Journal of Mediterranean Ecology **vol. 12, 2013: 13-19**

Invasive plants in the Mediterranean basin: which traits do they share?

C. Bresch[1], L. Mailleret[1], M.M. Muller[1], C. Poncet[1] and P. Parolin[1,2]

[1] *INRA, ISA - TEAPEA 1355, BP 167, F-06903 Sophia Antipolis*
[2] *University of Hamburg, Dept. Plant Diversity, Germany*

Key words: biological invasion, attributes, woody plants, herbaceous plants, ornamental species.

Abstract

Species extinction processes are closely linked to human activities. Among the human factors identified as responsible for the loss of species, introduced species are the second-leading cause after habitat degradation. Plant invasions are particularly important in the Mediterranean Basin. Attempts have been made to describe factors associated with the invasive characters of plants. However, only a weak proportion of exotic plants really becomes invasive. In this contribution we review typical morphological and physiological traits that favour the invasivibility of plants into the Mediterranean Basin with a focus on ornamental species in this region. The aim of this study is to review the factors linked to the invasibility of the Mediterranean Basin ecosystem and the attributes shared by invasive plants in the Mediterranean area. The review shows that there is no unique profile of a typical invasive plant.

Introduction

Invasions by alien plant species are environmental issues of global significance (Hulme, 2006). The diffusion and establishment of exotic organisms threaten the ecosystems, the species, the habitats, human health and induce an important economic impact (McNeely, 2001).

One major aim in ecology is identifying determinants of invasiveness (Van Kleunen et al. 2010). Attempts have been made to describe factors associated with the degree of invasion by alien plants in the Mediterranean Basin: the invasivity i.e. the set of traits of these species (Lloret et al., 2004; Lloret et al., 2005; Lambdon and Hulme, 2006; Cano et al., 2007), the invasibility i.e. the ecosystem resistance to invasion (Vilà et al., 2008; Lambdon et al., 2008; Sanz-Elorza et al., 2006) and the interactions between these factors (Troumbis et al., 2002). Furthermore, invasive species are more plastic in a variety of traits (Davidson et al. 2011).

The Mediterranean ecosystem could be considered less prone to invasion than similar ecosystems on other continents regarding the long history of interactions between its environment and humans (Quézel et al., 1990) and the harshness of the climatic conditions (Garcia-Serrano et al., 2009). However this perception has been revised in the present context of globalization of trade (Hulme, 2004). The disturbance degree of the habitats, the human population density (Sanz-Elorza, 2006) and the climatic changes (Vilà et al., 2008) may lead to a progressive invasion of the continental

regions of the Mediterranean Basin (Sanz-Elorza, 2006; Celesti-Grapow et al., 2010) and their islands (Hulme, 2004).

Mediterranean islands are particularly vulnerable to invasions (Hulme, 2004; Gimeno et al., 2006). This susceptibility can be attributed to the existence of unsaturated communities, a lower competitive ability of native species, a proportionally lower native diversity (Hulme, 2004) or a higher human population (Hulme et al., 2008). However in case of a low propagule pressure or limiting ecological factors at later life-history stages a relative resistance of Mediterranean island ecosystems can occur (Hulme et al., 2008).

The aim of this study is to review the factors linked to the invasibility of the Mediterranean Basin ecosystem and the attributes shared by invasive plants in the Mediterranean Basin.

Attributes of Mediterranean Invasive Plant Species

Biogeographic origin, habitats and history

The alien species introduced unvoluntarily and whose survival in the native flora appears to be definitive rarely originate from the other Mediterranean climate biomes of the world. They are mainly originated from North America and Tropical Africa. Only in the Western region the impact of the Eastern Mediterranean Basin is an important element (Sanz-Elorza et al., 2006). In eight Mediterranean islands the biogeographic origin zone even appears to play a more important role in invasion success than the life history traits of the species (Lloret et al., 2004a). This factor is also found to be significant concerning invasivity of woody plant species in North America (Reichard and Hamilton, 1997) and in Australia (Pheloung et al., 1999). Hulme et al. (2008) suggested that the climatic adaptation of alien species to the Mediterranean regime was not particularly important regarding the weak proportion of plants originating from the Mediterranean. However a certain climatic similarity is clearly obvious in the patterns of the origin of the alien invasive species i.e. origin from temperate to cold regions.

Whether it concerns the Mediterranean region, the subcontinental or the oceanic regions of Europe, the composition of alien floras are more comparable among different habitats of the same region than between the same habitats of different regions. Patterns of habitat invasions in each region seem to be determined above all by attributes of the habitats rather than by the identity of particular alien species. An analogous tendency was found by Weber (1997) in his analysis of alien plant occurrence in European countries and by Lloret et al. (2004a), who found more than 400 aliens on eight large Mediterranean islands, but only four of them were present on all the islands.

Notably, even if Mediterranean woodlands are exposed to invader pressure, they contain a low proportion and abundance of invaders compared to grasslands, old fields and ruderal ecosystems (Cano et al., 2007; Chytry et al., 2008). The presence of open shrublands can be a driving force for the invasion processes of introduced species in Mediterranean communities even when no disturbance occurs (Cano et al., 2007). Invasion is promoted after periods of rainfall in grassland and shrubland (Cano et al., 2007). Shrubs can act as nurse plants by protecting seedlings from drought and low temperatures (Pugnaire et al., 1996; Holmgren et al., 1997). The riparian zones are also known to be susceptible to biological invasions (Crawley, 1987) and they are the only habitats really favorable to invasions by exotic species (Quézel et al., 1990). In such habitats, the environmental stresses due to the Mediterranean characters are decreased and enable the establishment of mesophil and ubiquist plants (Quézel and Médail, 2003).

The knowledge that a species is invasive elsewhere in the world strongly contributes to the identification of invasive species (Reichard and Hamilton, 1997). This character was found by Daehler and Strong (1993) as having utility for predicting biological invasions and being associated with invasive plants in Australia (Scott and Panetta, 1993).

Reproduction, phenology and dispersal

Uniparental **reproduction** via agamospermy, selfing and/or clonal propagation is considered as essential for colonisation (Kolar and Lodge, 2001). One of the dominant trends of invasive alien flora in NE Spain is the propagation by seeds (Sanz-Elorza et al., 2006). In five Mediterranean islands, large seed size factor is over-represented in *Caryophyllales*, *Asterales* and *Poales* (Lloret et al., 2005).

Vegetative propagation in Mediterranean Basin is positively associated with an average alien abundance across five islands (Lloret et al., 2005). This attribute has also been found to correlate with invasiveness of woody plant species elsewhere (Reichard and Hamilton, 1997; Daehler, 1998). This trait enables the species to establish rapidly within suitable habitats, to be more competitive and to use more efficiently resources (Suehs et al., 2004).

Time of flowering is identified as important in the alien invasion of Mediterranean biomes (Lake and

Leishman, 2004) contrary to temperate floras (Thompson et al., 1995; Reichard and Hamilton, 1997). Flowering on summer enables the alien invasive species to avoid competitors with the exploitation of mutualists, such as pollinators. Summer flowering is a dominant trend of the invasive alien flora of NE Spain (Sanz-Elorza, 2006) and across five Mediterranean islands (Lloret et al., 2005). Long flowering periods especially in agricultural habitats explain alien species abundance across five Mediterranean islands (Lloret et al., 2005). Late flowering is a significant attribute over-represented with *Caryophyllales*, *Asterales* and *Poales* in five Mediterranean islands (Lloret et al., 2005).

Long flowering can increase the likelihood of cross-pollination and reproductive success in conditions of seasonal pollination and/or high competition for pollinators (Lloret et al., 2005). Phenology adjustment to periods of water availability and more efficient water consumption than native species is also a sparking element for invasion in the Mediterranean (Cano et al., 2007). Alien species can be not competitive against native vegetation (e.g. Garcia-Serrano et al., 2004; Sans et al., 2004) but their recruitment during periods of abundant rainfall can increase their competitive ability and allow a successful invasion (Cano et al., 2007).

In 79 Mediterranean islands, the rate of invasion is higher in species with good dispersal abilities (Lambdon and Hulme, 2006). Animal dispersal may be particularly important for the colonization of semi-natural habitats, where propagule pressure is often lower than in anthropogenic habitats (Vilà et al., 2003). Dispersal by vertebrates and anemochory are positively associated with the average alien abundance of exotic plant species in five Mediterranean islands (Lloret et al., 2005).

Genetics and phylogenetics

Hybridization between native and alien species and/or between aliens particularly in island habitats (Abbott, 1992) can result in negative genetic and ecological impacts on the native flora (Vilà et al., 2000). In the Hyères archipelago of the Southeastern coast of France, *Carpobrutus affine acinaciformis* shows a high hybrid vigour owing to its hybridisation with *C. edulis*. A high occurrence of introgression of *C. edulis* genes into the *C. affine acinaciformis* population increases the hybrid status of the latter (Suehs et al., 2004a). The hybrids arising from backcrosses can contribute gradually to increased invasion (Ellstrand and Schierenbeck, 2000) e.g. in *Carpobrotus* in California (Vilà and D'Antonio, 1998b).

The analysis of alien species composition of the Mediterranean region differs from the analysis of the alien floras of the subcontinental and oceanic regions of Europe which are more similar to each other (Chytry et al., 2008). In the Mediterranean islands, invasiveness appears highly unpredictable across lineages (Hulme et al., 2008; Lambdon, 2008). A high diversity of families represented by a low number of species is also a trait of the alien naturalized flora in Europe (Weber, 1997) and France (Maillet, 2000).

Morphology and physiology

The effect of summer water shortages on the physiological attributes of alien plant species is crucial to their success or failure of invasion. Some species are able to adapt to water restriction owing to their plasticity in ecophysiological traits (Monneveux and Belhassen, 1996). Succulence which enables species to resist efficiently the seasonal water deficit of the Mediterranean climate is correlated with invasion success in ruderal habitats of Mediterranean islands (e.g. *Opuntia spp., Agave americana*). This trait which is rare among native species from the Mediterranean Basin is however relatively common in other Mediterranean type regions and may be attributed to the presence of empty niches (Lloret at al., 2005). However sometimes a better ecophysiological adaptation of native species to environmental conditions can also be expected e.g. *Senecio malacitinus* (Garcia-Serrano et al., 2009) or *Spartina maritima* (Castillo et al., 2000).

Allelopathic interactions between invasive and native species are known to be involved in biological invasions, e.g. *Ailanthus altissima* which is able to inibit the development of neiborhood plants (Gomez-Aparicio and Canham, 2008)

Certain morphological traits can promote the invasive spread of a species. In NE Spain, the most invasive species are herbaceous agricultural weeds due to their widespread diffusion and to their adaptation to rapid changing environments (Sanz-Elorza et al., 2006). Annual established species are more abundant than perennial ones in ruderal habitats of five Mediterranean islands. However in all habitat types of this region, plant size attributes (e.g. growth form, height) or life cycle (e.g. longevity) are not positively associated with average alien abundance (Lloret et al., 2005). The importance of herbaceous species is corroborated by Pyšek et al. (1995). These data contrast with findings in the British Isles where introduced species appear to be larger than native plants (Crawley et al., 1996) and show the difficulty to identify a unique profile of invasive plants even for one type of traits.

Alien plant species with very large leaves are more

likely to become abundant in Mediteranean islands (Lloret et al., 2005). This attribute was also found to differ between alien and native species in Australia (Lake and Leishman, 2004). It is often associated with higher competitive ability, particularly in nutrient-rich moderately disturbed habitats (Grime, 1979).

Elements linked to introduction

The influence of the introduction pathway on the invasiveness of a species can be significant, as was demonstrated in NE Spain (Sanz-Elorza et al., 2006) and in the Mediterranean islands (Lambdon and Hulme, 2006). Whereas the majority of the naturalized species arise on Mediterranean islands from intentional introductions for forestry, agriculture or gardening purposes, one third are fortuitious (Hulme et al., 2008). Escapes of ornamental plants in the Mediterranean islands constitute the largest source of established alien species (Hulme et al., 2008; Lambdon and Hulme, 2006). This is corroborated by findings in the United States where horticulture is identified as the main pathway of invasive plant introductions (Reichard and White, 2001).

In Mediterranean islands, frequency of introduction is not linked to invasiveness even if the species introduced in invasible natural environments are more likely to benefit from high introduction frequencies than those confined to gardens (Lambdon and Hulme, 2006). Against all expectations, time since introduction also has a minor influence (Lambdon and Hulme, 2006) whereas a large residence time effect is usually reported (Rejmanek, 2000). Moreover the inclusion of the data relative to the importance of international trade routes are known to be a good indicator to prevent the invasions in the future (Thuillier et al., 2005) and it constitues an important element of the criteria necessary for the screening of species by the Pest Risk Analysis developed in Europe (EPPO, 2010).

Conclusion

Even if the alien flora of the Mediterranean basin has similarities with the attributes of the alien flora of other regions of the world, conflicting data demonstrate the extreme difficulty to define a unique suite of traits. Although numerous studies have attempted to identify species traits causing invasion success, there was no evidence for well defined invasive syndromes, be it in Mediterranean plants as in invasive plants in general (Lloret et al., 2005). These results support the hypothesis that a universal pattern of attributes is unlikely to explain invasion success (Thompson et al., 1995; Pyšek, 1998; Rejmánek, 2000).

Invasiveness is present in all ecosystems, in natural as well as in those altered by human activities. Semi-natural communities like the Mediterranean basin with its pluri-millenary human intervention appear particularly susceptible to biological invasions. Length of lag-phases, pathways and land-use changes (Hulme et al., 2008) may accelerate this process. Climate change in the Mediterranean ecosystems might induce fluctuations of water availability (Lavorel et al., 1998) and thus modify species distributions.

Concluding, the development of screening systems which integrate local and regional abundance patterns appears promising in order to identify invasive species already established in the Mediterranean Basin, an ecosystem where significant losses in local species richness and ecosystem structure and function are ongoing since several millennia (Hulme et al., 2008).

Acknowledgements

We dedicate this review to Jean-Paul Onesto.

Literature Cited

Abbott, RJ. 1992. Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends in Ecology and Evolution* 7: 401-405.

Andreu, J, Montserrat, V, Hulme, PE. 2009. An Assessment of Stakeholder perceptions and Management of Noxious Alien Plants in Spain. *Environmental Management* 43(6): 1244-1255.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody species. J. Veg. Sci. 7: 121–124.

Bousquet-Mélou, A, Sophie, L, Robles, C, Greff, S, Dupouyet, S, Fernandez, C. 2005. Allelopathic potential of *Medicago arborea*, a Mediterranean invasive shrub. *Chemoecology* 15(4): 193-198.

Cano, L, Escarre, J, Sans, FX. 2007. Factors affecting the invasion success of *Senecio inaequidens* and *S. pterophorus* in Mediterranean plant communities. *Journal of Vegetation Science* 18: 281-288.

Castillo, JM, Fernández-Baco, L, Castellanos, EM, Luque, CJ, Figueroa, ME, Davy, AJ. 2000. Lower limits of *Spartina densiflora* and *S. maritima* in a Mediterranean salt marsh determined by different ecophysiological tolerances. *Journal of Ecology* 88: 801-812.

Celesti-Grapow, L, Alessandrini, A, Arrigoni, PV, Assini, S, Banfi, E, Barni, E, Bovio, M, Brudu, G, Cagiotti, MR, Camarda, I, Carli, E, Conti, F, Del Guacchio, E, Domina, G, Fascetti, S, Galasso, G, Gubellini, L, Lucchese, F, Medagli, P, Passalacqua, NG, Peccenini, S, Poldini, L, Pretto, F, Prosser, F, Vidali, M, Viegi, L, Villani, MC, Wilhalm, T, Blasi, C. 2010. Non-native flora of Italy: Species distribution and threats. *Plant Biosystems* 144(1): 12-28.

Crawley, MJ. 1987. What makes a community invasible? p. 429-454. In: Crawley, M.J., Edwards, P.J, Gray, A.J. (eds). *Colonisation, succession and stability*. Blackwell Scientific, Oxford, England.

Crawley, MJ, Harvey, PH, Purvis, A. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society B* 351: 1251-1259.

Crooks, JA, Soulé, M.E. 1999. Lag times in population explosions of invasive species: causes and implications. p. 103 -125. In: Sandlund, O.T. et al. (eds). *Invasive species and biodiversity management*. Kluwer.

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

Daehler, CC, Strong, DR. 1993. Prediction and biological invasions. *Trends in Ecology and Evolution* 8: 380-380.

Davidson, A, Jennions, M, Nicotra, A. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419-431.

Ellstrand, NC, Schierenbeck, KA. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the United States of America*. 97: 7043-7050.

EPPO. 2010. *European and Mediterranean Plant Protection Organization*. http://archives.eppo.org/EPPOStandards/pra.htm.

Garcia-Serrano, H, Caño, L, Escarré, J, Fleck, I, Sans, FX. 2009. Physiological comparison of alien *Senecio inaequidens* and *S. pterophorus* and native *S. malacitanus*: implications for invasion. *Flora* 204: 445-455.

Gimeno, I, Vilà, M, Hulme, PE. 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.

Gómez-Aparicio, L, Canham, CD. 2008. Neighborhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. *Journal of Ecology* 96: 447-458.

Grime, JP. 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester.

Hulme, PE. 2004. Invasions, islands and impacts: A Mediterranean perspective. p. 337-361. In: Fernandez Palacios, J.M, Morici, C. (eds.). *Island ecology*. Asociación Española de Ecología Terrestre, La Laguna.

Hulme, PE. 2006. Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* 43: 835-847.

Hulme, PE, Brundu, G, Camarda, I, Dalias, P, Lambdon, P, Lloret, F, Médail, F, Moragues, E, Suehs ,C.M, Traveset, A, Troumbis, A, Vilà, M. 2008. Assessing the risks to Mediterranean islands ecosystems from alien plant introductions. p. 39-56. In: Tokarska-Guzik, B, Brock, J.H, Brundu, G, Child, L, Daehler, C.C, Pyšek, P. (eds.). *Plant invasions: Human perception, ecological impacts and management*. Backhuys Publishers, Leiden.

Kolar, CS, Lodge, DM. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* 16: 199-204.

Lake, JC, Leishman, MR. 2004. Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117: 215-226.

Lambdon, PW, Hulme, PE. 2006. Predicting the invasion success of Mediterranean alien plants from their introduction characteristics. *Ecography* 29: 853-865.

Lambdon, PW, Lloret, F, Hulme, PE. 2008. Do alien plants on Mediterranean islands tend to invade different niches from native species? *Biological Invasions* 10: 703-716.

Lambdon, PW. 2008. Is invasiveness a legacy of evolution? Phylogenetic patterns in the alien flora of Mediterranean Islands. *Journal of Ecology* 96: 46-57.

Lavorel, S, Canadell, J, Rambal, S, Terradas, J. 1998. Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology and Biogeography* 7: 157-166.

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

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

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

Maillet, J, Lopez-Garcia, C. 2000. What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France. *Weed Research* 40(1): 11-26.

McNeely, J. 2001. Invasive species: a costly catastrophe for native biodiversity. *Land Use and Water Resources Research* 1(2): 1-10.

Monneveux, P, Belhassen, E. 1996. The diversity of drought adaptation in the wide. *Plant Growth Regulation* 20: 85-92.

Pheloung, PC, Williams, PA, Halloy, SR. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57: 239-251.

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

Pyšek, P, Prach, K. & Smilauer, P. 1995. Relating invasion success to plant traits: an analysis of the czech alien flora. p. 39–60. In: P. Pyšek, K. Prach, M. Rejmánek & M. Wadw (eds.). *Plant Invasions – General Aspects and Social Problems*. SPB Academic, Amsterdam.

Quezel, P, Barbero, M, Bonin, G, Loisel, R. 1990. Recent plant invasions in the circum-mediterranean region. p. 51-60. In: Di Castri, F, Hansen, A.J, Debussche, M. (eds). *Biological invasions in Europe and the Mediterranean Basin*. Kluwer Academic Publisher, Dordrecht.

Reichard, SH, Hamilton, CW. 1997. Predicting invasions of woody plants introduced in North America. *Conservation Biology* 11: 193-203.

Reichard, SH, White, P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* 51: 103-113.

Rejmánek, M. 2000. Invasive plants: approaches and predictions. *Australian Ecology* 25: 497-506.

Sakai, AK, Allendorf, FW, Holt, JS, Lodge, DM, Molofsky, J, With, KA, Baughman, S, Cabin, RJ, Cohen, JE, Ellstrand, NC, McCauley, DE, O'Neil, P, Parker, IM, Thompson, JN, Weller, SG. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305-332.

Sans, FX, Garcia-Serrano, H, Afán, I. 2004. Life-history traits of alien and native senecio species in the Mediterranean region. *Acta Oecologica* 26: 167-178.

Sanz-Elorza, M, Dana, ED, Sobrino, E. 2006. Invasibility of an island area in NE Spain by alien plants. *Acta Oecologica* 29: 114-122.

Scott, JK, Panetta, FD. 1993. Predicting the Australian weed status of southern African plants. *Journal of Biogeography* 20: 87-93.

Suehs, CM, Affre, L, Médail, F. 2004a. Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. *Heredity* 92: 31-40.

Suehs, CM, Affre, L, Médail, F. 2004b. Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: II. Reproductive strategies. *Heredity* 92: 550-556.

Thuiller, W, Richardson, DM, Pyšek, P, Midgley, GF, Hughes, GO, Rouget, M. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234-2250.

Thompson, K, Hodgson, JG, Rich, TCG. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.

Troumbis, AY, Galanidis, A, Kokkoris, GD. 2002. Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* 98: 239-250.

van Kleunen, M, Weber, E, Fischer, M. 2009. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245.

Vilà, M, D'Antonio, C.M. 1998. Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in coastal California. *Ecologia Applicata* 8: 1196-1205.

Vilà, M, Siamantziouras, ASD, Brundu, G, Camarda, I, Lambdon, P, Medail, F, Moragues, E, Suehs, C.M, Traveset, A, Troumbis, A.Y, Hulme, PE. 2008. Widespread resistance of Mediterranean island ecosystems to the establishment of three alien species. *Diversity and Distributions* 14: 839-851.

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

Vilà, M, Burriel, JA, Pino, J, Chamizo, J, Llach, E, Porterias, M, 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, Basnou, C, Pyšek, P, Josefsson, M, Genovesi, P, Gollasch, S, Nentwig, W, Olenin, S, Roques, A, Roy, D, Hulme, PE, DAISIE partners. 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. *Frontiers in Ecology and Environment* 8(3): 135-144.

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