ISLANDS, INVASIONS AND IMPACTS: A MEDITERRANEAN PERSPECTIVE

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Abstract

The Mediterranean is one of the island-rich seas of the world but its insular biogeography has received little attention in the past. Its native vegetation reflects its dynamic history of island formation, connection and isolation but also the millenary impact of its well known ancient civilisations that altered most of the territory. The region is relatively susceptible to plant invasions and 12 species are here considered as the most widespread naturalised plants. Their spatial trends are here analysed. The Mediterranean islands are less susceptible to invasions than oceanic islands, yet they are more vulnerable than their comparable closest mainland areas. Finally, the role of plant invasions in the context of current threats to Mediterranean island plant diversity is considered.

Resumen

Pese a ser el Mediterráneo uno de los mares del mundo más rico en islas, su biogeografía insular ha recibido poca atención en el pasado. Su vegetación nativa refleja su historia dinámica de formación de islas, conexiones y aislamientos, pero también el impacto milenario de sus conocidas antiguas civilizaciones que alteraron gran parte del territorio. Esta región es relativamente susceptible a las invasiones de exóticas. En este capítulo se consideran las doce plantas naturalizadas más extendidas y sus tendencias espaciales. Las islas del Mediterráneo se muestran menos susceptibles a las invasiones que las oceánicas, siendo, sin embargo, más vulnerables que las áreas continentales cercanas. Finalmente, se considera el papel de las invasiones en el contexto de las amenazas actuales a la diversidad vegetal de esta región.

Introduction

Biological invasions by non-indigenous species are widely recognised as a major component of human-caused global environmental change, often resulting in a significant loss in the economic value, biological diversity and function of invaded ecosystems (Mooney & Hobbs 2000; Mack *et al.* 2000; Pimentel *et al.* 2001). Global biodiversity scenarios for 2010 (Sala *et al.* 2000) highlight dramatic future increases in biological invasions in Mediterranean ecosystems, proportionally more so than in any other global ecosystem. Furthermore, biological invasions are seen as one of the most important drivers of change in Mediterranean ecosystems, second only to land use change and more important than climate, nitrogen deposition or rising CO_2 concentration (Sala *et al.* 2000). In addition, interacting effects among drivers suggest that biological invasions will be facilitated by rising atmospheric CO_2 concentrations, warmer temperatures, greater nitrogen deposition, altered disturbance regimes and increased habitat fragmentation (Dukes & Mooney 1999). The urgency of the situation and the lack of coordinated problem solving are only just dawning on an unprepared Mediterranean Basin.

The ecology of islands is intimately associated with biological invasions (Carlquist 1974, Williamson 1981, Nunn 1994, Whitaker 1998). The species composition and community structure of islands is widely recognised to be a function of colonisation rates (Hubbell 2001) and it follows that where these have been accelerated by human activities, biological invasions will also play a significant role. Current understanding of the extent, character and consequences of the invasion of islands by non-native species is drawn largely from studies of tropical oceanic islands especially Hawaii (Vitousek 1988, Loope & Mueller-Dombois 1989, Simberloff 1995, Vitousek *et al.* 1995, Denslow 2003). In contrast, what might best be called continental islands, have received far less attention yet may in themselves shed considerable light on the drivers and impacts of island invasions. This paper aims to address this imbalance by focusing on the invasion by non-native plants of islands in the Mediterranean Basin.

The biogeographical context of Mediterranean island floras

There are nearly 5,000 islands in the Mediterranean Basin. Their wide ranges of sizes (from small islets to Sicily, the largest island at 25,708 km^2), maximum altitudes (from sea level to 3,260m for Mount Etna), substrates and morphologies, as well as human activities, have resulted in the evolution of a highly diversified flora (Greuter 1995, Delanoë *et al.* 1996). Surprisingly, although richer in islands than anywhere else in the

world apart from the Caribbean and the archipelagoes of the Pacific ocean, the biogeography of Mediterranean islands has received relatively little attention (Carlquist 1974, Williamson 1981, Nunn 1994, Whitaker 1998). This is surprising since the ecology of these islands present a fascinating opportunity to assess the impact of complex geological history, human impact and biogeography on the structure of ecological communities.

It is widely recognised that the key elements that shape the ecology of islands are their geological age, spatial and temporal isolation from continental land masses and the length of time since islands were first colonised by humans (Whittaker 1998). The formation of Mediterranean islands reflects a complex geological history (Blondel & Aronson 1999). The turbulent tectonic history of the Mediterranean led to the majority of islands arising from uplift of the sea floor as it buckled between the colliding Eurasian and African plates (Blondel & Aronson 1999). However, several islands were shaped by volcanic activity during the Pleistocene (Kos, Ustica, Kos, Alicudi, Filicudi) and Holocene ((Milos, Salina, Panarea) while others have been influenced by eruptions during relatively recent times (e.g. Santorini, Ischia, Stromboli, Pantelleria, Sicily). The islands have variously been connected to the mainland on several occasions. The Messinian Salinity Crisis that occurred between 5.6 and 5.3 million years ago resulted in the almost complete drying-up of the Mediterranean Sea and would undoubtedly have facilitated biotic interchange between Africa, Asia, Europe and the former islands. Following the restitution of the sea, islands were again connected to the mainland during the Quaternary sea level minima. Sea level dropped by between 100 and 200m during several glacial periods that not only helped connect islands to the mainland but also led to the amalgamation of archipelagoes into single islands (Sfikas 2000). Thus the Mediterranean contains a complex of islands differing in age, isolation, geology and colonization history.

The native vegetation of Mediterranean islands reflects this dynamic history of island formation, connection and isolation and comprises elements with Afro-tropical, Holarctic, Irano-Turanian, Saharo-Arabian and indigenous origins (Blondel & Aronson 1999). The result is that each of the larger islands in the Mediterranean has its own distinctive set of native species. Two further biotic influences have additionally shaped Mediterranean island floras- grazers and humans. Grazing and browsing mammals, including deer, rodents, dwarf elephants and hippos, were widespread on most of the larger Mediterranean islands during the Pleistocene. Evidence of human colonization stretches as far back as 20,000 years ago in Sardinia but it is likely that most islands were colonized soon after the end of the last glaciation around 11,000 years ago. Archaeological data suggests that by 7,000 years ago, Neolithic

humans had begun to cut a swathe through the Pleistocene mammal fauna to the extent that all that now remains on islands are a handful of small mammal species (Blondel & Aronson 1999). Humans accidentally and deliberately introduced mammals to the islands. Commensal rodents such as the house mouse, brown and black rats colonized islands as a result of human settlement. Domesticated animals included sheep, goats and pigs whose subsequent feralisation probably gave rise to mouflon, the Cretan wild goat and the Corsican wild boar. The pressure of grazing by domesticated livestock has profoundly shaped the Mediterranean flora but is not the only human influence that characterises the region.

As the cradle of agriculture, the Mediterranean Basin represents one of the most important centres of origin for crop plant worldwide. Current estimates approach 522 cultivated crop species in the Mediterranean Basin, including both native and non-native species first cultivated in the region (Blondel & Aronson 1999). Thus the Mediterranean possesses an extensive archaeophyte flora. Many species of cereals and pulses were introduced into Mediterranean islands in the Neolithic, where they have subsequently naturalised and on occasion hybridised with native species.

The Mediterranean was at the heart of some of the world's most ancient civilisations and the characteristics of the flora and fauna reflect this history. Many islands endured repeat invasions (by humans) and incessant wars because of their strategic position for defence, trade or natural resources. For example, Corsica has been invaded more than twenty times in the last 2500 years, first by the Phoenecians (565BC), then Etruscans (540BC), Carthaginians (270BC), Romans (259BC), Vandals (455AD), Byzantines (534AD), Goths (549AD), Sarrasins (704AD), Lombards (725AD), Pisanos (1015AD), Genoans (1195AD), Aragons (1297AD), Genoans again (1358), Milanians (1468AD) Franco-Ottomans (1553AD), French (1768AD), British (1794AD) and German-Italian Axis during the Second World War (Blondel & Aronson 1999). Similar invasion histories can be described for any other of the larger Mediterranean islands, although in each case the range of protagonists differ. With each invasion, islands suffered changes in land use and resource exploitation as well as the deliberate and accidental introduction of non-native plants and animals.

The foregoing has briefly described the processes that have shaped the vegetation, habitats and environment of Mediterranean islands. More so than any other set of islands, the flora of Mediterranean islands has been strongly shaped by successive periods of colonisation and the current trends in plant invasion must be viewed in this context. Having set the historical scene, it is now time to introduce the cast of characters that encapsulate the present series of island invasions.

A dirty dozen: an overview of the more widespread naturalised plants of the Mediterranean
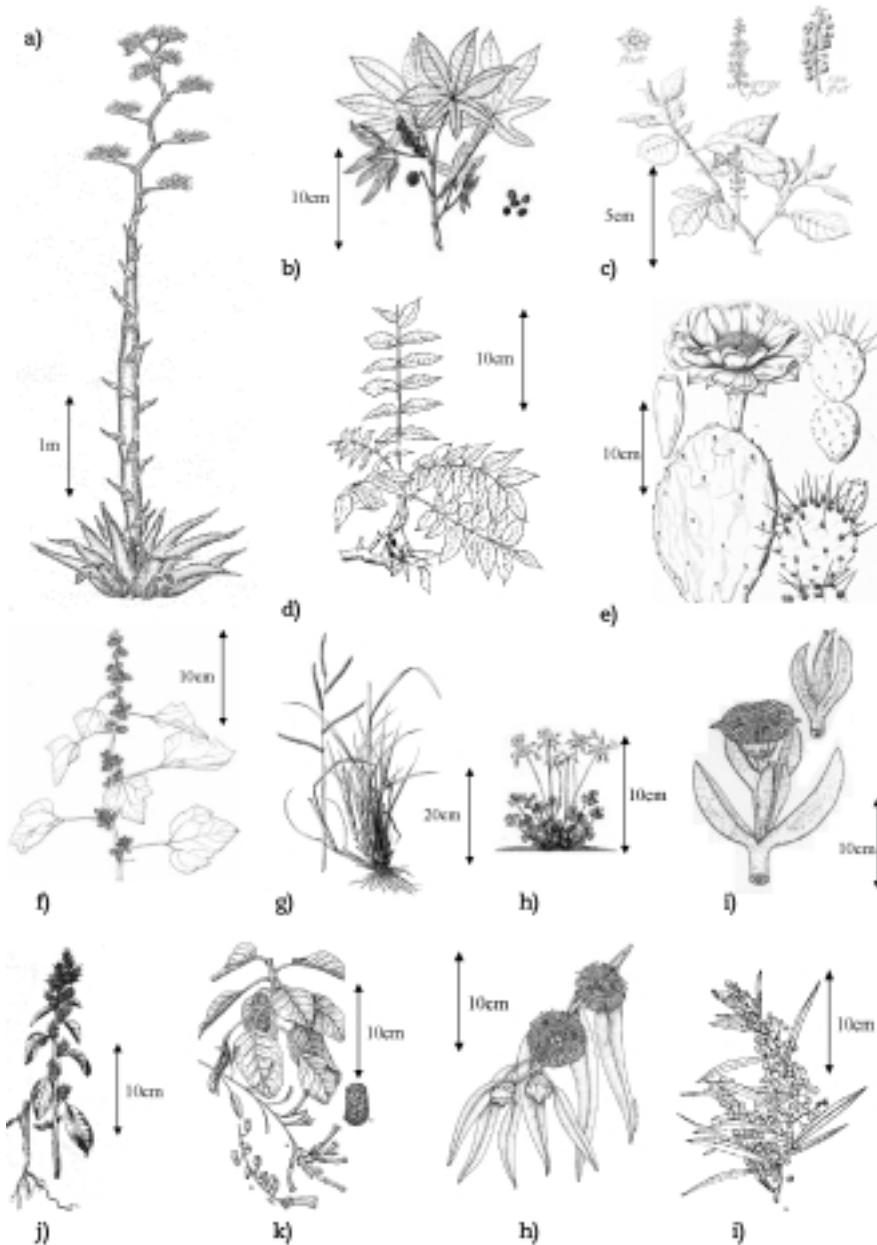
Until recently, invading plant species were not thought to be a major threat in Mediterranean ecosystems (Blondel & Aronson 1999). This view was partly as a result of the relatively few naturalised non-native species in the Mediterrranean (~250) that represent no more than 1% of the entire Mediterranean flora (Quezel *et al.* 1990). However, assessments of the percentage of the flora comprising non-native species is only one estimate of the risks posed by biological invasions. Another is the evidence that many species of non-native plant have become naturalised throughout large parts of the Mediterranean Basin, and particularly on islands. While it is impractical to describe all such species, a brief overview of twelve widespread species frequently invading natural vegetation provides a suitable introduction to the diversity and recent history of plant invasions in the Mediterranean (Fig. 1). The following descriptions are drawn from Polunin & Huxley (1987), Blamey & Grey Wilson (1993) and Sfikas (2000).

1.   ***Agave americana*** L (Agavaceae). A succulent perennial with large basal rosette that flowers once after 10-15 years producing a panicle that can reach heights of 10 m. The flowers are pollinated by moths and produce many small wind dispersed seeds. Seedlings and juveniles are sensitive to frost but adults are more hardy. Following flowering, the parent plant dies but also propagates new plants around its circumference. A native of Mexico it was introduced into Europe in the 16th century and has naturalised in many parts of the Mediterranean. It is grown as an ornamental in gardens, a hedging plant and is also a modern source of steroids. In the Mediterranean the species tolerates poor soil and drought and invades dry habitats, rocky outcrops, abandoned fields, roadsides and drainage lines. Contact with the fresh sap can cause dermatitis.

2.   ***Ailanthus altissima*** (Miller) Swingle (Simaroubaceae). A deciduous tree 8-10 m high with pinnate leaves that propagates both by seed and through vegetative suckers. An individual tree can produce as many 325,000 samaras per year and cut stems resprout vigorously, rapidly forming dense thickets. A native of China, it was introduced into the Mediterranean in the late 18th century both as an ornamental but also as hostplant for silkworms. It is widely grown as an ornamental in gardens and for landscaping in urban areas but has naturalised throughout much of Europe. The seedlings are relatively shade intolerant but benefit from disturbance and the species has invaded ditches, roadsides and river beds. Roots often clog drains, damage pavements and foundations. *Ailanthus* trees also produce toxins that prevent the establishment of other plant

Figure 1

Examples of widespread non-native plant invaders of Mediterranean islands
a) *Agave americana*, b) *Ricinus communis*, c) *Phytolacca americana*, d) *Ailanthus altissima*, e) *Opuntia ficus indica*, f) *Xanthium strumarium*, g) *Paspalum dilatatum*, h) *Oxalis pes caprae*, i) *Carpobrotus acinaciformis*, j) *Amaranthus retroflexus*, i) *Nicotiana glauca*, j) *Eucalyptus globulus*, k) *Acacia saligna*.

species. The quassinoid alkaloid ailanthone has been isolated from the plant and has potential as a broad spectrum herbicide.

3. ***Amaranthus retroflexus*** L. (Amaranthaceae) is a native riverbank pioneer in the central and eastern U.S.A. and adjacent regions in southeastern Canada and northeastern Mexico. The young leaves are edible, and the plant has been cultivated both for human consumption and for forage. It was introduced into Europe in the mid 18th century and by 1800 was becoming a common weed throughout much of the continent. Although an annual, it grows vigorously and may reach >2 metres. The monoecious flowers are minute, greenish-white and are borne in tall branched spikes. The tiny seeds are wind-dispersed, produced in great quantity and establish a persistent seed bank. The species is capable of invading disturbed ground very rapidly especially cultivated or abandoned fields, waste places, burned areas, roadsides and stream valleys. It infests crops and its toxic seeds subsequently contaminate seed harvests.

4. ***Carpobrotus acinaciformis*** and **C. edulis** L. (Aizoaceae). Succulent subshrubs, comprising trailing or hanging multiple stems, often reaching several meters in length. The thick, fleshy leaves reflect a strong adaptation to drought and saline conditions. Fruits are fleshy and dehiscent producing numerous seeds, usually dispersed by mammals. A genus native to the Cape Region (South Africa), it was first introduced into Europe in 1680 but subsequently widely planted as an ornamental and used for stabilization of dunes and slopes. The species invades dunes, coastal rocky slopes, maritime cliff ledges, coastal scrubs, grasslands, and shrubland. The expansion of *Carpobrotus* species reduces native species biomass, survival and reproductive performances through changes in soil properties (pH, nutrients, water balance).

5. ***Eucalyptus*** spp. (Myrtaceae). Eucalypts (especially *E. globulus* Labill., *E. camaldulensis* Schlecht, *E. cornuta* Labill.) are tall growing (50-60m) evergreen trees with straight trunks and well-developed crowns. They can be distinguished by their deciduous, grey mottled bark, two types of blue-grey leaves (broad, upright leaves on juveniles and long spear-shaped leaves on adults) and their feathery solitary flowers than can be white, yellow or pink. The fruit is a hard, woody capsule, broadly top shaped. The numerous small seeds are wind dispersed. Eucalypts were introduced to the Mediterranean in the late 19th century and are extensively planted both in plantations and as a landscaping tree. Their rapid growth and adaptability to a range of site conditions have been responsible for their popularity. The species grow best in areas having an annual rainfall of 60-110 cm and will grow on a wide range of substrates. Eucalypts remain very sensitive to frost as long as the immature foliage is retained. In the

coastal Mediterranean where it receives enough moisture to propagate from seed, the tree can naturalise freely in grasslands, waysides and streambeds, eliminating the diversity of native species as it colonizes new ground. Terpenes in leaves reduce decomposition rates leading to accumulation of litter and their leachates can reduce the abundance of native herbs. Although capable of surviving severe drought stress it is not economical with use of water, leading to a lowering of the watertable.

6. ***Nicotiana glauca*** Graham (Solanaceae). An evergreen shrub or small tree to 3 metres with erect sparsely branched stems. Long tubular yellow flowers are borne almost throughout the year on large leafless branches and the fruit is a many-seeded capsule. Large individuals can produce between 10,000 to 1,000,000 seeds that are dispersed by wind and water. It is drought resistant, tolerant of a wide range of environmental conditions and withstands mechanical damage although does not spread vegetatively. The species is native to South America and is naturalised as a shrubby weed growing in sandy or gravel soils along roadsides, stream beds, near cultivated areas, around old dwellings, building sites and ditches. The plants (especially the leaves and young stems) are poisonous to all kinds of livestock and to humans. Although tobacco plants are distasteful, frequent livestock poisonings from these plants are reported.

7. ***Opuntia ficus-indica*** Miller (Cactaceae). A 3-5m tall cactus with flattened spiny cladodes. The fleshy fruit is also often spiny yet the seeds are dispersed by both mammals and birds. In addition to reproduction by seed, vegetative propagation occurs by detached stem segments. A native of tropical and semi-arid Mexico, it was introduced into the Mediterranean in the early 16th century and cultivated for fruit consumption, forage and the production of cochineal. The cactus is also used in popular medicine, field management (windbreaks, soil erosion control, hedges) and as an ornamental. It is an aggressive invader of natural vegetation, especially dry and rocky places, pastureland and degraded garrigue. Dense infestations can invade fertile agricultural land preventing access to pasture.

8. ***Oxalis pes-caprae*** L. (Oxalidaceae). A rhizomatous geophyte up to 20 cm height that rarely reproduces by seed but rather by vegetative bulbils formed from the underground stem, fragments of which can also take root. Another native of the Cape Region it was introduced to the Mediterranean as an ornamental in the late 18th century and is presently widely naturalised throughout the region. It is a persistent and pernicious weed of cultivated areas (vineyards, olive groves, etc.) as well as roadsides and grassy places. Aggressive vegetative growth enables it to form monocultures that oust out native species. High concentration of soluble oxalates in leaves may lead to poisoning of livestock if no other feed is available.

9. **Paspalum dilatatum** Poir. (Gramineae). A deep-rooted perennial grass with numerous leaves emerging from a knotted basal tuft. Culms range in height from 40 to 175 cm and seed is spread by clinging to animals, clothing, machinery or vehicles, and by water. Fragments of the rhizome may also be broken up and spread during cultivation. A native of northeastern Argentina, Uruguay, and southern Brazil, it has been introduced to several Mediterranean islands as a highly palatable pasture grass providing good quality forage that is maintained late into the season. The species prefers wet situations but on low ground may extend from rather dry prairies to marshy meadows. The plant succeeds on both light or heavy clay soils and is drought-resistant but frost-sensitive. In the Mediterranean it is found naturalised in irrigated fields, on wetter parts of road verges but has the potential to become a major weed of wetland edges and native wet grasslands. Seed-heads parasitized by the ergot fungus *Claviceps paspali* can be toxic.

10. **Phytolacca americana** L. (Phytolaccaceae). A robust and foetid perennial herb growing from 1 to 3.5 m high that produces bird dispersed multi-seeded berries. A native to North and Central America (from Maine to Florida and Mexico), it was introduced into the Mediterranean as an ornamental in the mid 17th century and as a source of dyes to colour wine. The species is naturalized up to 700 m elevation along stream banks and river valleys, but usually beneath cultivated trees such as olives and oranges. The vegetative parts of the plant are toxic and may threaten livestock.

11. **Ricinus communis** L. (Euphorbiaceae). A shrub to about 3 m tall with large deeply lobed leaves. It is a perennial in the tropics but often an annual in Europe being killed by frost. Flowers are wind pollinated and seed set is usually high. Fruits occur in terminal clusters and are covered with soft spines. The seed pod explodes when ripe, scattering the seeds. The extremely viable seeds germinate readily in a variety of soils. A native of tropical south-eastern Africa it has now become naturalised in many parts of the world. It is grown as an ornamental in gardens but especially as a crop (castor oil) and has been recorded in the Mediterranean since the mid 19th century. It forms somewhat ephemeral thickets which can shade out other species. It grows in dry and mesic habitats and is commonly naturalized along stream beds and river beds as well as other open locations with warm, well-drained, high nutrient soils. Seeds contain the extremely toxic lectin ricin and as few as four are sufficient to kill a human if consumed and chewed.
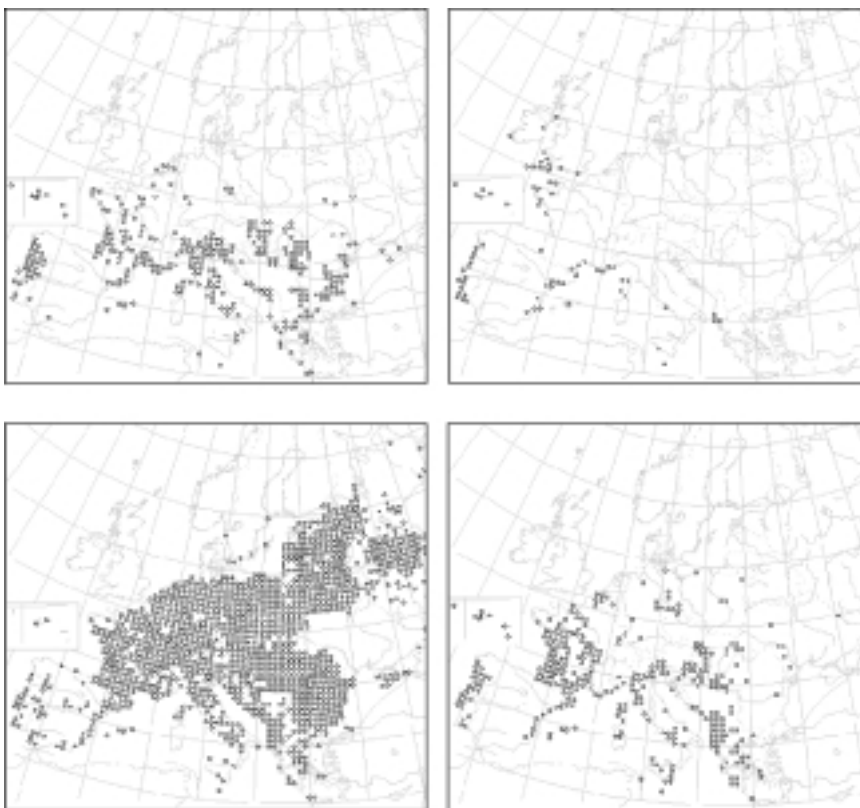
12. **Xanthium strumarium** L. (Asteraceae). A wind or self-pollinated annual weed that produces numerous spiny burrs spread by water, humans, or other animals. It is probably a native of North America

(especially the subspecies *strumarium*) but is a cosmopolitan weed, likely to have been introduced accidentally to the Mediterranean in the 16th century. It is often associated with open, disturbed areas, but it is found in a wide variety of habitats. It frequents roadsides, railway banks, small streams, and riverbanks, as well as the edges of ponds and freshwater marshes and overgrazed pastures. It does not tolerate shade, is toxic to certain animals and is considered one of the world's worst weeds.

These twelve taxa do not represent an exhaustive list but do provide examples of the diversity of growth forms, species origins and plant families that have successfully established themselves in the Mediterranean Basin. Several species are widely distributed throughout Europe (Fig. 2) and are known to be invasive in Macaronesia as well as on

Figure 2

European distributions of four naturalised exotic plant species introduced into Europe during the last 200 years. Species distribution maps (50km resolution) have been extracted from the *Atlas Florae Europaeae* (Jalas *et al.* 1972-1999).
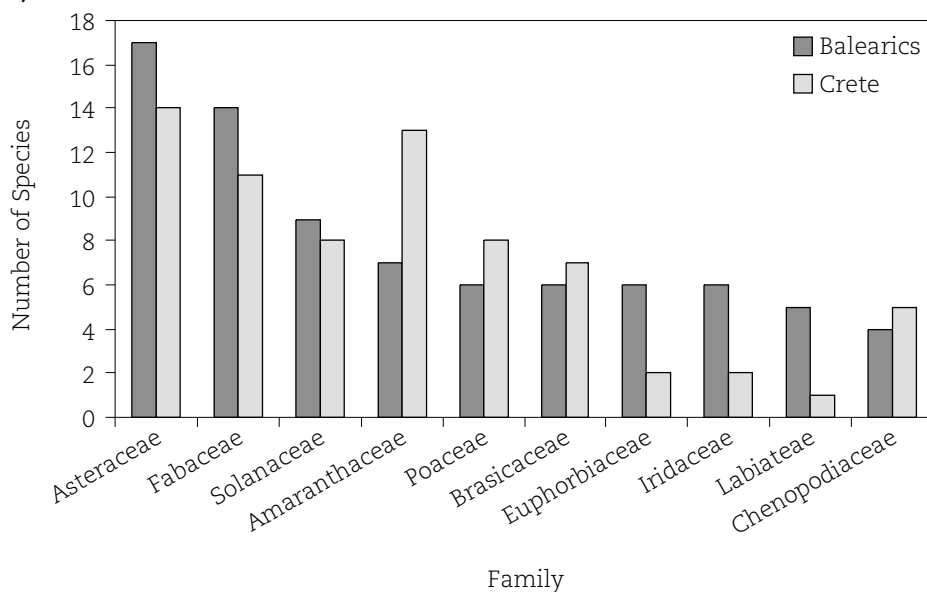
certain tropical islands. It is immediately evident that there is no single «invasive plant» syndrome since growth forms encompass annual and perennial herbs, succulents, shrubs and trees. The most widespread invaders tend to possess spines/thorns, or are unpalatable or even toxic to mammalian herbivores, particularly livestock. Rapid growth, vegetative reproduction and/or resprouting ability appears important as does a high output of small seeds. Pollination and seed dispersal syndromes are less consistent and possibly indicate that self-compatibility and both deliberate and accidental anthropogenic seed dispersal are of greater importance. Taken together, these traits make sense in an environment where overgrazing and possibly fire have shaped natural plant communities and in which tolerance and/or resistance to physical damage may play a key role in plant survival.

Comparison of the composition of non-native floras in Crete and the Balearics (Fig. 3) highlight that neither taxonomy or geographic origin are necesarily robust correlates of invasion success. Certainly, non-native floras are not a random draw from the available pool of potential colonists. There is an overrepresentation of the Asteraceae, Solanaceae and Amaranthaceae yet taxonomic composition can vary among islands with proportionally greater importance of the Chenopodiaceae, Brassicaceae and Poaceae in the eastern Mediterranean while Labiateae, Iridaceae and Euphorbiaceae are more prevalent in the West (Figure 3a). History and culture undoubtedly shape the non-native floras and may indeed reflect past trading relationships. Thus the Balearics have a greater representation of non-natives with Macaronesian, North American and Mediterranean origins, while Crete (possibly due to its lengthy Turkish occupation) has a marked Asian element (Figure 3b). Such findings suggest that the spatial trends in invasive species distribution, both within and among islands will reflect human, environmental and biogeographic processes.
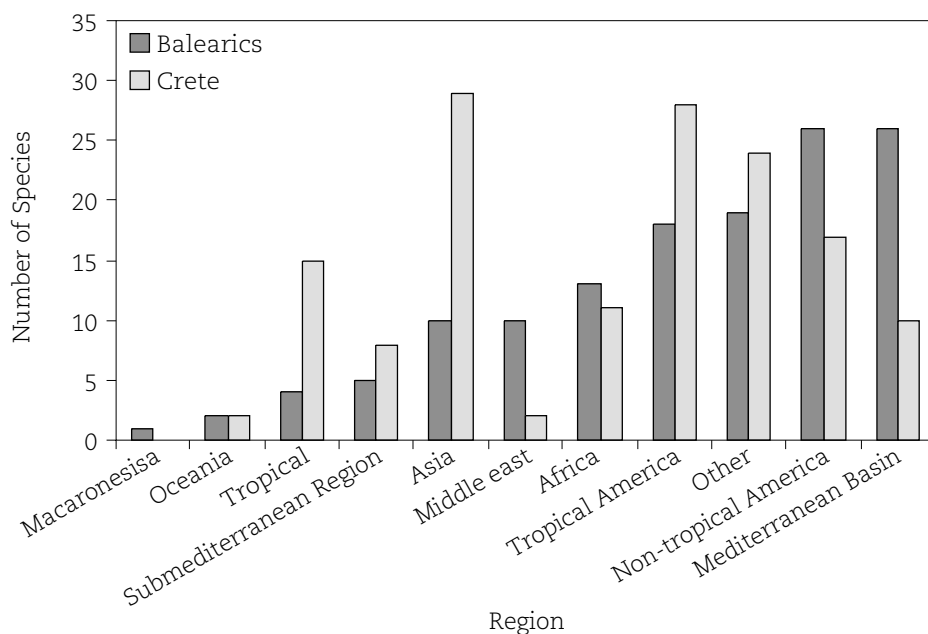
Figure 3

Comparison of the non-native flora of Crete (data from Yannitsaros 1991, Turland *et al.* 1993) and the Balearics (data from Vila & Munoz 1999) in relation to a) taxonomic and b) geographic origins.

a)

b)

Trends in the invasion of Mediterranean islands by non-native plants

Larger islands are expected to support a greater richness of native species (Whittaker 1998) and this hypothesis could be extended to cover non-native species as well. Globally, larger islands do possess greater non-native plant richness (Lonsdale 1999). For the major islands of the Mediterranean, a weak positive relationship does exist between island area and the number of non-native plant species (Fig. 4a). The relationship appears strongest for small to medium sized islands less than 10,000 km^2 and this range would encompass the vast majority of Mediterranean islands. However, the relationship disappears for larger islands suggesting that perhaps a form of species saturation occurs. This runs contrary to the ideas that as island size increases so should the diversity of habitats and opportunities for invasive species. Examination of the distribution of non-native plants in Crete and the Balearics highlight that not all habitats are equally susceptible to invasion (Fig. 4b). In general, agricultural, ruderal and riparian areas are most often invaded by non-native plants. While other habitats are colonised less frequently. Hence, while habitat diversity may indeed increase with increasing island size, the diversity of habitats susceptible to invasion may be less responsive to changes in island area.

Further insights into the scope for saturation arise from examination of spatial trends within islands (Fig. 5). Spatial patterns highlight invasion hotspots with *Nicotiana glauca* strongly associated with the four major urban centres on Crete, *Ailanthus altissima* distribution linked to the main transport network of major roads, *Oxalis pes-caprae* is widespread in lowland olive groves and orchards and both *Opuntia ficus indica* and *Agave americana* coincide in agricultural areas, probably colonizing areas of abandonment. However, most species exhibit a strong association with coastal areas (Fig. 5). Although natural coastal habitats themselves are not highly invasible (Fig. 4b), the more benign environment (lower elevation), higher degree of urbanisation and development as well as the often higher propagule influx (through ports etc.) leads to the frequent finding that a large number and higher percentage of non-native species occur along coastlines (D'Antonio & Dudley 1995). Thus perhaps a better correlate of the invasibility of islands is the extent of coastline rather than island area *per se*. If coastline is an important correlate, area based analyses may not pick up the often smaller perimeter/area ratios of larger islands that might give rise to the trend depicted in Figure 4a. This may be the simplest explanation as to why the largest Mediterranean islands have fewer non-native aliens than might be expected from species-area analyses.

Figure 4

a) Positive relationship between island size and the number of non-native species for Karpathos, Menorca, Mallorca, Crete, Corsica, Sardinia and Sicily (y=10.581ln(x) - 13.257, R^2=0.3942). b) Comparison of the non-native flora of Crete (data from Yannitsaros 1991, Turland *et al.* 1993) and the Balearics (data from Vila & Munoz 1999) in relation to habitat occurrence.
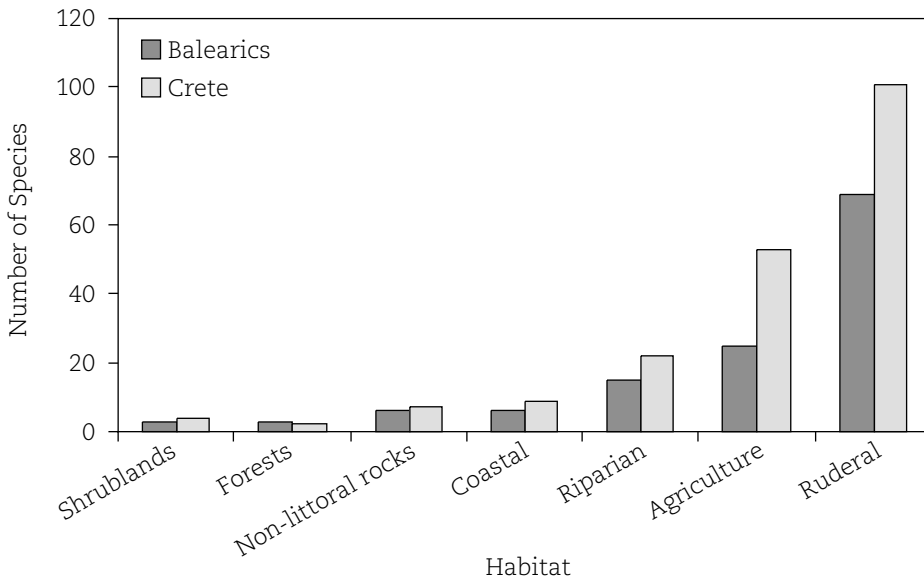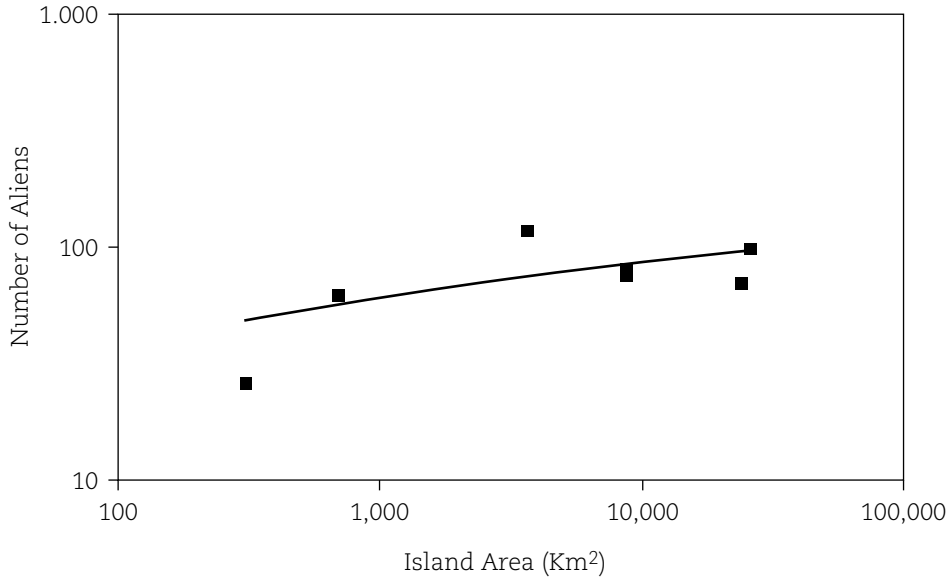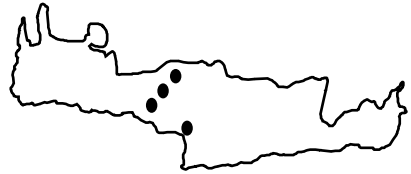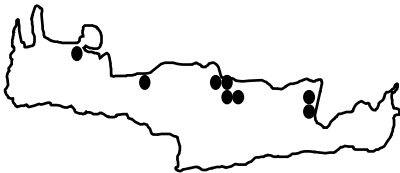
Figure 5

Distribution of six non-native plant species on the island of Crete (adapted from Turland *et al.* 1993) highlighting different spatial patterns of invasion.

a) Ailanthus altissima

d) Opuntia ficus-indica

b) Agave americana

e) Oxalis pes-caprae

c) Nicotiana glauca

f) Conyza canadensis

The relative susceptibility of Mediterranean islands to plant invasions

In contrast to the various monographs addressing plant invasions on oceanic islands e.g. Galapagos (Mauchamp 1997); Tiwi (Fensham & Cowie 1998); Guam (Fritts & Rodda 1998) there exist few detailed regional assessments of the threat from alien invasive plant species in Mediterranean islands. Mediterranean climate regions are particularly susceptible to biological invasions (Mooney 1988; Sala *et al.* 2000), although New World ecosystems appear more susceptible than those of the Mediterranean Basin (Fox 1990). Nevertheless, whereas the proportion of the flora of the Mediterranean Basin composed of non-natives has been estimated at only 1% (Quezel *et al.* 1990), it is substantially higher for Mediterranean islands (Table 1). However, when compared to oceanic islands, Mediterranean islands have fewer non-native species and they comprise a smaller proportion of their flora (Table 1).

Table 1

Characteristics of the floras of selected Mediterranean
(Both Old and New World) and oceanic islands

Region	Area (km²)	% ende-mics	# Alien	% Alien	# Alien/ log area	Reference
Balearics	5,014	7	124	8.4	33.4	Vila & Muñoz 1999
Mallorca	3,656	—	117	8.8	32.8	Vila & Muñoz 1999
Menorca	702	—	62	6.6	21.8	Vila & Muñoz 1999
Pithyusics	623	—	6	5.3	23.2	Vila & Muñoz 1999
Crete	8,700	10	76	4.7	19.3	Turland *et al.* 1993
Karpathos	305	—	26	2.7	10.5	Turland *et al.* 1993
Corsica	8,682	10	80	19.0	20.3	Jeanmonod 1998
Sardinia	24,090	10	70	9.0	16.0	Viegi 1993
Sicily	25,708	10	99	3.9	22.5	Weber 1997
California Channel Isles	900	22	227	26.8	76.8	Loope & Mueller-Dombois 1989
Canary Islands	7,300	28	700	29.2	181.2	Loope & Mueller-Dombois 1989
Hawaiian Islands	16,635	94	800	36.4	189.5	Loope & Mueller-Dombois 1989
Galapagos Islands	7,900	51	240	35.6	61.6	Loope & Mueller-Dombois 1989
Granitic Seychelles	241	31	165	42.6	69.3	Loope & Mueller-Dombois 1989
New Zealand	270,534	81	1623	39.9	298.9	Loope & Mueller-Dombois 1989

The difference between tropical and Mediterranean islands may in part reflect a larger pool of potentially invasive plant species in the tropics (Cronk & Fuller 1995, Binggelli 1996). However, of possibly greater relevance is the general finding that oceanic islands are of more recent geological origin and are considerably more isolated (both in time and space) from the nearest continent than equivalent Mediterranean islands (Table 2). These characteristics of oceanic islands are thought to lead to proportionally lower native diversity (Denslow 2003), greater disharmony in species composition arising from the absence of key plant functional groups (Carlquist 1974), lower competitive ability of native species and vacant niche space (D'Antonio & Dudley 1995) than either Mediterranean islands or equivalent mainland areas. Levels of endemism may reflect the degree to which floras have become specialised and the existence of

undersaturated communities. Thus, levels of endemism and extinction risk are correlated for tropical island floras (Loope & Mueller Dombois 1989). Comparison across a range of islands reveals a positive relationship between level of endemism and the proportion of non-native species in the flora (Fig. 6). The trend clearly separates relatively low endemic, low invasion Mediterreanean islands from high endemic, high invasion oceanic islands. Thus, undeniably other variables correlated with these two different groups could explain the trend. However, although the data are preliminary, positive relationships between rates of endemism and invasion can be discerned in each of the two island subgroups. The finding provides tentative support to the hypothesis that the more specialised a particular flora becomes, the greater the susceptibility to invasion by non-native species.
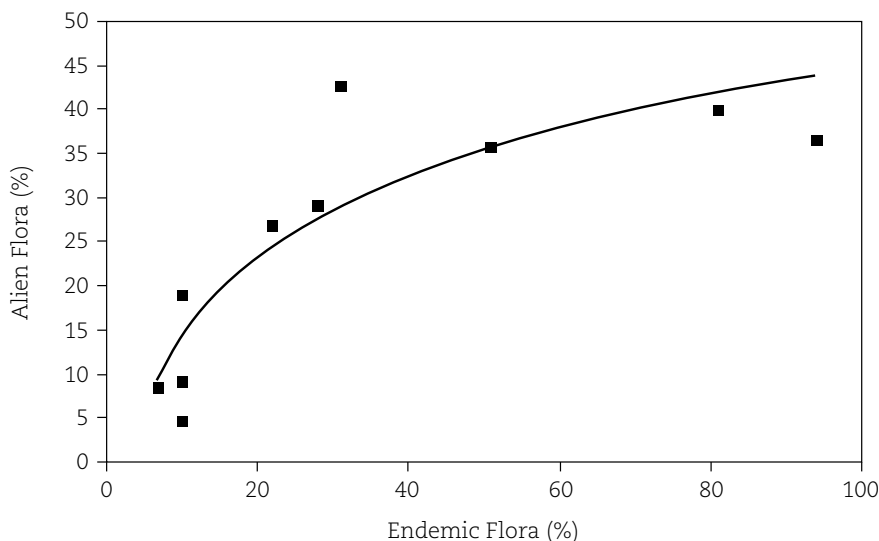
Table 2

Biogeographic characteristics Mediterranean and oceanic islands

Island	Hawaiian Islands	Gala-pagos Islands	Canary Islands	Granitic Sey-chelles	New Zealand	Medite-rranean Islands
Distance from nearest continent	3200	1050	115	1600	2000	2-135
Age of oldest islands (millions of years)	~70	~3	~80	~650	~200	~300
Total area of islands (km^2)	16,635	7,900	7,300	241	270,534	108,300
Highest elevation (meters)	4206	1707	3718	914	3765	3323
Number of invasive introduced plants	800	240	700	165	500	~300
First colonised by humans	1000AD	1800AD	1400BC	1770AD	100AD	8500BC
Human population density	1,193,000	16,000	1,665,117	70,260	3,635,388	10,663,000
Number of islands in group	132	8	13	115	33	5000

In addition, the particular nature of the flora of the Mediterranean Basin may increase its resistance to biological invasions. Unlike oceanic islands, 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). In contrast to California

Figure 6

Positive relationship between levels of plant endemism in island floras and the proportion of the flora composed of non-native species (y=13.32ln(x) - 16.906, R^2=0.7822, for sources see Table 1).

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, phrygana, matorral, garrigue, etc.) that form such a conspicuous part of Mediterranean landscapes. Naveh & Dan (1973) described the region as a whole as «composed of innumerable variants of different degradation and regeneration phases'. In particular, fire, water stress, grazing and cutting contribute to the high degree of floristic and ecological diversity shown by the region (Heywood 1995). 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 non-native plant species. Thus it is probably not surprising that Mediterranean islands are less susceptible to invasion than oceanic islands, they also appear less susceptible than equivalent continental islands off the coast of California (Table 1). It also explains why so many of the world's worst agricultural weeds have Mediterranean origins, since such species are often pre-adapted for human-altered environments (Sax & Brown 2000).

Given their close proximity to the mainland of the Mediterranean Basin, similar geological age and shared history of human disturbance,

why are Mediterranean islands more susceptible to invasion than comparable mainland areas? Island floras do reveal higher levels of endemism than many comparable mainland areas of the Mediterranean (Delanoë *et al.* 1996, Medail & Quezel 1999). However, differences are much less dramatic than comparisons with tropical oceanic islands. An additional pressure may be human population density which is a major correlate of invasion success (Lonsdale 1999). Frequently, islands have higher population densities than comparable mainland areas (e.g. Hawaii 71.7 *vs* USA 28.1; Canaries 228.1 and Mallorca 174.8 *vs.* Spain 77.3; Sicily 198.2 vs Italy 188 although on occasion the trend is reversed Galapagos 2.0 *vs.* Ecuador 45.3; and Corsica 86.3 *vs.* France 108; all values are persons per km^2). The Mediterranean islands have an average population density of nearly 100 persons per km^2, twice the average for the entire Mediterranean region. The individual islands themselves vary ranging from a claustrophobic 1,409 persons per km^2 on Malta to as few as 4 per km^2 on the neighbouring island of Comino. Furthermore, the human population density on Mediterranean islands can more than double during the summer due to the influx of tourists. Greater population density and tourist dynamics presents plenty of scope for accidental and deliberate introductions of non-native species.

It should be clear from the foregoing that the islands of the Mediterranean Basin are somewhat more susceptible to plant invasions than neighbouring mainland areas but less susceptible than tropical oceanic islands or continental islands of New World Mediterranean climate systems. Given this perspective, should the invasion of Mediterranean islands be a major global concern?

Plant invasions in the context of current threats to Mediterranean island plant diversity

Although levels of plant endemism on Mediterranean islands are often much lower than on oceanic islands (Table 1), they are relatively high for Europe, running at approximately 10% for the larger islands (Greuter 1991). Furthermore, a high proportion of plants of Mediterranean islands is endemic to the Mediterranean Basin and includes several wild relatives of crops (Heywood 1995). However, over the last few decades changes in agriculture towards large-scale operations have resulted in a loss of species rich habitat boundaries and widespread application of herbicides and fertilizer have lead to a consequent loss of biodiversity. Tourism has not only led to migration from agricultural to urban areas but has placed increasing pressure on coastal ecosystems. These trends are not unique to islands but their small size increases the effects of anthropogenic impacts making them particularly vulnerable (Delanoë *et al.* 1996).

A review of the globally threatened taxa on Mediterranean islands (Delanoë *et al.* 1996) highlighted that, for the larger islands, on average 4% of taxa are threatened and that the number of taxa viewed as threatened with extinction is sufficiently high that priority conservation actions must be implemented quickly (Table 3). Unfortunately, legal protective measures are in general scarce, and poorly implemented. Protected areas are insufficient in number, and the management of existing protected areas needs to be improved. The combination of endemism and high species richness faced with severe environmental threats has led the majority of Mediterranean islands (with the exception of Malta and certain small Aegean islands) to be classed as global biodiversity hotspots (Medail & Quezel 1999). The main threats to Mediterranean islands include: deforestation and fire, overgrazing by sheep and goats, cultivation of lower slopes and invasion by non-native species (Heywood 1995). These threats lead to consequential changes such as reduction in rainfall, the establishment and spread of new types of plant community (e.g. secondary forest, subseral communities), the opening up of marginal habitats and their subsequent invasion by non-native species. Clearly, the biodiversity of Mediterranean islands face a variety of environmental threats. Biological invasions are both a consequence of these threats (e.g. agricultural land abandonment, coastal development) and a potential threat in themselves. What impacts are likely to arise from non-native plant invasions?

Table 3

Conservation status of threatened plant species on large islands of the Mediterranean Basin (from Delanoe *et al.* 1996)

Island	Extinct	Endan-gered	Vulne-rable	Rare	Un-certain	Total	% Island Flora
Balearics	1	10	14	43	1	69	5
Corsica	1	8	27	10	1	47	2
Sardinia	0	11	30	21	1	63	3
Sicily	1	11	26	45	4	87	3
Crete	0	11	61	118	3	193	11
Malta	1	0	1	10	4	16	2
Cyprus	0	9	14	22	6	51	3

The impact of invasive plants on Mediterranean ecosystems

The impact of exotic plants on biodiversity remains poorly documented in the Mediterranean Basin (di Castri *et al.* 1990; Groves & di

Castri 1991). Several non-native plants are weeds of major economic significance e.g. *Chenopodium ambrosioides*, *Paspalum distichum*, *Conyza canadensis*, *Oxalis pes-caprae*. Others may also be hosts of plant pathogens e.g. *Bromus catharticus* as host for barley yellow dwarf virus and wheat stem rust. Both the intensive planting of exotic species and agricultural abandonment significantly increase the risk of invasion by feral crops (Guillerm *et al.* 1990). Non-native plants are frequently planted commercially, for example, economically important crops e.g. *Eucalyptus globulus* (Blue Gum), *Helianthus tuberosus* (Jerusalem artichoke) are becoming widely naturalised in the Mediterranean basin. Non-native plants may also impact on human and animal health as in the cases of eruptive dermatitis following contact with *Agave americana*, and poisoning of humans and livestock though consumption of toxic fruit e.g. *Phytollaca americana*, *Solanum eleagnifolium*. Non-native plants may also have profound environmental consequences, exacting a significant toll on ecosystems. These range from wholesale ecosystem changes (e.g. colonisation of sand dunes by *Acacia saligna*) and extinction of indigenous species (e.g. threats to endemic coastal plants following expansion of *Carpobrotus edulis* (García 1999), to more subtle ecological changes and increased biological homogeneity. The physiognomy of exotic plants differs substantially from native Mediterranean species (Le Floc'h *et al.* 1990) and many of the most widespread non-native species belong to families otherwise not represented in the Mediterranean Basin e.g. Agavaceae, Cactaceae, Phytolaccaceae, Simaroubaceae (Figure 1). This suggests the potential ecosystem impacts could be considerable (Vitousek 1990) and is supported by studies that reveal reduced nutrient inputs due to the recalcitrant foliage of *Eucalyptus* spp. (Robles & Chapin 1995) and altered soil pH and nutrient availability following deposition of salt by *Carpobrotus edulis* (D'Antonio 1990). Finally, it is highly likely that global warming will favour non-native species currently limited by climate, e.g. *Opuntia ficus-indica* (Le Floc'h *et al.* 1990) and *Acacia dealbata* (Quezel *et al.* 1990).

The problems of invasive species are often viewed as those of disturbed and anthropogenic habitats rather than intact ecosystems (Figure 4b). However, a unique element of indigenous Mediterranean biodiversity is the anthropogenic component, a distinct subflora of around 1,500 segetal and 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 non-native plant species. Many of these endemic weeds have restricted distributions and could represent the elements of the Mediterranean flora most at risk from invasions.

Future outlook

To date, and in comparison with other island ecosystems, relatively little is known about the distribution and impacts of non-native species on Mediterranean islands. It is within this background that the EU funded project EPIDEMIE (Exotic Plant Invasions: Deleterious Effects on Mediterranean Island Ecosystems) was initiated. EPIDEMIE aims to raise awareness and advance existing understanding of the vulnerability of Mediterranean ecosystems to invasion by harmful exotic plants, in order to promote sustainable management of habitats and species, in line with European Community obligations under the Biodiversity Convention. The project is the result of a collaboration among eight European partners and currently assesses, both locally and regionally, the relative importance of the environmental and socio-economic factors that determine the likelihood of exotic plant invasions in order to evaluate the sustainability of management strategies directed towards reducing these risks of invasion. In addition to drawing together data from published floras to produce MIDAS (Mediterranean Islands Database of Alien Species) detailed studies focus on the Balearics, les Iles d'Hyeres, Sardinia, Corsica, Lesbos and Crete. Research includes mapping species distributions, assessing their performance and impacts as well as determining the attitudes of stakeholders to non-native species. These studies are currently being integrated so as to predict the current and future vulnerability of ecosystems to exotic plant invasions, identify optimum management strategies and highlight appropriate planning and policy development to mitigate harmful impacts. It is hoped that project outputs will increase awareness and understanding among the general public (including tourists), stakeholders, scientists, teachers, and both local and regional policy makers of the vulnerability of semi-natural ecosystems to exotic invasion and the ecological and economic consequences of invasion in Mediterranean islands.

Acknowledgements

References

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science* 7: 121-124.

Blamey, M. & Grey-Wilson, C. 1993. *Mediterranean Wild Flowers*. Harper Collins, London.

Blondel J. & Aronson J. 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford Univ. Press, Oxford.

Carlquist, S. 1974. *Island Biology*. Columbia University Press, New York.

Cronk, Q.C.B & Fuller J.L. 1995. *Plant Invaders. The threat to natural ecosystems.* Chapman & Hall, London.

D'Antonio, C.M. 1990. Invasion of coastal plant communities by the introduced succulent *Carpobrotus edulis* (Aizoaceae). PhD dissertation, University of California, Santa Barbara. California.

D'Antonio, C.M. & Dudley, T.L. 1995. Biological invasions as agents of change on islands versus mainlands. *Ecological Studies* 115, 103-121.

Delanoë, O., de Montmollin, B. & Olivier, L. 1996. *Conservation of Mediterranean Island Plants 1. Strategy for Action*. IUCN Gland.

Denslow, J.S. 2003. Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* 90: 119-127.

DiCastri, F., Hansen A.J. & Debussche M. 1990. *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht.

Dukes, J.S. & Mooney, H.A. 1999. Does global change increases the success of biological invaders? *Trends in Ecology and Evolution* 14: 135-139.

Fensham, R.J. & 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 between the five Mediterranean regions of the world. In: di Castri, F., Hansen, A.J. & Debussche. M. (eds.). *Biological Invasions in Europe and the Mediterranean Basin.* pp. 179-200. Kluwer Academic Publishers, Dordrecht.

Fritts, T.H. & Rodda, G.H. 1998. The role of introduced species in the degradation of island ecosystems, a case study of Guam. *Annual Review of Ecology and Systematics* 29: 113-140.

García O. 1999. *Carpobrotus edulis*, una amenaza para la flora endémica de Menorca. *Quercus* 158: 50-51.

Greuter, W. 1991. Botanical Diversity, Endemism, Rarity and Extinction in the Mediterranean Area: An Analysis. *Botanical Chronicles* 10: 63-79.

Greuter, W. 1995. Origin and peculiarities of Mediterranean island floras. *Ecologia Mediterranea* 21: 1-10.

Groves, R.H. & di Castri, F. 1991. *Biogeography of Mediterranean invasions*. Cambridge University Press, Cambridge.

Guillerm, J.L., Le Floc'h, E., Maillet, J. & Boulet, C. 1990. The invading weeds within the Western Mediterranean. In: di Castri, F., Hansen, A.J. & 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 Monographs in Population biology, Princeton University Press. Princeton.

Jalas, J., Suominen, J., Lampinen, R. & Curto, A. 1972-1999. *Atlas Flora Europaeae.* Vanamo, Helsinki.

Jeanmonod D. 1998. Les plantes introduites en Corse: impact, menaces et propositions de protection de la flore indigene. *Biocosme Mèsogèen* 15: 45-68.

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

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

Loope, L.L. & Mueller-Dombois, D. 1989. Characteristics of invaded islands, with special reference to Hawaii. En: Drake, J.A., Di Castri, F., Groves, R.H., Kruger, F.J., Mooney, H.A., Rejmanek M. & Williamson, M.H. (eds.) *Biological Invasions: a Global Perspective.* pp. 257-280. Wiley, Nueva York.

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.

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

Medail, F. & Quezel, P. 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. *Conservation Biology* 13: 1510-1513.

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.

Mooney, H.A. & Hobbs, R.J. 2000. *Invasive Species in a Changing World.* Island Press, Washington.

Naveh, Z. & Dan, J. 1973. The human degradation of Mediterranean landscapes in Israel. In: Di Castri, F. & Mooney, H.A. (eds.). *Mediterranean Type Ecosystems: Origin and Structure* pp. 373-390. Springer, Berlin.

Nunn, P.D. 1994. *Oceanic Islands.* Blackwell Publishers, Oxford.

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 *Agroecosystems and Environment* 84:1-20.

Polunin, O. & Huxley, A. 1987. *Flowers of the Mediterranean.* Chatto & Windus, London.

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

Robles, M. & Chapin, F.S. III. 1995. Comparison of the influence of two exotic species on ecosystem processes in the Berkely Hills. *Madroño* 42: 349-357.

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. & Wall, D.H. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770-1774.

Sax, D.F. & Brown J.H. 2000. The paradox of invasion. *Global Ecology & Biogeography* 9: 363-371.

SFIKAS, G. 2000. *Wildflowers of Crete*. Efstathiadis Group, Athens.

SIMBERLOFF, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49: 97-97.

TURLAND, N.J., CHILTON, L. & PRESS, J.R. 1993. *Flora of the Cretan Area*. The Natural History Museum, HMSO, London.

VIEGI, L. 1993. Contributo alla conoscenza della biologia delle infestanti dell colture della Sardegna nord-occidentale. I. Censimento delle specie esotiche della Sardegna. *Boll. Soc. Sarda Sci. Nat*. 29: 131-234.

VILÁ, M. & MUÑOZ, I. 1999. Patterns and correlates of exotic and endemic plant taxa in the Balearic islands. *Ecologia Mediterranea* 25: 153-161.

VITOUSEK, P.M. 1988. Diversity and biological invasions of oceanic islands. In: Wilson, E.O. (ed.). *Biodiversity* pp. 181-189; National Academy of Sciences/ Smithsonian Institution, Washington DC.

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

VITOUSEK, P.M., LOOPE, L.L. & ADSERSEN H. (eds.). 1995. *Islands: Biological Diversity and Ecosystem Function*. Springer, Berlin.

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

WHITTAKER, R.J. 1998. *Island Biogeography. Ecology, Evolution, and Conservation*. Oxford University Press, Oxford.

WILLIAMSON, M. 1981. *Island Populations*. Oxford University Press, Oxford.

YANNITSAROS, A. 1991. Adventive flora of Crete: history, phytogeography, ecology and agricultural aspects. *Botanika Chronika* 10: 299-307.