

The ecological impact of invasive plants

In addition to impacts upon cultural heritage (Celesti-Grapow & Blasi 2004), human health (Belmonte & Vilà 2004) and landscape, alien plants may have profound environmental consequences, exacting a significant toll on Mediterranean ecosystems. These include wholesale ecosystem changes e.g. colonization of sand dunes by *Acacia saligna* (Labill.) H.Wendl. (Bar *et al.* 2004), threats to indigenous species e.g. endemic or rare coastal plants in relation to expansion of *Carpobrotus edulis* (L.) N. E. Br. (Suehs *et al.* 2001) or *Cortaderia selloana* (Schultes et Shultes. f.) Asch. & Gr. (Domenech *et al.* 2005), as well as more subtle ecological changes and increased biological homogeneity. The physiognomy of alien plants may differ substantially from native Mediterranean species (Le Floc'h *et al.* 1990) and many of the most widespread alien species belong to families otherwise not represented in the Mediterranean Basin e.g. Agavaceae, Cactaceae, Phytolaccaceae, Simaroubaceae. This suggests the potential ecosystem impacts could be considerable (Vitousek 1990).

Detailed comparative studies on the impacts of *Ailanthus altissima* (Mill.) Swingle, *Carpobrotus edulis* and *C. acinaciformis* L. (L. Bol.) hereafter described as *Carpobrotus* spp. and *Oxalis pes-caprae* on up to eight Mediterranean islands revealed that, on average, the presence of the invaders was associated with reduced species richness and diversity but the relative impact was dependent on the island of study and was positively related to species richness of the recipient community (Vilà *et al.* 2006b). Thus in relatively species-poor communities, the presence of the invasive species leads to a net increase in species richness while in species-rich communities there is a net loss of species. Invasion also changes plant species composition. For example, the percentage of therophytes is reduced in plots invaded by *A. altissima* and *Carpobrotus* spp. but not in those invaded by *O. pes-caprae*. Taken as a whole, invasion had a negative effect on plant community structure but the effect of invasion on soil properties was variable and reflects individual species impacts on soil C, N and pH.

Although invasive plant species are often considered as potential competitors of native species due to their usually greater capacity for colonization and expansion, only scarce information exists on whether invasive plants also compete for pollination services with natives (see review in Traveset & Richardson 2006). Many alien species have been introduced for aesthetic reasons and have attractive insect-pollinated flowers that are presented over a relatively long flowering season (Lloret *et al.* 2005). For example, the large, brightly coloured flowers of the invasive *Carpobrotus* spp. may compete with native species (*Cistus* spp., *Anthyllis* spp. and *Lotus* spp.) with which it shares habitat and flowering time, influencing pollinator visitation. To test this, insects visiting the flowers of native species in the field in Majorca (Spain) and the Hyeres archipelago (France) were censused and the number of flowers visited in areas with and without the presence of *Carpobrotus* recorded (Moragues *et al.* 2004, Moragues & Traveset 2005; Fig. 5). Both potential competitive and facilitative effects were found with *Carpobrotus* but patterns were dependent on the native taxon, island and year of study. Thus, the role of the invasive *Carpobrotus* in promoting or constraining the natural pollination dynamics is likely to vary considerably among native species.



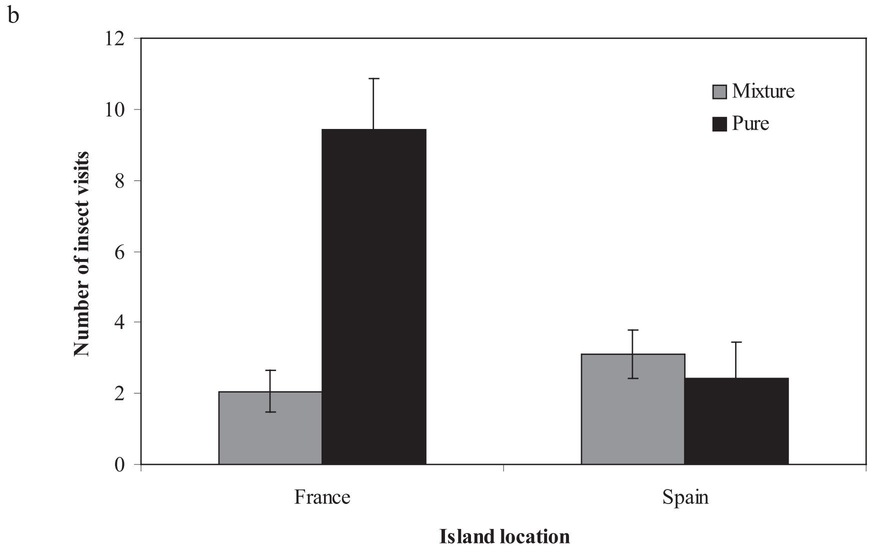


Fig. 5. Number of visits by insects to the flowers of (a) *Lotus cytisoides* L. and (b) *Cistus monspeliensis* L. when occurring as pure stands or in a mixture with the alien *Carpobrotus* spp. Data are shown for patterns observed on two different Mediterranean islands during 2002: Bagaud (France) and Majorca (Spain).

A confounding factor when assessing the potential impact of invasive plant species is that any correlative trends may reflect underlying environmental gradients rather than an effect of the invasive species *per se*. For example, a distinct invertebrate fauna was found to be associated with *Carpobrotus* spp. in Majorca.

However, analysis of associated environmental variables revealed that variation in the invertebrate fauna could be explained by distance from urban centres, soil type and the vegetation community (Palmer *et al.* 2004). The presence of *Carpobrotus* did not explain any additional variation in invertebrate species composition and the results highlight that any correlative assessment of impact should account for gradients of anthropogenic influence.

Conclusions: future threats and possible responses

The evidence presented in this paper highlights that (a) a wide range of semi-natural communities are vulnerable to invasion, (b) if lag-phases are important then the problem is likely to get much worse in the future, (c) the future trends in drivers of invasion, especially pathways and land-use change will accelerate the spread of alien species, (d) the consequences for native biodiversity and ecosystem function are complex and potentially severe and (e) the tools for prevention are limited, while attempts to eradicate alien species are costly and not entirely successful (Carta *et al.* 2004).

For the islands of the Mediterranean, a clear message is that the deliberate introduction of alien species through forestry, agriculture and the ornamental nursery trade represents the major source of naturalized species. These sources of introduction are exempt from current legislation, thus a potential conflict exists between the economic and environmental sectors. For example, *Opuntia ficus-indica* is still promoted as a fruit crop, defensive hedge, fodder crop and for erosion control (Le Houerou 1996). Yet, evidence highlights the significant spread of this and related species following land abandonment, resulting in considerable invasion in shrublands close to urban centres (Vilà *et al.* 2003). New introductions in the forestry sector are foreseen as possible results of commitments to the Kyoto protocol and the promotion of short rotation forestry for biomass production. The forestry sector is also responsible for subtle invasion processes at the level of the gene pool (Petit 2004), as clearly demonstrated in riparian ecosystems where native black poplar is threatened by intermingling with alien clones (Cagelli & Lèfevre 1995).

Resolving these potential conflicts will not be easy yet screening species on the basis of their life-history characteristics may prove challenging since there is little evidence for well-defined and correlated sets of attributes constituting a global syndrome of invasiveness. Furthermore, decision theory analysis highlights that even a risk assessment system with an accuracy of 85% would be better ignored, unless the damage caused by introducing a pest is eight times that caused by not introducing a non-invasive plant species that is potentially useful (Smith *et al.* 1999). The difficulties arising from screening new introductions suggest that development of an “invasion index” that integrates local and regional abundance patterns may prove a useful tool to identify species already established in the Mediterranean that pose a wider threat. The idiosyncratic nature of many alien plant assemblages on different islands (Lloret *et al.* 2005) such that even the most widespread alien, *Oxalis pes-caprae*, is still only found on around half the islands of the Mediterranean. Indeed most alien plants established on Mediterranean islands have the potential to become naturalized on more islands and regional ecological surveys may provide an adequate means to assess this risk. Scope therefore exists for prevention, and much might be gained from information sharing across the Mediterranean Basin. Accidental introductions are currently not covered by legislation yet present a significant source of naturalized species on Mediterranean islands. Managing accidental introductions requires considerable improvement in biosecurity policy and appropriate management of trade and transport, including regular inspection of imported commodities (Hulme 2006). It is highly unlikely that every airport and harbour on the numerous Mediterranean islands can be successfully monitored and this proves to be an area where management response requires the greatest attention. To address this threat, mechanisms should be put in place to limit the further spread of known problem species across the Mediterranean through awareness raising and better regulation of the import and disposal of alien plant material.

Acknowledgements

The work presented here was largely drawn from the results of EPIDEMIE (Exotic Plant Invasions: Deleterious Effects on Mediterranean Island Ecosystems) a research project supported by the European Commission under the 5th Framework, contributing to the implementation of Key Action 2.2.1 (Ecosystem Vulnerability) within the Energy, Environment and Sustainable Development thematic program (Contract no. EVK2-CT-2000-00074). Further details of the project and the data bank can be found at www.ceh.ac.uk/epidemie.

References

Bar, P., Cohen, O. and Shoshany, M. 2004. Invasion rate of the alien species *Acacia saligna* within coastal sand dune habitats in Israel. Israel Journal of Plant Science 52: 115-124.

Belmont, J. and Vilà, M. 2004. Atmospheric invasion of non-native pollen in the Mediterranean region. American Journal of Botany 91: 1243-1250.

Blondel, J. and Aronson, J. 1999. Biology and wildlife of the Mediterranean region. Oxford University Press, Oxford UK.

Cadotte, M.W. and Lovett-Doust, J. 2001. Ecological and taxonomic differences between native and introduced plants of south-western Ontario. Ecoscience 8: 230-238.

Cagelli, L. and Lefèvre, F. 1995. The conservation of *Populus nigra* L. and gene flow with cultivated poplars in Europe. Forest Genetics 2: 135-144.

Campbell, F.T. 1997. Exotic pest plant councils: cooperating to assess and control invasive nonindigenous plant species. In: Luken, J.O. and Thieret, J.W. (eds), Assessment and Management of Plant Invasions*,* pp. 228-243. Springer-Verlag, New York.

Carta, L., Manca, M. and Brundu, G. 2004. Removal of *Carpobrotus acinaciformis* (L.) L. Bolus from environmental sensitive areas in Sardinia, Italy. In: Arianoutsou, M. and Papanastasis, V. P. (eds.), Proceedings of the 10' MEDECOS – International Conference on Ecology, Conservation and Management. Millpress Science Publishers, Rotterdam.

Celesti-Grapow, L. and Blasi, C. 2004. The role of alien and native weeds in the deterioration of archaeological remains in Italy. Weed Technology 18: 1508-1513.

Collingham, Y.C., Wadsworth, R.A., Willis, S.G., Huntley, B. and 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. and 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.

Crawley, M.J. 1987. What makes a community invasible? In: Crawley, M.J., Edwards, P.J. and Gray, A.J. (eds.), Colonisation, succession and stability, pp. 429-454, Blackwell Scientific Publications, Oxford.
Crosby, A.W. 1986. Ecological imperialism: the ecological expansion of Europe, 900-1900. Cambridge University Press, Cambridge.
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. 1989. History of biological invasions with special emphasis on the Old World. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M. and Williamson, M. (eds.), Biological Invasions: a Global Perspective, pp. 1-30. John Wiley and Sons, Chichester.
di Castri, F., Hansen, A.J. and Debussche, M. 1990. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht.
Domenech, R., Vilà, M., Pino, J. and Gesti, J. 2005. Historical land-use legacy and *Cortaderia selloana* invasion in the Mediterranean region. Global Change Biology 11: 1054-1064.
Duncan, R.P. and Williams, P.A. 2002. Darwin's naturalization hypothesis challenged. Nature 417: 608-609.
Fensham, R.J. and Cowie, I.D. 1998. Alien plant invasions on Tiwi Islands. Extent, implication and priorities for control. Biological Conservation 83: 55-68.
Fox, M.D. 1990. Mediterranean weeds: exchanges of invasive plants btween the five Mediterranean regions of the world. In: di Castri, F., Hansen, A.J. and Debussche M. (eds.), Biological invasions in Europe and the Mediterranean Basin, pp. 179-200. Kluwer Academic Publishers, Dordrecht.
Fritts, T.H. and Rodda, G.H. 1998. The role of introduced species in the degradation of island ecosystems, a case study of Guam. Annual Review of Ecology Evolution and Systematics 29: 113-140.
Gimeno, I., Vilà, M. and Hulme, P.E. 2006. Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* in the western Mediterranean. Journal of Biogeography 33: 1559-1565.
Guillerm, J.L., Le Floc'h, E., Maillet, J. and Boulet, C. 1990. The invading weeds within the Western Mediterranean. In: di Castri, F., Hansen, A.J. and Debussche M. (eds.), Biological invasions in Europe and the Mediterranean Basin, pp. 61-84. Kluwer Academic Publishers, Dordrecht.
Heywood, V.H. 1995. The Mediterranean flora in the context of world biodiversity. Ecologia Mediterranea 20: 11-18.
Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
Hulme, P.E. 2003. Biological Invasions: winning the science battles but losing the conservation war? Oryx 37: 178-193.
Hulme, P.E. 2004. Invasions, islands and impacts: A Mediterranean perspective. In: Fernandez Palacios, J.M. and Morici, C. (eds.), Island ecology, pp. 337-361. Asociación Española de Ecología Terrestre, La Laguna.
Hulme, P.E. 2005. Nursery crimes: agriculture as victim and perpetrator in the spread of invasive species In: Crop science and technology, pp. 733-740, British Crop Protection Council, Farnham.
Hulme, P.E. 2006 Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835-847.
IPPC 2004. International standards for phytosanitary measures. Pest risk analysis for quarantine pests, including analysis of environmental risks and living modified organisms. ISPM 11, FAO, Rome.
Island Commission 2000. What status for Europe's islands? L'Harmattan, Paris.
Jeanmonod, D. 1998. Les plantes introduites en Corse: impact, menaces et propositions de protection de la flore indigene. Biocosme Mésogéen 15: 45-68.
Lambdon, P.W. and Hulme, P.E. 2006a. Predicting the invasion success of Mediterranean alien plants from their introduction characteristics. Ecography 29: 853-865.
Lambdon, P.W. and Hulme, P.E. 2006b. How strongly do interactions with closely-related native species influence plant invasions? Darwin's naturalization hypothesis assessed on Mediterranean islands. Journal of Biogeography 33: 1116-1125.

Le Floc'h, E., Le Houerou, H.N. and Mathez, J. 1990. History and patterns of plant invasion in Northern Africa. In: di Castri, F., Hansen, A.J. and Debussche, M. (eds.), Biological invasions in Europe and the Mediterranean Basin, pp. 105-133. Kluwer Academic Publishers, Dordrecht.

Le Houerou, H.N. 1996. The role of cacti (*Opuntia* spp.) in erosion control, land reclamation, rehabilitation and agricultural development in the Mediterranean basin. Journal of Arid Environments 33: 135-159.

Lloret, F., Lambdon, P., Camarda, I., Brundu, G., Médail, F. and Hulme, P. E. 2004a. Local and regional abundance of exotic plant species on Mediterranean islands: species traits or island attributes? In: Arianoutsou, M. and Papanastasis, V.P. (eds.), Proceedings of the 10' MEDECOS – International Conference on Ecology, Conservation and Management. Millpress Science Publishers, Rotterdam.

Lloret, F., Médail, F., Brundu, G. and Hulme, P.E. 2004b. Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? Global Ecology and Biogeography 13: 37-45.

Lloret, F., Médail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P. and Hulme, P.E. 2005. Species attributes and invasion success by alien plants in Mediterranean islands. Journal of Ecology 93: 512-520.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

Mauchamp, A. 1997. Threats from alien invasive plant species in the Galapagos Islands. Conservation Biology 11: 260-263.

McNeeley, J.A., Mooney, H.A., Neville, L.E., Schei, P. and Waage, J.K. 2001. A global strategy on invasive alien species. IUCN, Gland.

Mooney, H.A. 1988. Lessons from Mediterranean climate regions. In: Wilson, E.O. (ed.), Biodiversity, pp. 157-165. National Academy of Sciences/Smithsonian Institution, Washington DC.

Moragues, E. and Rita, J. 2005. Els vegetals introduïts a les Illes Balears. Technical Report from the Conselleria de Medi Ambient, Govern de les Illes Balears.

Moragues, E. and Traveset, A. 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122: 611-619.

Moragues, E., Traveset, A., Suehs, C.M., Affre, L. and Medial, F. 2004. Effect of *Carpobrotus* spp. on the pollination success of native species. Interspecific pollen transfer as a mechanism of competition. In: Arianoutsou, M. and Papanastasis, V.P. (eds.), Proceedings of the 10' MEDECOS – International Conference on Ecology, Conservation and Management. Millpress Science Publishers, Rotterdam.

Palmer, M., Linde, M. and Pons, G.X. 2004. Correlational patterns between invertebrate species composition and the presence of an invasive plant. Acta Oecologica 26: 219-226.

Parker, I.M., Simberloff, D., Lonsdale, W.M, Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. and Goldwasser, L. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-19.

Pauchard, A., Cavieres, L.A. and Bustamante, R.O. 2004. Comparing alien plant invasions among regions with similar climates: where to from here? Diversity and Distributions 10: 371-375.

Petit, R.J. 2004. Biological invasions at the gene level. Diversity and Distributions 10: 159-165.

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

Pino, J., Font, X., Carbo, J., Jove, M. and Pallares, L. 2005. Large-scale correlates of alien invasion in Catalonia (NE of Spain). Biological Conservation 122: 339-350.

Pyšek, P. 1998. Is there a taxonomic pattern to plant invasions? Oikos 82: 282-294.

Pyšek, P. and Hulme, P.E. 2005. Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience 12: 302-315.

Quézel P., Barbero, M., Boni, G. and Loisel, R. 1990. Recent plant invasions in the Circum-Mediterranean Region. In: di Castri, F., Hansen, A.J. and Debussche M. (eds.), Biological invasions in Europe and the Mediterranean Basin, pp. 51-60. Kluwer Academic Publishers, Dordrecht.

Rejmánek, M. 1999. Invasive plant species and invasible ecosystems. In: Sandlund, O.T., Schei, P.J. and Viken, A. (eds.), Invasive species and Biodiversity Management, pp. 79-102. Kluwer, Dordrecht.

Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., LeRoy Poff, N., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770-1774.

Smith, C.S, Lonsdale, W.M. and Fortune, J. 1999. When to ignore advice: invasion predictions and decision theory. Biological Invasions 1: 89-96.

Strahm, W. 1999. Invasive species in Mauritius: examining the past and charting the future. In: Sandlund, O.T., Schei, P.J. and Viken, A. (eds.), Invasive species and biodiversity management, pp. 325-348. Kluwer Academic Publishers, Dordrecht.

Suehs, C. M., Médail, F. and Affre, L. 2001. Ecological and genetic features of the invasion by the alien *Carpobrotus* plants in Mediterranean island habitats. In: Brundu, G., Brock, J., Camarda, I., Child, L. and Wade, M. (eds.), Plant invasions: species ecology and ecosystem management, pp. 145-158. Backhuys Publishers, Leiden, The Netherlands.

Suehs, C.M., Affre, L. and Médail, F. 2005. Unexpected insularity effects in invasive plant mating systems: the case of *Carpobrotus* (Aizoaceae) taxa in the Mediterranean Basin. Botanical Journal of the Linnean Society 85: 65-79.

Thompson, J.D. 2005. Plant evolution in the Mediterranean. Oxford University Press, Oxford.

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

Traveset, A. and Richardson, D.M. 2006 Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution 21: 208-216.

Viegi, L. 1993. Contributo alla conoscenza della biologia delle infestanti dell colture della Sardegna nord-occidentale. I. Censimento delle specie esotiche della Sardegna. Bollettino Società Sarde Scienze Naturali 29: 131-234.

Vilà, M., Burriel, J.A., Pino, J., Chamizo, J., Llach, E., Porterias, M. and Vives, M. 2003. Association between *Opuntia* species invasion and changes in land cover in the Mediterranean region. Global Change Biology 9: 1234-1239.

Vilà, M., Bartomeus, I., Gimeno, I., Traveset, A. and Moragues, E. 2006a. Demography of the invasive geophyte *Oxalis pes-caprae* across a Mediterranean island. Annali di Botanica 97: 1055-1062.

Vilà, M. and Gimeno, I. 2006. Potential for higher invasiveness of the alien *Oxalis pes caprae* on islands than on the mainland. Plant Ecology 183: 47-53.

Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galinidis, A., Lambdon, P., Manca, M., Medail, F., Moragues, E., Traveset, A., Troumbis, A.Y. and Hulme, P.E. 2006b. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. Journal of Biogeography 33: 853-861.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57: 7-13.

Weber E.F. 1997. The alien flora of Europe: a taxonomic and biogeographic review. Journal of Vegetation Science 8: 565-572.

Wittenberg, R. and Cock, M.J.W. 2001. Invasive alien species: A toolkit for best prevention and management practices. CAB International, Wallingford.