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ORIGINAL PAPER

The alien flora of Greece: taxonomy, life traits and habitat preferences

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Abstract The aim of the paper is the state-of-the-art assessment of the alien flora of Greece and its traits. The dataset consists of a total of 343 alien taxa, including 49 archaeophytes. The taxonomy, life traits and habitat of the 294 neophytes are analysed vs their naturalisation status. Out of the 122 (41%) naturalised neophytes, 50 are identified as exhibiting invasive behaviour. Poaceae, Asteraceae, Amaranthaceae, Solanaceae, Fabaceae, and Polygonaceae are the plant families richest in alien taxa. The majority of them are of American origin, followed by those of Asiatic and Mediterranean origin. The neophytes are predominantly herbs, most of them annuals. Yet, the perennial life cycle is equally frequent with the annual one and the proportion of phanerophytes in the alien flora is increased compared to the one of the native flora. Regarding flowering traits, most of the aliens have a long flowering period (over 1 month) and flower in late spring, summer and autumn, when few of the native plants are in bloom. Vertebrate zoochory and anemochory are the two dispersal modes mostly utilised by the alien plants (43 and 28%, respectively), while more than one dispersal mechanisms are functional for 56% of them. Artificial habitats have the highest frequencies of alien plants. The natural habitats with the highest numbers of aliens are the coastal ones and inland surface waters. *Opuntia ficus-barbarica*, *Ailanthus altissima*, *Oxalis pes-caprae*, *Erigeron bonariensis*, *Amaranthus albus* and *Symphyotrichum squamatum* are typical cases of plants characterised as invasive, having established in almost all the habitat groups identified. The diversity of the ecological characteristics of the plants suggests a potential of impacts that needs to be further assessed.

Keywords Plant invasions · Species traits · Habitats · Mediterranean basin

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Introduction

Although the phenomenon of biological invasions has been noted for some time (Elton 1958), it is only during the last two decades that the biological consequences of exotic invasions have been researched extensively. This is due to the realisation

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of the significant losses of the biological diversity and function of the ecosystems invaded and the economic impacts caused (Mooney and Hobbs 2000; Mack et al. 2000; Vilà et al. 2009). Vascular plants are among the most ubiquitous invasive organisms. The majority of the plants have been introduced for agricultural, silvicultural, ornamental or medicinal purposes (Williamson 1996), while many have been accidental introductions (Newsome and Noble 1986).

Two basic questions have fascinated ecologists since biological invasions have become a focal issue of the global change (Pyšek and Richardson 2006). The first question articulated was "which species invade and under which conditions?" This question has stimulated the search for traits that make plant species potential successful invaders (e.g. Lloret et al. 2004; Pyšek et al. 1995, 2009). The second question was "what features of ecosystems make them either prone or resistant to invasions?" This has lead to studies on community characteristics and environmental conditions under which an invasive event is realised (e.g. Davis et al. 2000; Vilà et al. 2007). It is only recently that these two questions have been considered in concert (Richardson and Pyšek 2006; Weber et al. 2008).

Despite the fact that there are several independent research efforts in the field of invasion ecology in Europe, it is only recently that a systematic and synthetic approach has been adopted on investigations into alien species in Europe (DAISIE 2009). Prior to the DAISIE work only few European countries had sound information on the composition of their alien floras, available in specialised checklists, namely Austria (Essl and Rabitsch 2002), the Czech Republic (Pyšek et al. 2002), Germany (Klotz et al. 2002; Kühn and Klotz 2003), Ireland (Reynolds 2002), the United Kingdom (Clement and Foster 1994; Preston et al. 2002, 2004) and recently Italy (Celesti-Grapow et al. 2009).

The study of the alien vascular flora of Greece started in the early 1970's (Yannitsaros 1982). It became more intense and systematic during the last two decades and many new records were added. Some of the Greek regions for which there is sufficient knowledge of the alien flora are Attica (Yannitsaros 1982), the island of Crete (Yannitsaros 1991; Turland et al. 1995), the urban areas of Thessaloniki (Krigas and Kokkini 2004) and Patras (Chronopoulos and Christodoulakis 2000) and some Aegean Islands, e.g. Lesvos (Bazos 2005), Chios (Snogerup et al. 2001), Kalymnos (Zervou and Yannitsaros 2009). However, there had been no checklist of the alien taxa of Greece. The current paper is based on the data inventory carried out under the DAISIE project (http://www.europe-aliens.org/), which was complemented by information on plant traits and habitats. It provides for the first time a complete catalogue of the alien plants of Greece based on up-to-date information, and it aims to address basic but essential questions such as the number and naturalisation status of the neophytes, their taxonomic identity and origin, and their biological and ecological profile.

Methods

Area of study

Greece occupies the southernmost part of the Balkan Peninsula and has a total land territory of approx. 132,000 km^2. By land it is bordered by Albania, Former Yugoslav Republic of Macedonia and Bulgaria from the north, and the European part of Turkey from the northeast. The continental mainland is surrounded by the Aegean Sea to the east, the Libyan Sea to the south, and the Ionian Sea to the west. The insular part occupies more than one-fifth of its total area and includes more than 2000 islands (only 227 of which are inhabited) (Strid and Tan 1997).

Although a small country, Greece, owing to its geomorphology and dissected landscape, has an extremely wide range of natural habitats ranging from alpine to almost xeric. Eighty percent of Greece consists of mountains or hills which make it the third most mountainous country in Europe (Dax and Hovorka 2005). The mountains, many of which exceed 2,000 m in height, provide a wide range of habitats, including a large variety of shrublands, forests, and meadows. The lowlands include lakes, streams, river deltas and lagoons of international importance. In terms of ecosystem types Greece possesses a great diversity, as a result of the complex relief and the relatively mild, until recently, human activities. The most extended ecosystems are the Mediterranean maquis, phrygana and forests covering 40% of the area (Arianoutsou and Diamantopoulos 1985). Greece has the tenth longest coastline in the

World (15,000 km total, 7,300 continental and 7,700 in the islands), hence coastal, marine and island habitats comprise a priority for the country (Strid and Tan 1997).

Greece, being part of the Mediterranean Basin was settled by humans very early. As a consequence Mediterranean landscapes have long ago experienced the human impact. Indigenous agriculture and animal husbandry have been practiced here for more than 10,000 years (Naveh 1998) in combination with deforestation practices and fire management. Plant community structure and diversity patterns have therefore evolved under the influence of this interaction, as is also the case for the other Mediterranean type regions of the world (Cowling et al. 1996). These patterns were kept at a dynamic equilibrium at least until the Second World War (Caravello and Giacomin 1993). Since 1950, major changes have occurred to the economies, the livelihood and hence the landscapes of the country. Initially, there were extensive rural migrations followed by agricultural intensification from the introduction of new farm machinery, new strains of cereals and tree crops and extensive application of fertilisers. The invention of new irrigation techniques made the use of hilly areas possible, so agriculture spread further. Land abandonment, tourism development, population concentration along the coast, and the building of extended transportation networks characterized the last two decades of the twentieth century (Burke and Thornes 1998). The common agricultural policy (CAP) set by the European Union is also part of the puzzle. The accelerated socio-economic changes during these two decades have caused major changes in the landscape patterns and the biodiversity they support (see Arianoutsou 2001 for an extensive review).

The total population of Greece is about 11 million (2001 census data, NSSG 2005). Approximately 90% of the population lives in the coastal region (population density is about 78/km^2 or 0.6/km of coast). Population density in Greece is generally lower than in North Europe (UN 2004; Eurostat 2005), but it is high in Athens and Thessaloniki metropolitan areas where half of the Greek population is concentrated. The urbanisation rate in 1985 was 60% but had reached 68% by the year 2000. Rural population has gradually decreased since the early 1960s and currently most of the Greeks inhabit either big cities or coastal areas thriving by tourism. This intensification and shift of economic activities to the secondary and tertiary sector has increased environmental problems and threats to Greece's natural environment. The most serious human impacts are wetland reclamation, desertification due to repeated fires, frequently coupled with grazing, development of coastal housing and tourism infrastructure. Increased emissions of various kinds of pollutants and pollution of air, water, and soil have also been recognised as significant problems.

Data sources-database

The dataset analysed here originates from the database "Alien", an upgraded version of the one compiled for the DAISIE project (Pyšek et al. 2009; http://www.europe-aliens.org/), complemented with additional and updated information. The database includes tables with multiple records for the status, distribution, introduction and ecological traits of each plant. The data recorded were based on the investigation of 283 sources of which 234 were used for the plants of "Appendix IV". The sources ("Appendices I and II") include mainly original articles and standard floras and checklists such as Flora Hellenica (Strid and Tan 1997, 2002), Flora Europaea (Tutin et al. 1968–1980, 1993) and Med-Checklist (Greuter et al. 1984–1989; Greuter and von Raab-Straube 2008). Internet databases, such as the International Plant Names Index, and unpublished vegetation relevés databases (available to the authors) were also used. Circumstantial field observations and expert opinion by our research team were used for c. 50 records. The bulk of the sources (84%) consist of research results published from the 1980s onwards ("Appendix II") and 33% of the sources were published during the last decade.

Characterisation of species

The dataset includes all alien species recorded at terrestrial habitats of the territory of Greece published in the literature since 1939. Taxa native in some parts of the Greek territory but alien in others as well as cryptogenic taxa were excluded.

Nomenclature of taxa follow mainly Tutin et al. (1968–1980, 1993), Strid and Tan (1997, 2002), Greuter et al. (1984–1989), Greuter and von Raab-Straube (2008), while that of families' the

APG system (Stevens 2001 onwards). All other data, including the characterisation of species' status, were recorded based on different sources, on a case by case basis.

The species entries are supplemented with data on taxonomic position (family), chorology, life habit characteristics (life and growth form, life cycle), habitats, ecological characteristics (flowering period and duration, dispersal type and mode, dispersal agent and dispersal unit) and status.

Status is defined as either casual or naturalised (after Richardson et al. 2000; Pyšek et al. 2004), or as unknown if existing information is insufficient for the classification of an alien plant to one of the previous categories. Taxa were also characterised as archaeophytes or neophytes and as being invasive or not.

Life forms are identified according to the system proposed by Raunkiaer (1934, 1937) and modified by Ellenberg (1956) and Ellenberg and Müller-Dombois (1967). Plant chorological categories for the native range of the plants are defined according to Pignatti (1982) while in some cases several additional sources are used.

Habitat classification is made according to the EUNIS system levels 1, 2 and 3. The EUNIS codes are assembled to broad habitat groups which are also distinguished in artificial (a)/natural (n) and dry (d)/water related (w) for analysis ("Appendix III").

Results

Species status

The alien flora of Greece includes 343 taxa ("Appendix IV"). The neophytes (294 taxa) amount to 86% of the alien flora ("Appendix IV"). Of them, 41% (122 taxa) are classified as naturalised and 26% (77 taxa) are classified as casual. There is, however, a relatively high percentage of neophytes (95 taxa, 32%) whose naturalisation status is unknown. These are either recent introductions or recently recorded in Greece. A total of 50 naturalised neophytes ("Appendix IV") fulfil the criteria to be characterised as invasive (after Richardson et al. 2000; Pyšek et al. 2004), based on expert opinion and taking into account their distribution across the Greek floristic regions, number of records, and number and types of habitats occupied. Some of the most prominent among the invasive species are: *Ailanthus altissima*, *Amaranthus* spp., *Chenopodium ambrosioides*, *Datura stramonium*, *Eleusine indica*, *Erigeron* spp., *Nicotiana glauca*, *Opuntia ficus-barbarica*, *Oxalis pes-caprae*, *Paspalum distichum*, *Solanum elaeagnifolium*, *Symphyotrichum squamatum* and *Xanthium spinosum*.

Further analysis of data concerns only the neophytes.

Taxonomy

Out of the 343 alien taxa recorded in Greece, 18 are recorded at subspecific level, but only two species are represented by more than one subspecies in the database, namely *Medicago sativa* (an archaeophyte) and *Narcissus tazetta*. A total of four species are of hybrid origin ("Appendix IV").

The neophytes belong to 199 genera and 76 families (Fig. 1). The majority of the taxa recorded belong to the families of Poaceae (39 taxa), Asteraceae (31 taxa), Amaranthaceae (29 taxa), Solanaceae (18 taxa), Fabaceae (18 taxa), and Polygonaceae (9 taxa). Approximately half of the families are represented by only one taxon (e.g. Acanthaceae, Agavaceae, Caprifoliaceae, Caryophyllaceae, Elaeagnaceae, Elatinaceae, Geraniaceae). The families richest in naturalised taxa are Poaceae (16 taxa), Amaranthaceae (16 taxa), Asteraceae (13 taxa), Solanaceae (7 taxa), Convolvulaceae (7 taxa) and Fabaceae (5 taxa) (Fig. 1).

Amaranthus is by far the richest genus including 18 taxa, followed by *Solanum* including 6 taxa and *Euphorbia* including 5 taxa.

Chorology

The American continent is the origin of the majority of the neophytes (133 taxa, 46%) and notably of an even larger percentage of the naturalised neophytes (68 taxa, 56%) in Greece (Fig. 2). Within this group, 44 taxa are South-American, 48 are North-American and only 4 are Central-American, while the rest have a wider distribution. The next most frequent areas of origin for the sum of the neophytes are Asia, Africa, and the Mediterranean basin (43, 30, and 24 taxa, respectively) while the native range of 20 taxa includes the Tropical and/or Subtropical areas of the world. This chorological pattern is more or less

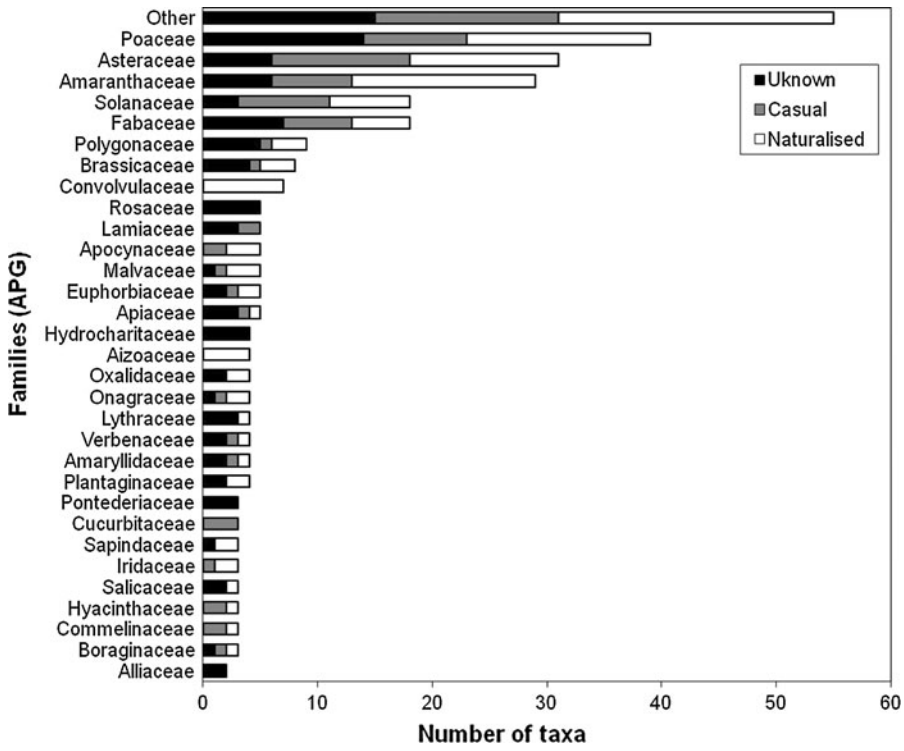

Fig. 1 The richest families of the neophyte flora of Greece classified according to the Angiosperm Phylogeny Group (Stevens 2001 onwards). Families are ranked according to the number of taxa they include. Taxa are characterised as of Unknown status, Casual and Naturalised

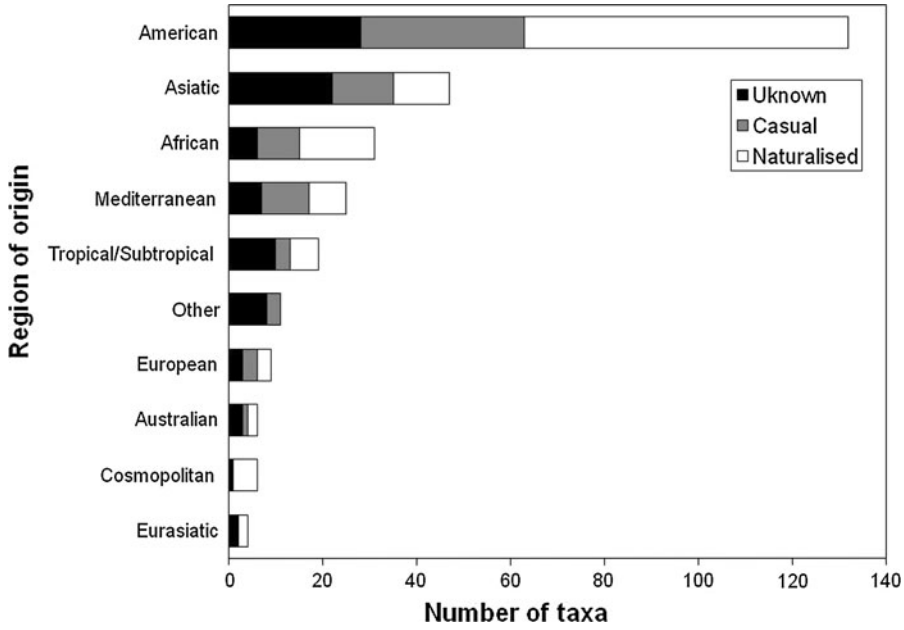

Fig. 2 Regions of origin for the neophytes of Greece. Taxa are classified as of Unknown status, Casual and Naturalised

followed by the naturalised neophytes, as well (Fig. 2). Notably, while the Asiatic naturalised neophytes originate from various regions, most of the African naturalised neophytes originate from South Africa (11 out of 15).

Mode of introduction

Our sources do not allow us to properly assess the mode of introduction for all alien taxa reported from Greece so far. Preliminary available data indicate that

most neophytes (75%) are introduced intentionally for agricultural or ornamental purposes. On the other hand, contamination of crop seed propagules has apparently been a main pathway of accidental introduction.

Life habits

Most neophytes are herbs (over 75%), while shrubs and trees account for 16 and 8%, respectively, and this pattern was observed in all status categories (Fig. 3).

The perennial life cycle is somewhat more frequent in the alien taxa than the annual one (52 and 43%, respectively) (Fig. 4). Naturalised taxa follow the same pattern (50% perennials and 46% annuals) and in the casual taxa the two categories have almost the same frequency (48% perennials and 44% annuals) (Fig. 4). Moreover, there are few taxa that appear with more than one type of life cycle, e.g. annuals/biennials (*Lunaria annua* subsp. *annua*), annual/perennials (*Amaranthus deflexus*, *Brassica napus*, *Chenopodium pumilio*, *Ch. ambrosioides*, *Eragrostis leptocarpa*, *Oenothera laciniata*, *Symphyotrichum squamatum*) and biennials/perennials (*Oenothera glazioviana*, *Peucedamum chryseum*).

Regarding life forms, therophytes are the most prominent group, comprising 45% of the neophytes (Fig. 5). The perennials are mostly phanerophytes (20%) and hemicryptophytes (14%). This general pattern is again similar in the groups of naturalised and casual neophytes (Fig. 5).

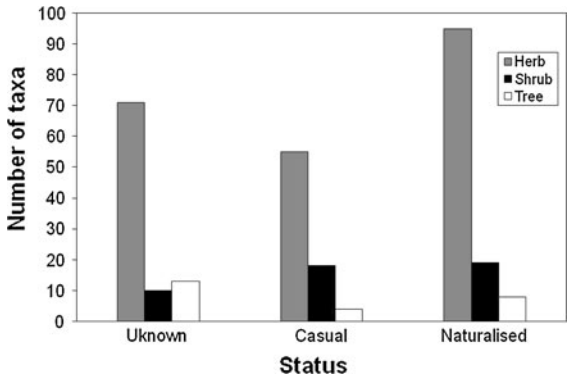

Fig. 3 Growth forms of the neophytes of Greece according to their status. Taxa are classified as of Unknown status, Casual and Naturalised

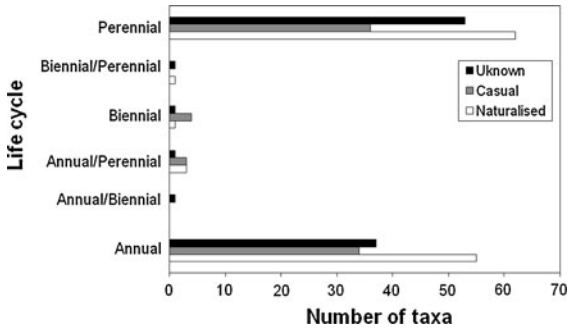

Fig. 4 Life cycle of the neophytes of Greece. Taxa are classified as of Unknown status, Casual and Naturalised

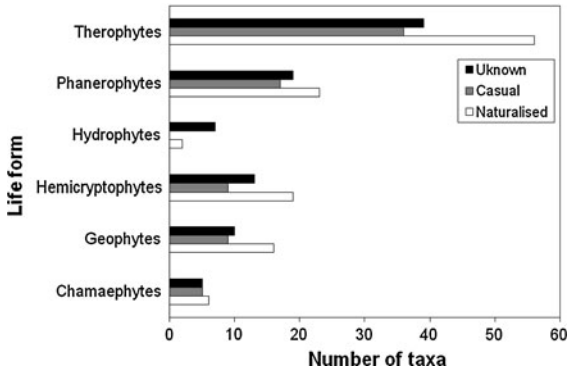

Fig. 5 Life forms of the neophytes of Greece. Taxa are classified as of Unknown status, Casual and Naturalised

The flowering period for the majority of neophytes extents in more than one seasons, mainly initiating in spring and lasting through summer to autumn (Fig. 6a). Summer flowering aliens are the most frequent while winter flowering ones are few. This flowering season pattern is repeated in all the status groups. The duration of flowering (Fig. 6b) ranges from 2 to 4 months for most aliens (e.g. *Bassia hyssopifolia*, *Phalaris canariensis*). Few of them flower for only 1 month. On the contrary, a considerable number of aliens have an extended flowering period, from 7 (e.g. *Amaranthus quitensis*, *Ipomoea indica*, *Solanum cornutum*) up to 12 months (e.g., *Aeonium aboreum*, *Nicotiana glauca*).

Dispersal of most of the neophytes is mediated by mammals and birds (43%) and by the wind (28%) (Fig. 7), that is by agents which provide the chance for long distance dispersal. The casual aliens follow the same dispersal agent pattern but in the naturalised aliens dispersal by the wind and by

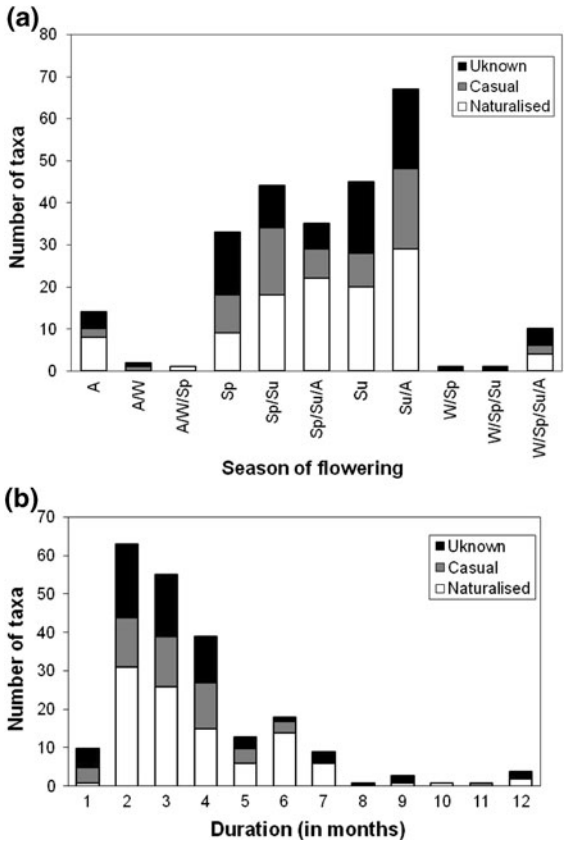

Fig. 6 Flowering season (**a**) and duration of flowering (**b**) for the neophytes of Greece. Taxa are classified as of Unknown status, Casual, and Naturalised (*A*, Autumn; *W*, Winter; *Sp*, Spring; *Su*, Summer)

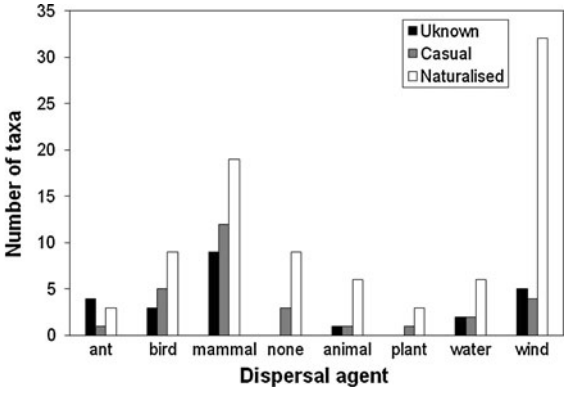

Fig. 7 Dispersal agents of alien neophytes in Greece. Taxa are classified as of Unknown status, Casual and Naturalised

animals are equally frequent. Most of the neophytes (67%), in all status categories, possess some adaptation that ensures dispersal at some distance, usually zoochory (e.g., adhesive dispersal unit as in *Xanthium* spp. or endozoochorous fruits as in *Carpobrotus edulis*) or anemochory (e.g., flying device as in *Acer negundo* and *Erigeron* spp.). Moreover, for most of the neophytes (56%) more than one dispersal mechanisms are available either the plants have developed specific morphological features or not (data not shown). For example, the rolling seeds of *Amaranthus albus* are anemochorous (medium distance) but they are occasionally further transferred by animals.

Habitats

The distribution of neophytes per habitat group is shown in Table 1.

Artificial habitats, especially cultivations (Cu) and road networks (At), host the highest numbers of neophytes, in all status categories. Plant habitats of urban and inhabited rural areas (Au, Aw, Ap—see "Appendix III" for details), such as walls, pavements, construction sites and abandoned constructions are also often colonised by neophytes. The natural habitats that host the highest numbers of neophytes are the coastal zones (C) and inland surface waters (W). Artificial habitats host the highest numbers of naturalised taxa, as well. However, the naturalised neophytes occur more frequently in natural habitats than casuals, especially in coastal and water related ones.

Less than half of the alien neophytes (38%) occur in only one habitat group and 33% occur in 2–3 habitat groups (Fig. 8). This trend is different for the naturalised taxa, since only 16% of them occur in only one habitat group, half of them (49%) occur in more than 3 habitat groups and one species (*Oxalis pes-caprae*) is in fact omnipresent in all the 18 habitat groups. Another three naturalised plants, namely *Erigeron bonariensis*, *Amaranthus albus* and *Symphyotrichum squamatum*, have also been found in a wide range of habitats (in 16, 15, and 14 groups, respectively).

Poaceae and Fabaceae are the families with the largest numbers of naturalised taxa recorded in only one habitat type (18 and 9 taxa, respectively) followed by Amaranthaceae (8 taxa), Solanaceae (4 taxa), and Lythraceae (4 taxa). Naturalised taxa inhabiting more than one habitat are of diverse status and taxonomy.

Table 1 Number of neophytes in Greece occurring in each habitat group (*n*, natural habitat; *a*, artificial habitat; *w*, water-related habitat; *d*, dry habitat; detailed description of habitats in "Appendix II")

Habitat group	Unknown	Casual	Naturalised
Marine			
M.n.w	1 (1)	0	0
Coastal			
C.n.d	7 (10)	6 (11)	44 (39)
C.n.w	2 (3)	2 (4)	15 (13)
Inland water bodies, Fens, Bogs			
W.n.w	7 (10)	7 (13)	50 (44)
Grasslands			
G.n.d	1 (1)	4 (8)	12 (11)
G.n.w	2 (3)	0	13 (11)
Shrubs			
S.n.d	6 (8)	5 (9)	14 (12)
S.n.w	1 (1)	1 (2)	12 (11)
Forests			
F.n.d	3 (4)	4 (8)	10 (9)
F.n.w	8 (11)	1 (2)	19 (17)
Rocks, screes			
R.n.d	1 (1)	1 (2)	12 (11)
Cultivations (arable land and market gardens)			
Cu.a.d	12 (17)	11 (21)	62 (54)
Cu.a.w	16 (22)	0	2 (2)
Cultivated areas of gardens and parks			
Cp.a.d	15 (21)	6 (11)	33 (29)
Woody cultivations			
Ct.a.d	5 (7)	5 (9)	34 (30)
Artificial constructed			
Au.a.d	7 (10)	8 (15)	34 (30)
Au.a.w	0	0	11 (10)
Artificial constructed, transportation			
At.a.d	21 (29)	22 (42)	69 (61)
Artificial constructed, walls			
Aw.a.d	2 (3)	4 (8)	36 (32)
Artificial constructed, abandoned			
Ap.a.d	3 (4)	2 (4)	29 (25)
Anthropogenic grasslands			
G.a.d	4 (6)	7 (13)	26 (23)

Numbers in brackets represent percentage of plants of each status category occurring in each habitat group

Discussion

The total number of the alien taxa reported for Greece (343) is relatively low compared to those of other

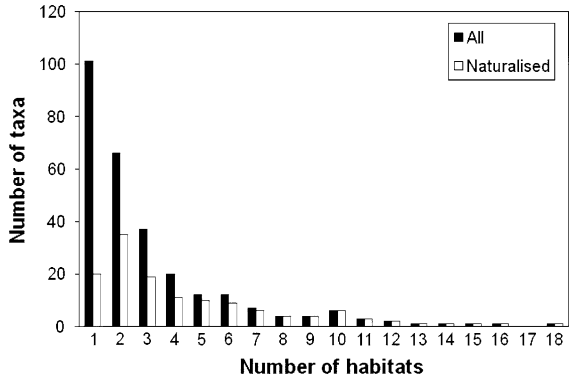

Fig. 8 Distribution of neophytes according to the number of habitats they invade in Greece

Mediterranean and Southern European countries, namely Italy, Spain and Portugal (1023, 933, 547, respectively, Lambdon et al. 2008; Celesti-Grapow et al. 2009; Arianoutsou et al. 2010). Taking the factor of area into account, Greece has a lower density of alien taxa (log species/log area = 0.49, compared to 0.59, 0.55, 0.52 and 0.55 for Cyprus, Italy, Spain and Portugal, respectively). The density of naturalised neophytes is also lower (log species/log area = 0.41, 0.53, 0.49, 0.46 and 0.48 for Greece, Cyprus, Italy, Spain and Portugal, respectively). Besides, the rate of naturalisation (proportion of naturalised to all aliens) in Greece (41%) is lower to that of Cyprus (68%), Spain (53%), Portugal (47%) (based on Lambdon et al. 2008) and Italy (51%, based on Celesti-Grapow et al. 2009). Moreover, the total number of alien taxa accounts for only c. 5% of the native flora of Greece, which is markedly low compared to that of other countries, for example aliens reach to 13.4% of the Italian flora (Conti et al. 2005), to 12% of the Spanish flora (Sanz-Elorza et al. 2004), 25% in the German flora (Kühn and Klotz 2003), 29% in the flora of Poland (Tokarska-Guzik 2005) and 33.4% in the flora of the Czech Republic (Pyšek et al. 2002).

Obviously, area cannot be the main explanatory factor for the apparent lower presence of alien plants in Greece compared to other Mediterranean countries, since its area is similar to that of Portugal and much larger than that of Cyprus. Besides, it has been shown that in Europe, area is among the determinants of alien species richness, but it is neither the sole nor the main determinant (Lambdon et al. 2008).

The smaller number and density of alien plant species observed in Greece may be related to the fact

that it has lower levels of industrialisation and of transportation network development, a higher proportion of scarcely if at all populated or cultivated mountainous areas, and a highly dissected physiography with many high and often inaccessible mountain ranges spreading across the mainland (Dax and Hovorka 2005).

The number of casual species (77 out of 294 neophytes) is strikingly lower than those reported from other countries, mainly of central or north Europe, e.g. 1,486 for Belgium (Verloove 2006), 891 for Czech Republic (Pyšek et al. 2002), 835 (neophytes alone) for Austria (Rabitsch and Essl 2006) and 566 for Hungary (Balogh et al. 2004), but as a percentage of the total alien flora, it is close to that reported for Italy (42%) by Celesti-Grapow et al. (2009).

In terms of taxonomy, the richest families of the alien flora of Greece are the large global plant families of Poaceae, Amaranthaceae, Asteraceae, Fabaceae, Solanaceae and Brassicacae which are also dominant in other alien floras of Europe (e.g. Baker 1974; Heywood 1989; Weber 1997; Daehler 1998; Pyšek et al. 2002; Lambdon et al. 2008; Celesti-Grapow et al. 2009) or of other continents, e.g. China in Asia (Weber et al. 2008). Poaceae, Fabaceae, Asteraceae, and Brassicaceae are the largest families in the native flora and in the Mediterranean basin, as well, but have a global distribution and include cultivated plants (Heywood et al. 2007). On the other hand, the families of Amaranthaceae and Solanaceae, have much fewer representatives in the native flora, but the first is a family of cosmopolitan weeds including some cultivated taxa (Strid and Tan 1997) and the second is a mainly extra-European plant family with many cultivated, agricultural or ornamental plants (Tutin et al. 1972).

Amaranthus, the genus with the highest number of representatives in the plant list, is also prominent in other regions of the world, regardless of their differences in size, climate and history (e.g. Czech Republic, see Pyšek et al. 2002; Italy, see Celesti-Grapow et al. 2009, China, see Weber et al. 2008, the entire European continent, see Lambdon et al. 2008). This genus is of North American origin and comprises mainly urban and agricultural weeds, whose habitat in their native range is similar to the usual anthropogenic habitats where they establish as aliens.

Taxa of American and Asiatic origin are predominant in the alien flora of Greece, in all status categories. This is reported for alien floras of other Mediterranean countries as well (see for example Celesti-Grapow et al. 2009).

The life form spectrum of the alien taxa is characterised by a high proportion of herbaceous taxa and among them the most frequent life form is the therophytic one (47% of all aliens). This is a trend observed in other regional alien floras as well (see for example Pyšek et al. 2002; Weber et al. 2008) or even broader regions (see Lambdon et al. 2008). The perennial life cycle, which implies vegetative propagation, a trait correlated with alien abundance (Hulme et al. 2008; Milbau and Stout 2008), was equally frequent with the annual one. Compared to the life form spectra of the native flora (Georghiou and Delipetrou 2010), the neophyte life form spectra are characterised by a larger proportion of phanerophytes and a lower of hemicryptophytes and chamaephytes. This may be a result of the higher frequency of introduction and widespread use of trees and shrubs as ornamentals (Crawley et al. 1996). It has been found that for Mediterranean islands growth form and life cycle do not explain invasion success (Lloret et al. 2005). The analysis of our data does not allow to test such a correlation, but indicates that the patterns of these traits in the naturalised aliens may be related to other factors (e.g., history of introduction), as well.

Hulme et al. (2008), assessing the risk to Mediterranean islands by plant introductions, concluded that among the plant traits they studied, five attributes were positively associated with average alien abundance across the islands studied: vegetative propagation, large leaf size, summer flowering, long flowering period, and dispersal by wind or vertebrates. Moreover, they found that different attributes appear important in different habitats: long flowering period in agricultural habitats and vertebrate seed dispersal in semi-natural habitats, implying that these traits appear to reflect different strategies: empty niches, avoidance of competitors and exploitation of mutualists.

In support of this finding, most of the naturalised taxa with adequate dispersal information in our study are wind or vertebrate dispersed and they have more than one option in their long-distance dispersal. Dispersal mode is an attribute of the spatial distribution of plants. It is known that the colonisation process depends on the vegetative propagation mode and on the seed dispersal patterns (D'Antonio 1990; Lonsdale 1993; Higgins et al. 1996; Rejmánek 2000).

Species with structures that favour wind and animal dispersal have been also found to show better regional and local invasion success in studies of Mediterranean islands (Lloret et al. 2004).

It is generally considered that climatic conditions under which plants have evolved determine flowering phenology. However, this trait may change when a plant grows in a new region (Ratchke and Lacey 1985; Dlugosch and Parker 2008). If the climate in the new range of the development of the alien plants was similar to the original, then they would not have to change their phenological pattern. In the opposite case, they would face a challenge to adapt, their success being depended upon a combination of factors such as the amplitude of the climatic oscillations, their intrinsic ability to flower despite the different conditions, their phenotypic plasticity etc. (Dudley 2004). This process may lead to different phenologies than those of the natives so that invasive alien species can either start flowering earlier and for longer periods (Pyšek and Richardson 2007) or later (Celesti-Grapow et al. 2003) than the native plants. Most of the aliens recorded in Greece, present a flowering period that starts in late spring or in summer and some of them even in autumn when few of the native plants are in bloom. Also for most of the aliens, the flowering period lasts for more than 1 month and some present a remarkably long flowering period. Most of the native plants of Greece flower in spring (Arianoutsou and Diamantopoulos 1985) usually for 1 month, with species alternating in their flowering display (Petanidou et al. 1995; personal observations). The delayed flowering pattern observed in many aliens may be an advantage since it reduces their competition with natives for abiotic (e.g. water, nutrients) and biotic resources (e.g. pollinators). Our data are in agreement with those observed for Spain by Godoy et al. (2009). However, autumn flowering of alien plants (26%) in particular, may be a threat in a way, since most plants of low altitudes germinate in autumn when the abundance of aliens may smother the new seedlings.

According to Pyšek and Richardson (2008) at global scale, the ecosystems most transformed by invasions of alien plants are: Mediterranean-climate areas (with the exception of the Mediterranean Basin itself) in South Africa, California, Chile, and Australia; temperate grasslands in North America, South America, and Australia that have been invaded by annual grasses mostly from Europe (e.g., *Bromus tectorum*). The Mediterranean Basin exception is confirmed for Greece, as the habitats mostly invaded by alien taxa are the artificial ones, and more specifically the transportation networks (At), the cultivated areas (Cu, Cp, Ct) and the highly disturbed urban or rural areas (Au, Aw, Ap). A high frequency of aliens in man-made habitats characterised by frequent disturbance and fluctuating nutrient availability in contrast to a very low frequency in extreme and nutrient poor habitats (i.e. mires, heathlands and high mountain grasslands) was also found in the quantitative comparison among Mediterranean, sub-continental and oceanic regions of Europe by Chytrý et al. (2008). The increased frequency of neophytes in coastal and water related habitats that we observed in Greece is a trait reported both by Chytrý et al. (op. cit.) for neophytes, which were frequent in coastal, littoral and riverine habitats, and by Celesti-Grapow et al. (2010) for naturalised aliens in Italy, which are confound to wetlands.

These data allow us to attempt the ecological profile of an alien plant in the terrestrial environment of Greece. Once a taxon is accidentally released to the wild it is easier for it to spread if it is an annual herb as it has more possibilities to grow in a relatively short period exploiting possible gaps in the niches of the native flora, thus minimizing its competition with natives and hence the possibility of being wiped out. A taxon which can be transported by animals or by the wind has better access to more environments thus it multiplies its possibility of becoming established. The above type of opportunistic establishment strategy is displayed, for example, by the successful invaders *Amaranthus* spp. and *Erigeron* spp. The occurrence of *Amaranthus albus*, *Erigeron bonariensis*, and *Symphyotrichum squamatum* in the majority of the habitat groups distinguished in this study should be stressed as an indicator for their invasiveness potential. The success of a perennial plant, on the other hand, is based on the fact that after surpassing the difficulties of the initial establishment phase, it is able to occupy the same space for a long term and even expand its territory. When such a plant manages to colonise a new area and if it propagates effectively, either vegetatively or sexually, it may gain way over the native plants. This is the case of *Opuntia ficus-barbarica* and *Ailanthus altissima*, which invade abandoned rangelands, very often excluding the native herbs and shrubs that would have otherwise been the pioneer plants in this old

field succession. Extended areas in Central and South Greece, many of the islands of the Aegean, previously used as grazing lands, and now abandoned are heavily contaminated by the prickly pear (*Opuntia ficus-barbarica*), which has no natural predator to control its population spread. However, and despite these problematic landmarks of the Greek landscapes, most aliens are found in artificial habitats, leaving the natural ones relatively intact.

The renowned *Oxalis pes-caprae*, the ecology of which has been extensively studied in the Mediterranean (Gimeno et al. 2006; Vilà et al. 2006; Vilà and Gimeno 2007; Traveset et al. 2008) is becoming increasingly common at urban and suburban ruderal sites, olive groves and shrub and forest edges where it forms dense mats preventing the growth of other species, especially during the important for the Mediterranean habitats autumn to early spring growth period. However, it rarely penetrates natural habitats and is actually restricted to disturbed sites, such as the remnant forest stands on islands and the reedbeds at wetlands with degraded hydromorphology. Nevertheless, *Oxalis pes-caprae* constitutes a serious threat for species of transitional zones and for those species (including orchids and rare bulbs) that use to find a refuge in traditional olive groves.

This work, being the first comprehensive compilation and analysis of all available records on alien plant taxa in Greece, has provided a first assessment of these plants, their status and traits and has also pinpointed knowledge gaps such as the geographic distribution and the quantification of ecological and economic impact. We hope that our results will increase the environmental awareness on invasive species in Southern Europe and, most importantly, that they will induce and guide further work, especially field orientated studies, on this subject in Greece. No management strategy can be designed unless a thorough knowledge of the problem exists.

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Appendix I

See Table 2.

Table 2 Type of data sources used for the alien plants of Greece

Type of source	Number of sources	Number of plants	Number of records
Article (peer reviewed)	126	297	3,482
Article (proceedings)	8	9	237
Article (non peer reviewed)	9	59	31
Standard flora—checklist	50	327	3,653
PhD	11	166	941
Book	19	88	156
Database	2	75	1,176
Internet database	6	68	153
Field observation/expert opinion	3	43	51

Multiple records correspond to one record per type of data per plant per source

Appendix II

See Table 3.

Table 3 Time course of publication for the data sources used for the alien plants of Greece

Decade	Number of sources
1930	1
1940	1
1950	8
1960	7
1970	20
1980	53
1990	63
2000	75
	(Total) 228

Internet databases are not included

Appendix III

See Table 4.

Table 4 Habitat groups with classification in natural (n)/artificial (a) and dry (d)/water-related (w) categories and correspondence to EUNIS codes levels 2 and 3

Habitat group	Natural/artificial	Dry/water-related	EUNIS ID	Description
Marine				
M	n	w	A5.5	Sublittoral macrophyte-dominated sediment
Coastal				
C	n	d	B1	Coastal dunes and sandy shores
C	n	d	B1.1	Sand beach driftlines
C	n	d	B1.2	Sand beaches above the driftline
C	n	d	B1.3	Shifting coastal dunes
C	n	d	B1.4	Coastal stable dune grassland (grey dunes)
C	n	d	B1.6	Coastal dune scrub
C	n	d	B1.7	Coastal dune woods
C	n	d	B2	Coastal shingle
C	n	d	B2.4	Fixed shingle beaches, with herbaceous vegetation
C	n	d	B3	Rock cliffs, ledges and shores, including the supralittoral
C	n	d	B3.3	Rock cliffs, ledges and shores, with angiosperms
C	n	d	B3.4	Soft sea-cliffs, often vegetated
C	n	w	A2.5	Coastal saltmarshes and saline reedbeds
C	n	w	B1.8	Moist and wet dune slacks
C	n	w	X1	Estuaries
Inland water bodies, fens, bogs				
W	n	w	C1.3	Permanent eutrophic lakes, ponds and pools
W	n	w	C1.6	Temporary lakes, ponds and pools
W	n	w	C2	Surface running waters
W	n	w	C3	Littoral zone of inland surface waterbodies
W	n	w	C3.2	Water-fringing reedbeds and tall helophytes other than canes
W	n	w	C3.4	Species-poor beds of low-growing water-fringing or amphibious vegetation
W	n	w	C3.5	Periodically inundated shores with pioneer and ephemeral vegetation
W	n	w	D	Mire, bog and fen habitats
Grasslands				
G	a	d	E5.1	Anthropogenic herb stands
G	n	d	E1	Dry grasslands
G	n	d	E1.1	Inland sand and rock with open vegetation
G	n	d	E1.2	Perennial calcareous grassland and basic steppes
G	n	d	E1.3	Mediterranean xeric grassland
G	n	d	E1.6	Subnitrophilous annual grassland
G	n	d	E2.2	Low and medium altitude hay meadows
G	n	w	E3	Seasonally wet and wet grasslands

Table 4 continued

Habitat group	Natural/artificial	Dry/water-related	EUNIS ID	Description
G	n	w	E3.1	Mediterranean tall humid grassland
G	n	w	E3.4	Moist or wet eutrophic and mesotrophic grassland
Shrubs				
S	n	d	F3.1	Temperate thickets and scrub
S	n	d	F3.2	Submediterranean deciduous thickets and brushes
S	n	d	F5.1	Arborescent matorral
S	n	d	F5.2	Maquis
S	n	d	F5.3	Pseudomaquis
S	n	d	F5.5	Thermo-Mediterranean scrub
S	n	d	F6	Garrigue
S	n	d	F6.2	Eastern garrigues
S	n	d	F7	Spiny Mediterranean heaths (phrygana, hedgehog-heaths and related coastal cliff vegetation)
S	n	d	F7.3	East Mediterranean phrygana
S	n	d	F7.4	Hedgehog-heaths
S	n	w	F9.3	Southern riparian galleries and thickets
Forests				
F	n	d	G1.6	Fagus woodland
F	n	d	G1.7	Thermophilous deciduous woodland
F	n	d	G1.A	Meso- and eutrophic Quercus, Carpinus, Fraxinus, Acer, Tilia, Ulmus and related woodland
F	n	d	G2.1	Mediterranean evergreen Quercus woodland
F	n	d	G2.5	Phoenix groves
F	n	d	G3.1	Abies and Picea woodland
F	n	d	G3.5	Pinus nigra woodland
F	n	d	G3.7	Lowland to montane mediterranean Pinus woodland (excluding Pinus nigra)
F	n	d	G3.9	Coniferous woodland dominated by Cupressaceae or Taxaceae
F	n	w	G1.1	Riparian and gallery woodland, with dominant Alnus, Betula, Populus or Salix
F	n	w	G1.2	Mixed riparian floodplain and gallery woodland
F	n	w	G1.3	Mediterranean riparian woodland
Rocks/screes				
R	n	d	H3	Inland cliffs, rock pavements and outcrops
R	n	d	H3.2	Basic and ultra-basic inland cliffs
Cultivations (arable land and market gardens)				
Cu	a	d	I1	Arable land and market gardens
Cu	a	d	I1.1	Intensive unmixed crops
Cu	a	d	I1.3	Arable land with unmixed crops grown by low-intensity agricultural methods
Cu	a	d	I1.5	Bare tilled, fallow or recently abandoned arable land
Cu	a	w	I1.4	Inundated or inundatable croplands, including rice fields
Cultivated areas of gardens and parks				
Cp	a	d	FA	Hedgerows

Table 4 continued

Habitat group	Natural/artificial	Dry/water-related	EUNIS ID	Description
Cp	a	d	I2	Cultivated areas of gardens and parks
Cp	a	d	I2.2	Small-scale ornamental and domestic garden areas
Cp	a	d	I2.3	Recently abandoned garden areas
Woody cultivations				
Ct	a	d	FB.4	Vineyards
Ct	a	d	G1.D	Fruit and nut tree orchards
Ct	a	d	G2.9	Evergreen orchards and groves
Ct	a	d	G2.91	Olea europaea groves
Artificial constructed				
Au	a	d	J1	Buildings of cities, towns and villages
Au	a	d	J1.2	Residential buildings of villages and urban peripheries
Au	a	d	J1.5	Disused constructions of cities, towns and villages
Au	a	d	J1.6	Urban and suburban construction and demolition sites
Au	a	d	J2	Low density buildings
Au	a	d	J2.2	Rural public buildings
Au	a	d	J6	Waste deposits
Au	a	d	J6.4	Agricultural and horticultural waste
Au	a	d	X21	Archaeological sites
Au	a	w	J5	Highly artificial man-made waters and associated structures
Au	a	w	J5.2	Highly artificial saline and brackish running waters
Au	a	w	J5.4	Highly artificial non-saline running waters
Artificial constructed/transportation				
At	a	d	J4.2	Road networks
At	a	d	J4.3	Rail networks
At	a	d	J4.5	Hard-surfaced areas of ports
At	a	d	J4.6	Pavements and recreation areas
At	a	d	J4.7	Constructed parts of cemeteries
Artificial constructed/walls				
Aw	a	d	J2.5	Constructed boundaries
Artificial constructed/abandoned places				
Ap	a	d	J2.6	Disused rural constructions

Appendix IV

See Table 5.

Table 5 Checklist of alien plant species recorded in Greece

Taxon	Family	Status	History	Chorology
Acacia farnesiana (L.) Willd.	Fabaceae	C	neo	S American
Acacia saligna (Labill.) H.L. Wendl.	Fabaceae	U	neo	W Australian
Acanthus mollis L.	Acanthaceae	C	neo	W Mediterranean

Table 5 continued

Taxon	Family	Status	History	Chorology
Acer negundo L.	Sapindaceae	N+	neo	N American
Achyranthes sicula (L.) All.	Amaranthaceae	U	neo	SW Mediterranean
Aegilops tauschii Coss.	Poaceae	C	neo	Iranoturanian
Aeonium arboreum (L.) Webb & Berth.	Crassulaceae	N+	neo	Macaronesian
Agave americana L.	Agavaceae	N+	neo	N American
Ageratina adenophora (Spreng.) R.M. King & H. Rob.	Asteraceae	N	neo	N American
Agrostis lachnantha Nees	Poaceae	C	neo	Arabian-African
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	N+	neo	E Asiatic
Albizia julibrissin Durazz.	Fabaceae	U	neo	Paleotropical
Alcea rosea L.	Malvaceae	U	neo	Unknown
Allium cepa L.	Alliaceae	U	arch	W Asiatic
Aloë vera (L.) Burm. f.	Asphodelaceae	N	arch*	Arabian-NE African
Aloysia citriodora Palau	Verbenaceae	U	neo	S American
Amaranthus × *ozanonii* Thell.	Amaranthaceae	U	neo	European hybrid of American taxa
Amaranthus albus L.	Amaranthaceae	N+	neo	N American
Amaranthus blitoides S. Watson	Amaranthaceae	N+	neo	N American
Amaranthus bouchonii Thell.	Amaranthaceae	U	neo	N American
Amaranthus caudatus L.	Amaranthaceae	U	neo	Paleotropical
Amaranthus cruentus L.	Amaranthaceae	C	neo	Neotropical
Amaranthus deflexus L.	Amaranthaceae	N+	neo	S American
Amaranthus emarginatus Uline & Bray	Amaranthaceae	U	neo	Pantropical
Amaranthus hybridus L.	Amaranthaceae	N+	neo	N American
Amaranthus hypochondriacus L.	Amaranthaceae	N	neo	N American
Amaranthus muricatus (Gillies ex Moq.) Hieron.	Amaranthaceae	N	neo	S American
Amaranthus palmeri S. Watson	Amaranthaceae	N	neo	N American
Amaranthus powellii S. Watson	Amaranthaceae	N	neo	American
Amaranthus quitensis Kunth	Amaranthaceae	N+	neo	S American
Amaranthus retroflexus L.	Amaranthaceae	N+	neo	N American
Amaranthus spinosus L.	Amaranthaceae	C	neo	Neotropical
Amaranthus viridis L.	Amaranthaceae	N+	neo	S American
Amaranthus watsonii Standl.	Amaranthaceae	C	neo	N American
Amaryllis belladonna L.	Amaryllidaceae	N	neo	S African
Ambrosia artemisiifolia L.	Asteraceae	U	neo	N American
Ammannia baccifera L.	Lythraceae	U	neo	Paleotropical/subtropical
Ammannia coccinea Rottb.	Lythraceae	N	neo	Neotropical
Ammannia senegalensis Lam.	Lythraceae	U	neo	African
Amorpha fruticosa L.	Fabaceae	N	neo	N American
Amsinckia lycopsoides Lehm.	Boraginaceae	C	neo	N American
Amsinckia micrantha Suksd.	Boraginaceae	U	neo	American
Anethum graveolens L.	Apiaceae	U	arch	SW Asiatic
Anredera cordifolia (Ten.) Steenis	Basellaceae	N	neo	S American
Antirrhinum majus L.	Plantaginaceae	N	arch*	W Mediterranean
Antirrhinum majus L. subsp. *tortuosum* (Bosc ex Lam.) Rouy	Plantaginaceae	N	arch*	W Mediterranean

Table 5 continued

Taxon	Family	Status	History	Chorology
Antirrhinum siculum Mill.	Plantaginaceae	U	neo	S European
Apium leptophyllum (Pers.) F. Müller ex Bentham	Apiaceae	U	neo	S American
Aptenia cordifolia (L. f.) Schwantes	Aizoaceae	N+	neo	S African
Araujia sericifera Brot.	Apocynaceae	N	neo	S American
Arctotheca calendula (L.) Levyns	Asteraceae	C	neo	S African
Artemisia verlotiorum Lamotte	Asteraceae	U	neo	Asiatic
Arundo donax L.	Poaceae	N+	arch	C Asiatic
Asclepias curassavica L.	Apocynaceae	C	neo	Neotropical
Asclepias fruticosa L.	Apocynaceae	N+	neo	S African
Asclepias physocarpa (E. Mey.) Schltr.	Apocynaceae	N	neo	S African
Asparagus densiflorus (Kunth) Jessop	Asparagaceae	C	neo	S African
Atriplex hortensis L.	Amaranthaceae	N	arch	C Asiatic
Atriplex sagittata Borkh.	Amaranthaceae	C	neo	E European
Avena byzantina C. Koch	Poaceae	C	neo	Mediterranean-Turanian
Azolla caroliniana Willd.	Azollaceae	N	neo	Neotropical
Azolla filiculoides Lam.	Azollaceae	N+	neo	Neotropical
Bacopa rotundifolia (Michaux) Wettst.	Plantaginaceae	U	neo	American
Basella rubra L.	Basellaceae	C	neo	Pantropical
Bassia hyssopifolia (Pall.) Kuntze	Amaranthaceae	C	neo	C Asiatic
Bassia scoparia (L.) A. J. Scott	Amaranthaceae	N	neo	C Asiatic
Bergia capensis L.	Elatinaceae	U	neo	Paleotropical/subtropical
Beta vulgaris L. subsp. *vulgaris*	Amaranthaceae	C	neo	Unknown
Bidens pilosus L.	Asteraceae	U	neo	S American
Bouteloua dactyloides (Nutt.) Columbus	Poaceae	U	neo	N American
Brassica napus L.	Brassicaceae	N	arch*	Unknown
Brassica oleracea L.	Brassicaceae	N	arch	W European
Bromus catharticus Vahl	Poaceae	N	neo	S American
Broussonetia papyrifera (L.) Vent.	Moraceae	N	neo	E Asiatic
Buddleja madagascariensis Lam.	Scrophulariaceae	C	neo	E African
Caesalpinia gilliesii (Hooker) Dietr.	Fabaceae	U	neo	S American
Calendula officinalis L.	Asteraceae	C	neo	Tropical/subtropical
Campanula medium L.	Campanulaceae	C	neo	NW Mediterranean-Mont
Campsis radicans Seem.	Bignoniaceae	C	neo	N American
Cannabis sativa L.	Cannabaceae	U	arch*	C Asiatic
Cardiospermum halicacabum L.	Sapindaceae	N	neo*	Neotropical
Carpobrotus edulis (L.) N. E. Br.	Aizoaceae	N+	neo	S African
Catharanthus roseus (L.) G. Don	Apocynaceae	C	neo	African
Cenchrus ciliaris L.	Poaceae	N	neo	Saharo-Sindian
Cenchrus incertus M. A. Curtis	Poaceae	N+	neo	Neotropical
Centranthus macrosiphon Boiss.	Valerianaceae	N	neo	W Mediterranean
Cestrum parqui L'Hér.	Solanaceae	C	neo	Neotropical
Chasmanthe vittigera (Salisb.) N. E. Br.	Iridaceae	C	neo	S African
Chenopodium ambrosioides L.	Amaranthaceae	N+	neo	Neotropical
Chenopodium giganteum D. Don	Amaranthaceae	N	neo	Pantropical

Table 5 continued

Taxon	Family	Status	History	Chorology
Chenopodium multifidum L.	Amaranthaceae	N+	neo	S American
Chenopodium pumilio R. Br.	Amaranthaceae	U	neo	Australian
Chorispora tenella (Pallas) DC	Brassicaceae	U	neo	Eurasiatic
Cicer arietinum L.	Fabaceae	C	arch	Pontic
Citrullus lanatus (Thunb.) Matsum. & Nakai	Cucurbitaceae	U	arch	Paleotropical
Coix lacryma-jobi L.	Poaceae	N	neo	Paleotropical
Commelina communis L.	Commelinaceae	C	neo	E Asiatic
Convolvulus sabatius Viv.	Convolvulaceae	N	neo	W Mediterranean
Coriandrum sativum L.	Apiaceae	C	arch	SW Mediterranean
Coronopus didymus (L.) Sm.	Brassicaceae	N+	neo	S American
Cosmos bipinnatus Cav.	Asteraceae	C	neo	N American
Cotula coronopifolia L.	Asteraceae	N+	neo	S African
Cucurbita maxima Lam.	Cucurbitaceae	C	neo	C American
Cucurbita pepo L.	Cucurbitaceae	C	neo	C American
Cuscuta campestris Yuncker	Convolvulaceae	N+	neo	N American
Cuscuta suaveolens Ser.	Convolvulaceae	N	neo	S American
Cymbalaria muralis P. Gaertn., B. Mey. & Scherb	Plantaginaceae	N+	neo	S European
Cynara scolymus L.	Asteraceae	C	neo	Unknown
Cyperus alternifolius L.	Cyperaceae	N	neo	African
Dactyloctenium aegyptium (L.) Beauv.	Poaceae	N	neo	Paleotropical/subtropical
Datura ferox L.	Solanaceae	C	neo	E Asiatic
Datura innoxia Mill.	Solanaceae	C	neo	C American
Datura stramonium L.	Solanaceae	N+	neo	Cosmopolitan
Daucus carota L. subsp. *sativus* (Hoffm.) Arcangeli	Apiaceae	U	neo	Unknown
Dichanthium annulatum (Forssk.) Stapf	Poaceae	U	neo	Paleotropical
Dichondra micrantha Urban	Convolvulaceae	N	neo	American
Digitaria ciliaris (Retz.) Koeler	Poaceae	N	neo	Pantropical/subtropical
Digitaria ischaemum (Schreber) Muhl	Poaceae	N	neo	Sub-cosmopolitan
Diospyros lotus L.	Ebenaceae	N	neo	Asiatic
Diplotaxis erucoides (L.) DC	Brassicaceae	U	neo	W Mediterranean
Echinochloa colona (L.) Link	Poaceae	N	arch	Paleotropical/subtropical
Echinochloa crus-galli (L.) P. Beauv. subsp. *hispidula* (Retz.) Honda	Poaceae	U	neo	E Asiatic
Echinochloa frumentacea (Roxb.) Link	Poaceae	U	arch*	Eurasiatic
Echinochloa oryzoides (Ard.) Fritsch	Poaceae	U	neo	Unknown
Eclipta prostrata (L.) L.	Asteraceae	U	neo	Neotropical
Elaeagnus angustifolia L.	Elaeagnaceae	N+	neo	Temperate Asiatic
Eleocharis parvula (Roem. & Schult.) Bluff & al.	Cyperaceae	U	neo	Sub-cosmopolitan
Eleusine indica (L.) Gaertn.	Poaceae	N+	neo	Cosmopolitan
Eragrostis curvula (Schrad.) Nees	Poaceae	C	neo	S African
Eragrostis leptocarpa Benth.	Poaceae	C	neo	Australian
Eragrostis pectinacea (Michx.) Ness	Poaceae	N	neo	N American
Erigeron bonariensis L.	Asteraceae	N+	neo	Neotropical
Erigeron canadensis L.	Asteraceae	N+	neo	N American

Table 5 continued

Taxon	Family	Status	History	Chorology
Erigeron sumatrensis Retz.	Asteraceae	N+	neo	Neotropical
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	U	neo	E Asiatic
Eriochloa contracta Hitchc.	Poaceae	C	neo	American
Erysimum cheiri (L.) Crantz	Brassicaceae	N	arch	Euri-Mediterranean
Eschscholzia californica Cham.	Papaveraceae	C	neo	N American
Eucalyptus camaldulensis Dehnh.	Myrtaceae	N	neo	Australian
Euphorbia maculata L.	Euphorbiaceae	N+	neo	N American
Euphorbia marginata Pursh	Euphorbiaceae	C	neo	N American
Euphorbia nutans Lag.	Euphorbiaceae	U	neo	N American
Euphorbia prostrata Aiton	Euphorbiaceae	N+	neo	N American
Euphorbia serpens Kunth	Euphorbiaceae	U	neo	N American
Fagopyrum esculentum Moench	Polygonaceae	U	neo	C Asiatic
Fallopia aubertii (L. Henry) J. Holub	Polygonaceae	N	neo	C Asiatic
Fallopia baldschuanica (Regel) J. Holub	Polygonaceae	C	neo	C Asiatic
Fallopia japonica (Houtt.) Ronse Decr.	Polygonaceae	U	neo	E Asiatic
Fallopia sachalinensis (F. Schmidt) Ronse Decr.	Polygonaceae	U	neo	E Asiatic
Flaveria bidentis (L.) Kuntze	Asteraceae	U	neo	N American
Freesia refracta (Jacq.) Ecklon ex Klatt	Iridaceae	N	neo	S African
Galinsoga parviflora Cav.	Asteraceae	N	neo	S American
Galinsoga quadriradiata Ruiz & Pav.	Asteraceae	N	neo	S American
Gleditsia triacanthos L.	Fabaceae	C	neo	N American
Gossypium herbaceum L.	Malvaceae	N	arch*	SE Asiatic
Gossypium hirsutum L.	Malvaceae	N	neo	N American
Hablitzia tamnoides M. Bieb.	Amaranthaceae	N	neo	Caucasian
Halophila stipulacea (Forssk.) Ascherson	Hydrocharitaceae	U+	neo	W Indian Ocean, Red Sea
Hedysarum coronarium L.	Fabaceae	N	neo*	W Mediterranean
Helianthus × *laetiflorus* Pers.	Asteraceae	N	neo	N American
Helianthus annuus L.	Asteraceae	C	neo	S American
Helianthus tuberosus L.	Asteraceae	C	neo	N American
Heliotropium curassavicum L.	Boraginaceae	N+	neo	Neotropical
Hemerocallis fulva L.	Hemerocallidaceae	U	neo	E Asiatic
Heteranthera limosa (Sw.) Willd.	Pontederiaceae	U	neo	Neosubtropical/Neotropical
Heteranthera reniformis Ruiz & Pav.	Pontederiaceae	U	neo	Neotropical
Heteranthera rotundifolia (Kunth) Griseb.	Pontederiaceae	U	neo	American
Hibiscus syriacus L.	Malvaceae	N	neo*	E Asiatic
Hordeum distichon L.	Poaceae	C	arch	SW & C Asiatic
Hordeum vulgare L.	Poaceae	C	arch	E African
Humulus lupulus L.	Cannabaceae	U	neo	European-Caucasian
Hyacinthoides hispanica (Mill.) Rothm.	Hyacinthaceae	C	neo	W Mediterranean
Hyacinthus orientalis L.	Hyacinthaceae	C	neo*	SW Asiatic
Ibicella lutea (Lindl.) van Eseltine	Martyniaceae	N	neo	S American
Impatiens balfourii Hook. Fil.	Balsaminaceae	N	neo	Tropical Asiatic
Ipheion uniflorum (R. C. Graham) Rafin	Alliaceae	U	neo	S American
Ipomoea hederacea Jacq.	Convolvulaceae	N	neo	Neotropical

Table 5 continued

Taxon	Family	Status	History	Chorology
Ipomoea indica (Burm.) Merr.	Convolvulaceae	N	neo	Pantropical
Ipomoea purpurea (L.) Roth	Convolvulaceae	N	neo	Neotropical
Iris albicans Lange	Iridaceae	N	neo*	Arabian
Iris germanica L.	Iridaceae	N	arch	Unknown
Jacobaea maritima (L.) Pelser & Meijden subsp. *maritima*	Asteraceae	C	neo	W Mediterranean
Jonopsidium albiflorum Durieu	Brassicaceae	U	neo	SW Mediterranean
Koelreuteria paniculata Laxmann	Sapindaceae	U	neo	E Asiatic
Lactuca sativa L.	Asteraceae	C	neo	Unknown
Lagenaria siceraria (Molina) Standl.	Cucurbitaceae	C	neo	E Asiatic
Lantana camara L.	Verbenaceae	C	neo	Neotropical
Lathyrus odoratus L.	Fabaceae	C	arch	Mediterranean
Lathyrus sativus L.	Fabaceae	N	arch	Unknown
Lavandula angustifolia Mill.	Lamiaceae	U	neo	W Mediterranean
Lens culinaris Medik.	Fabaceae	C	arch	Unknown
Lepidium sativum L.	Brassicaceae	C	arch	Unknown
Lepidium virginicum L.	Brassicaceae	C	neo	N American
Leptochloa fusca (L.) Kunth	Poaceae	U	neo	Tropical/subtropical
Lindernia dubia (L.) Pennell	Linderniaceae	N	neo	N American
Linum grandiflorum Desf.	Linaceae	C	neo	African
Linum usitatissimum L.	Linaceae	N	arch	Unknown
Lippia canescens Kunth	Verbenaceae	U	neo	S American
Lobularia libyca (Viv.) Meissner	Brassicaceae	N	neo	S Mediterranean-Saharo-Sind
Lobularia maritima (L.) Desv.	Brassicaceae	N	neo*	Mediterranean
Lonicera japonica Thunb.	Caprifoliaceae	U	neo	E Asiatic
Lunaria annua L. subsp. *annua*	Brassicaceae	U	neo	Unknown
Lupinus luteus L.	Fabaceae	U	neo	W Mediterranean
Lycium barbarum L.	Solanaceae	N	neo	E Asiatic
Lycium chinense Mill.	Solanaceae	U	neo	E Asiatic
Lycopersicon esculentum Mill.	Solanaceae	C	neo	C & S American
Malephora purpuro-crocea (Haw.) Schwantes	Aizoaceae	N+	neo	S African
Malus domestica Borkh.	Rosaceae	C	arch	Unknown
Malva verticillata L.	Malvaceae	N	arch	E Asiatic
Matricaria discoidea DC	Asteraceae	U	neo	S American
Medicago blancheana Boiss. subsp. *blancheana*	Fabaceae	C	neo	E Mediterranean
Medicago sativa L. subsp. *microcarpa*	Fabaceae	C	neo	C & SW Asiatic
Medicago sativa L. subsp. *sativa*	Fabaceae	N+	neo	Paleotemperate
Melia azedarach L.	Meliaceae	U	neo	C & E Asiatic
Mirabilis jalapa L.	Nyctaginaceae	N	neo	S American
Morus alba L.	Moraceae	N	arch	E Asiatic
Morus nigra L.	Moraceae	N	arch*	SW Asiatic
Najas gracillima (Engelm.) Magn.	Hydrocharitaceae	U	neo	E Asiatic
Najas graminea Delile	Hydrocharitaceae	U	neo	Paleotropical
Najas orientalis Triest & Uotila	Hydrocharitaceae	U	neo	E Asiatic
Narcissus pseudonarcissus L.	Amaryllidaceae	C	neo	W European

Table 5 continued

Taxon	Family	Status	History	Chorology
Narcissus tazetta L. subsp. *aureus* (Loisel.) Baker	Amaryllidaceae	U	neo	SW European
Narcissus tazetta L. subsp. *italicus* (Ker-Gawler) Baker	Amaryllidaceae	U	neo	N & E Mediterranean
Nasella neesiana (Trin. & Rupr.) Barkworth	Poaceae	U	neo	S American
Nicandra physalodes (L.) Gaertn.	Solanaceae	U	neo	S American
Nicotiana glauca R. C. Graham	Solanaceae	N+	neo	S American
Nicotiana tabacum L.	Solanaceae	C	neo	N American
Nigella sativa L.	Ranunculaceae	U	neo*	SW Asiatic
Nothoscordum gracile (Aiton) Stearn	Alliaceae	U	neo	Neosubtropical/neotropical
Ocimum basilicum L.	Lamiaceae	C	arch	Tropical Asiatic
Oenothera biennis L.	Onagraceae	N	neo	Sub-cosmopolitan
Oenothera glazioviana M. Micheli	Onagraceae	U	neo	Australian
Oenothera indecora Camb. subsp. *indecora*	Onagraceae	N	neo	S American
Oenothera laciniata Hill	Onagraceae	C	neo	N American
Onobrychis viciifolia Scop.	Fabaceae	U	neo	Mediterranean-Montane
Opuntia ficus-barbarica A. Berger	Cactaceae	N+	neo	Neotropical
Opuntia vulgaris Mill.	Cactaceae	N+	neo	N American
Origanum majorana L.	Lamiaceae	U	arch*	Saharo-Sindian
Ornithogalum arabicum L.	Hyacinthaceae	N	neo	S Mediterranean
Oryza sativa L.	Poaceae	C	neo*	SE Asiatic
Osteospermum barberiae (Harv.) Norlind	Asteraceae	C	neo	S African
Oxalis articulata Savigny	Oxalidaceae	U	neo	S American
Oxalis debilis Kunth var. *corymbosa* (DC.) Lourteig	Oxalidaceae	N+	neo	S American
Oxalis exilis A. Cunn.	Oxalidaceae	U	neo	Australian
Oxalis pes-caprae L.	Oxalidaceae	N+	neo	S African
Panicum capillare L.	Poaceae	N	neo	N American
Panicum dichotomiflorum Michx.	Poaceae	U	neo	N American
Panicum hillmanii Chase	Poaceae	C	neo	N American
Panicum miliaceum L.	Poaceae	C	arch*	C Asiatic
Panicum repentellum Napper	Poaceae	U	neo	E African
Papaver somniferum L. subsp. *somniferum*	Papaveraceae	C	arch	SW Asiatic
Parkinsonia aculeata L.	Fabaceae	C	neo	Neotropical
Parthenocissus inserta (A. Kern) Fritsch	Vitaceae	N	neo	N American
Parthenocissus quinquefolia (L.) Planch.	Vitaceae	C	neo	American
Paspalum dilatatum Poiret	Poaceae	N+	neo	S American
Paspalum distichum L.	Poaceae	N+	neo	Neotropical
Paspalum notatum Flüggé	Poaceae	U	neo	American
Passiflora caerulea L.	Passifloraceae	C	neo	S American
Pelargonium peltatum (L.) L'Hér.	Geraniaceae	C	neo	S African
Pennisetum clandestinum Chiov.	Poaceae	N	neo	E African
Pennisetum villosum R. Br. ex Fresen.	Poaceae	U	neo	Paleotropical
Persicaria capitata (D. Don) H. Gross	Polygonaceae	U	neo	C Asiatic
Persicaria orientalis (L.) Spach	Polygonaceae	U	neo	Tropical Asiatic
Persicaria senegalensis (Meisner) Soják	Polygonaceae	N	neo	African-Australian
Petroselinum crispum (Mill.) A. W. Hill	Apiaceae	C	arch*	E Mediterranean

Table 5 continued

Taxon	Family	Status	History	Chorology
Peucedanum chryseum (Boiss. & Heldr.) D. F. Chamb.	Apiaceae	N	neo	E Mediterranean
Phacelia tanacetifolia Bentham	Hydrophyllaceae	U	neo	N American
Phalaris canariensis L.	Poaceae	N	neo	Macaronesian
Philadelphus coronarius L.	Hydrangeaceae	C	neo	European
Phoenix canariensis Chabaud	Arecaceae	U	neo	Macaronesian
Phoenix dactylifera L.	Arecaceae	C	neo*	Paleosubtropical
Physalis angulata L.	Solanaceae	C	neo	Neotropical
Physalis ixocarpa Brot. ex Hornem	Solanaceae	N	neo	American
Phytolacca americana L.	Phytolaccaceae	N+	neo	N American
Phytolacca dioica L.	Phytolaccaceae	N	neo	S American
Pimpinella anisum L.	Apiaceae	U	arch	Asiatic
Pisum sativum L. subsp. *sativum*	Fabaceae	N	arch	Sub-cosmopolitan
Pleuraphis jamesii Torr.	Poaceae	U	neo	N American
Plumbago auriculata Lam.	Plumbaginaceae	N	neo	S African
Populus × *canadensis* Moench	Salicaceae	U	neo	Unknown
Portulaca grandiflora Hooker	Portulacaceae	C	neo	S American
Prunus armeniaca L.	Rosaceae	U	arch*	C Asiatic
Prunus cerasus L.	Rosaceae	U	neo	Pontic
Prunus domestica L. subsp. *domestica*	Rosaceae	U	neo	Unknown
Prunus dulcis (Mill.) D. A. Webb	Rosaceae	C	arch	S Mediterranean
Prunus persica (L.) Batsch	Rosaceae	U	neo	E Asiatic
Punica granatum L.	Lythraceae	N	arch	SW Asiatic
Pyrus communis L.	Rosaceae	U	neo	European-SW Asiatic
Raphanus sativus L.	Brassicaceae	U	arch	Unknown
Retama monosperma (L.) Boiss.	Fabaceae	N	neo	W Mediterranean
Ribes odoratum H. L. Wendl	Grossulariaceae	C	neo	N American
Ricinus communis L.	Euphorbiaceae	N+	arch	Paleotropical
Robinia pseudoacacia L.	Fabaceae	N+	neo	N American
Rotala ramosior (L.) Koehne	Lythraceae	U	neo	Neotropical
Rumex vesicarius L.	Polygonaceae	N	neo	Paleosubtropical
Ruscus hypoglossum L.	Ruscaceae	C	neo	Euri-Mediterranean
Salix × *rubens* Schrank	Salicaceae	U	neo	Unknown
Salix fragilis L.	Salicaceae	N+	neo	Eurosibirian
Santolina chamaecyparissus L.	Asteraceae	C	neo	W & C Mediterranean
Schinus molle L.	Anacardiaceae	U	neo	S American
Scolymus grandiflorus Desf.	Asteraceae	C	neo	SW Mediterranean
Secale cereale L.	Poaceae	C	arch	C Asiatic
Sesamum indicum L.	Pedaliaceae	U	arch*	Paleotropical
Setaria adhaerens (Forssk.) Chiov.	Poaceae	N+	neo	Sub-cosmopolitan
Setaria italica (L.) Beauv.	Poaceae	U	neo	Tropical Asiatic
Sida spinosa L.	Malvaceae	C	neo	Tropical/subtropical
Silene pendula L.	Caryophyllaceae	U	neo	NE Mediterranean-Mont
Sinapis alba L. subsp. *alba*	Brassicaceae	N	arch	Unknown
Solanum cornutum Lam.	Solanaceae	N	neo	N American

Table 5 continued

Taxon	Family	Status	History	Chorology
Solanum elaeagnifolium Cav.	Solanaceae	N+	neo	S American
Solanum physalifolium Rusby	Solanaceae	N	neo	S American
Solanum pseudocapsicum L.	Solanaceae	C	neo	S American
Solanum sodomeum L.	Solanaceae	U	neo	S African
Solanum tuberosum L.	Solanaceae	C	neo	S American
Sorghum bicolor (L.) Moench	Poaceae	U	neo	Paleotropical
Sorghum sudanense (Piper) Stapf	Poaceae	U	neo	E African
Spinacia oleracea L.	Amaranthaceae	C	neo*	SW Asiatic
Sporobolus indicus (L.) R. Br.	Poaceae	N	neo	Neotropical
Symphyotrichum novi-belgii (L.) G. L. Nesom	Asteraceae	N	neo	N American
Symphyotrichum squamatum (Spreng.) G. L. Nesom	Asteraceae	N+	neo	Neotropical
Tagetes minuta L.	Asteraceae	N	neo	S American
Tagetes patula L.	Asteraceae	C	neo	S American
Tetragonia tetragonioides (Pall.) Kuntze	Aizoaceae	N	neo	Australian
Teucrium fruticans L.	Lamiaceae	C	neo	W Mediterranean
Thymus odoratissimus Mill.	Lamiaceae	U	neo	Euro-Siberian
Tradescantia fluminensis Vell.	Commelinaceae	N	neo	S American
Tradescantia virginiana L.	Commelinaceae	C	neo	N American
Trigonella caerulea (L.) Ser.	Fabaceae	U	neo	W Asiatic
Trigonella foenum-graecum L.	Fabaceae	U	arch	SW Asiatic
Triticum aestivum L.	Poaceae	C	arch*	SW Asiatic
Triticum durum Desf.	Poaceae	C	arch	SW Asiatic
Triticum turgidum L.	Poaceae	C	arch*	SW Asiatic
Tropaeolum majus L.	Tropaeolaceae	U	neo	S American
Verbena aristigera S. Moore	Verbenaceae	N	neo	S American
Veronica persica Poiret	Plantaginaceae	N+	neo*	W Asiatic
Vicia faba L.	Fabaceae	U	neo	Unknown
Vicia sativa L. subsp. *sativa*	Fabaceae	N	arch	Mediterranean-Turanian
Wisteria sinensis (Sims) Sweet	Fabaceae	C	neo	E Asiatic
Xanthium orientale L. subsp. *italicum* (Moretti) Greuter	Asteraceae	N+	neo	S European
Xanthium spinosum L.	Asteraceae	N+	neo	S American
Zantedeschia aethiopica (L.) Spreng.	Araceae	N+	neo	S African
Zea mays L.	Poaceae	C	neo	Neotropical
Zizyphus zizyphus (L.) Meikle	Rhamnaceae	U	neo	SE & E Asiatic

N naturalised alien; *C* casual alien; *U* alien of unknown naturalisation status; + plants with an invasive behaviour; *arch* archaeophyte; *neo* neophyte

* Diverging or inadequate data/expert opinion on plant history

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