Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs

Zavlečená flóra Evropy: druhová diverzita, časové trendy, zákonitosti geografického rozšíření a oblasti budoucího výzkumu

Philip W. Lambdon[1,2#], Petr Pyšek[3,4*], Corina Basnou[5], Martin Hejda[3,4], Margarita Arianoutsou[6], Franz Essl[7], Vojtěch Jarošík[4,3], Jan Pergl[3], Marten Winter[8], Paulina Anastasiu[9], Pavlos Andriopoulos[6], Ioannis Bazos[6], Giuseppe Brundu[10], Laura Celesti-Grapow[11], Philippe Chassot[12], Pinelopi Delipetrou[13], Melanie Josefsson[14], Salit Kark[15], Stefan Klotz[8], Yannis Kokkoris[6], Ingolf Kühn[8], Hélia Marchante[16], Irena Perglová[3], Joan Pino[5], Montserrat Vilà[17], Andreas Zikos[6], David Roy[1] & Philip E. Hulme[18]

[1]*Centre for Ecology and Hydrology, Hill of Brathens, Banchory, Aberdeenshire AB31 4BW, Scotland, e-mail; plambdon@googlemail.com, dbr@ceh.ac.uk;* [2]*Kew Herbarium, Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3AB, United Kingdom;* [3]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic, e-mail: pysek@ibot.cas.cz, hejda@ibot.cas.cz, pergl@ibot.cas.cz, perglova@ibot.cas.cz;* [4]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 01 Praha 2, Czech Republic; e-mail: jarosik@cesnet.cz;* [5]*Center for Ecological Research and Forestry Applications, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain, e-mail: c.basnou@creaf.uab.es, joan.pino@uab.es;* [6]*University of Athens, Faculty of Biology, Department of Ecology & Systematics, 15784 Athens, Greece, e-mail: marianou@biol.uoa.gr, pandriop@biol.uoa.gr, ibazos@biol.uoa.gr, ikokkori@biol.uoa.gr, azikos@biol.uoa.gr;* [7]*Federal Environment Agency, Department of Nature Conservation, Spittelauer Lände 5, 1090 Vienna, Austria, e-mail: franz.essl@umweltbundesamt.at;* [8]*Helmholtz Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, D-06120 Halle, Germany; e-mail: marten.winter@ufz.de, stefan.klotz@ufz.de, ingolf.kuehn@ufz.de;* [9]*University of Bucharest, Faculty of Biology, Department of Botany & Microbiology, Aleea Portocalelor 1-3, 060101 Bucharest, Romania, e-mail: anastasiup @yahoo.com;* [10]*Department of Botany and Plant Ecology, University of Sassari, Italy, e-mail: gbrundu@tin.it;* [11]*Department of Plant Biology, Sapienza University of Rome, piazzale Aldo Moro 5, I-00185 Rome, Italy, e-mail: laura.celesti@uniroma1.it;* [12]*UMR1210 Biologie et Gestion des Adventices, INRA-ENESAD-Université de Bourgogne, 17 rue Sully, BP 86510, 21065 Dijon CEDEX, France, e-mail: philippe.chassot@unine.ch;* [13]*University of Athens, Faculty of Biology, Department of Botany, 15784 Athens, Greece, e-mail: pindel@biol.uoa.gr;* [14]*Swedish Environmental Protection Agency, Uppsala, Sweden, e-mail: melanie.josefsson@snv.slu.se;* [15]*The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, The Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel, e-mail: salit@hebrew.edu;* [16]*Department of Pure and Environmental Sciences, Escola*

[#] present address: Global Programmes Department, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, United Kingdom

[*] corresponding author

Superior Agrária de Coimbra, Bencanta 3040-316, Coimbra, Portugal, e-mail: hmarchante@esac.pt; [17]*Estación Biológica de Doñana (EBD-CSIC), Avd/María Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain, e-mail: montse.vila@ebd.csic.es;* [19]*National Centre for Advanced Bio-Protection Technologies, PO Box 84, Lincoln University, Canterbury, New Zealand, e-mail: hulmep@ lincoln.ac.nz*

Lambdon P. W., Pyšek P., Basnou C., Hejda M., Arianoutsou M., Essl F., Jarošík V., Pergl J., Winter M., Anastasiu P., Andriopoulos P., Bazos I., Brundu G., Celesti-Grapow L., Chassot P., Delipetrou P., Josefsson M., Kark S., Klotz S., Kokkoris Y., Kühn I., Marchante H., Perglová I., Pino J., Vilà M., Zikos A., Roy D. & Hulme P. E. (2008): Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. – Preslia 80: 101–149.

The paper provides the first estimate of the composition and structure of alien plants occurring in the wild in the European continent, based on the results of the DAISIE project (2004–2008), funded by the 6th Framework Programme of the European Union and aimed at "creating an inventory of invasive species that threaten European terrestrial, freshwater and marine environments". The plant section of the DAISIE database is based on national checklists from 48 European countries/regions and Israel; for many of them the data were compiled during the project and for some countries DAISIE collected the first comprehensive checklists of alien species, based on primary data (e.g., Cyprus, Greece, F. Y. R. O. Macedonia, Slovenia, Ukraine). In total, the database contains records of 5789 alien plant species in Europe (including those native to a part of Europe but alien to another part), of which 2843 are alien to Europe (of extra-European origin). The research focus was on naturalized species; there are in total 3749 naturalized aliens in Europe, of which 1780 are alien to Europe. This represents a marked increase compared to 1568 alien species reported by a previous analysis of data in Flora Europaea (1964–1980). Casual aliens were marginally considered and are represented by 1507 species with European origins and 872 species whose native range falls outside Europe. The highest diversity of alien species is concentrated in industrialized countries with a tradition of good botanical recording or intensive recent research. The highest number of all alien species, regardless of status, is reported from Belgium (1969), the United Kingdom (1779) and Czech Republic (1378). The United Kingdom (857), Germany (450), Belgium (447) and Italy (440) are countries with the most naturalized neophytes. The number of naturalized neophytes in European countries is determined mainly by the interaction of temperature and precipitation; it increases with increasing precipitation but only in climatically warm and moderately warm regions. Of the nowadays naturalized neophytes alien to Europe, 50% arrived after 1899, 25% after 1962 and 10% after 1989. At present, approximately 6.2 new species, that are capable of naturalization, are arriving each year. Most alien species have relatively restricted European distributions; half of all naturalized species occur in four or fewer countries/regions, whereas 70% of non-naturalized species occur in only one region. Alien species are drawn from 213 families, dominated by large global plant families which have a weedy tendency and have undergone major radiations in temperate regions (*Asteraceae*, *Poaceae*, *Rosaceae*, *Fabaceae*, *Brassicaceae*). There are 1567 genera, which have alien members in European countries, the commonest being globally-diverse genera comprising mainly urban and agricultural weeds (e.g., *Amaranthus*, *Chenopodium* and *Solanum*) or cultivated for ornamental purposes (*Cotoneaster*, the genus richest in alien species). Only a few large genera which have successfully invaded (e.g., *Oenothera*, *Oxalis*, *Panicum*, *Helianthus*) are predominantly of non-European origin. *Conyza canadensis*, *Helianthus tuberosus* and *Robinia pseudoacacia* are most widely distributed alien species. Of all naturalized aliens present in Europe, 64.1% occur in industrial habitats and 58.5% on arable land and in parks and gardens. Grasslands and woodlands are also highly invaded, with 37.4 and 31.5%, respectively, of all naturalized aliens in Europe present in these habitats. Mires, bogs and fens are least invaded; only approximately 10% of aliens in Europe occur there. Intentional introductions to Europe (62.8% of the total number of naturalized aliens) prevail over unintentional (37.2%). Ornamental and horticultural introductions escaped from cultivation account for the highest number of species, 52.2% of the total. Among unintentional introductions, contaminants of seed, mineral materials and other commodities are responsible for 1091 alien species introductions to Europe (76.6% of all species introduced unintentionally) and 363 species are assumed to have arrived as stowaways (directly associated with human transport but arriving independently of commodity). Most aliens in Europe have a native range in the same continent (28.6% of all donor region records are from another part of Europe where the plant is native); in terms of species numbers the contribution of Europe as a region of origin is 53.2%. Considering aliens to Europe separately, 45.8% of species have their native distribution in North and South America, 45.9% in Asia, 20.7% in Africa and 5.3% in Australasia. Based on species composition, European alien flora can be classified into five major groups: (1) north-western, comprising Scandinavia and the UK; (2) west-central, extending from Belgium and the Netherlands to Germany and Switzerland; (3) Baltic, including only the former Soviet Baltic states; (4) east-central, comprizing the remainder of central and eastern Europe; (5) southern, covering the entire Mediterranean region. The clustering patterns cut across some European bioclimatic zones; cultural factors such as regional trade links and traditional local preferences for crop, forestry and ornamental species are also important by influencing the introduced species pool. Finally, the paper evaluates a state of the art in the field of plant invasions in Europe, points to research gaps and outlines avenues of further research towards documenting alien plant invasions in Europe. The data are of varying quality and need to be further assessed with respect to the invasion status and residence time of the species included. This concerns especially the naturalized/casual status; so far, this information is available comprehensively for only 19 countries/regions of the 49 considered. Collating an integrated database on the alien flora of Europe can form a principal contribution to developing a European-wide management strategy of alien species.

K e y w o r d s: alien plants, biogeographical pattern, donor regions, Europe, habitat affinity, naturalization, neophytes, plant invasions, residence time, temporal trends

Introduction

Biological invasions by alien species are widely recognized as a significant component of human-caused global environmental change, often resulting in a significant loss in the economic value, biological diversity and function of invaded ecosystems (Mack et al. 2000, Mooney & Hobbs 2000, Pimentel et al. 2000, 2001, Hulme 2003, Weber 2003, Pyšek et al. 2006, Richardson & Pyšek 2006, Stohlgren et al. 2006). They are large-scale phenomena of widespread importance and represent one of the major threats to European biodiversity. Numerous invasive alien species, many introduced into Europe little more than 200 years ago, have become successfully established over large areas of the European Community, and the geographical range of a large number of species is increasing (Pyšek & Hulme 2005, Hulme 2007). European states recognize the risk that activities within their jurisdiction or control may pose to other states as a potential source of invasions; appropriate individual and cooperative actions are needed to minimize that risk (Miller et al. 2006, Hulme et al. 2008c). This is particularly important within Europe, with its shared coastline, transboundary mountain ranges and protected areas and international watercourses, as species introduced into the territory of one state can easily spread to neighbouring states, subregions or the entire region. From this it follows that a continental approach to biological invasions is a necessary precondition to successful management; political boundaries are not an ideal framework because they do not correspond to biological and ecological barriers that are crucial in determining the limits of plant invasions (Richardson et al. 2000). The awareness of accelerating problems with biological invasions resulted in this topic being included in framework research programs of the European Union, and specifically addressed by the DAISIE project in 2005–2008 (DAISIE 2008, see www.europe-aliens.org for details).

However, information on the (invasive) alien species present in Europe is incomplete. As far as plants, which are in the focus of the present paper, are concerned, there are case studies on particular alien species (e.g., Moravcová et al. 2006, Perglová et al. 2006, Essl

2007, Kollmann et al. 2007), but only a few states had assembled a specialized checklist on the composition of their alien flora before DAISIE: Austria (Essl & Rabitsch 2002), Czech Republic (Pyšek et al. 2002b), Germany (Klotz et al. 2002, Kühn & Klotz 2003), Ireland (Reynolds 2002) and UK (Clement & Foster 1994, Preston et al. 2002, 2004), and the only available continental analysis of plant invasion patterns in Europe (Weber 1997) was based on data from Flora Europaea (Tutin et al. 1964–1980), the only synthetic source of information on the flora of all European countries, including alien species. This source is, however, now outdated and contains numerous inaccuracies in data for individual countries (Pyšek 2003). In general, information on the presence and distribution of alien plant species for most European countries was scattered in a variety of published and unpublished accounts and databases. Therefore, the funding of DAISIE was motivated by need for a regional network of invasive alien species information, and one of the project's major tasks was "to create an inventory of invasive species that threaten European terrestrial, freshwater and marine environments" (Hulme et al. 2008c).

Reliable data on the composition of alien floras from a number of regions make it possible to describe the extent of invasion in different parts of the world and reveal robust biogeographical patterns (Lonsdale 1999, Sax 2001, Lloret et al. 2004, Cadotte et al. 2006, Daehler 2006, Palmer 2006, Pyšek & Richardson 2006, Hulme et al. 2008b). Such studies provide a critical first step in the search for the explanation of invasion patterns, and for characterizing invasive taxa and invaded ecosystems (e.g., Crawley et al. 1996, Cadotte & Lovett-Doust 2001, Kühn et al. 2003, 2004, Lloret et al. 2004, 2005, Hamilton et al. 2005; see Pyšek & Richardson 2007 for a review). In addition, conclusions drawn from such studies can be used to formulate hypotheses which can be tested by other approaches (Daehler 2001). However, such analyses using previously published information depend crucially on the quality of assessment of particular species with respect to their taxonomic identity, time of immigration and invasion status (Pyšek 2003, Pyšek et al. 2004a).

On a more practical side, collating an integrated database on the alien flora of Europe can form a principal contribution to developing a European-wide management strategy of alien species (Wittenberg & Cock 2001). Dispersed and disconnected knowledge cannot easily be marshalled to deliver the information and knowledge required to address policy of biological invasions at a European scale. Improving information exchange can build regional capacity to identify and manage invasive alien species threats (Hulme et al. 2008c). The European Strategy on Invasive Alien Species, launched in 2002, encouraged the development of a pan-European inventory of invasive alien species (Genovesi & Shine 2003).

This paper brings an overview of the alien flora of Europe, based on the results of the DAISIE project, with aims to (i) inform about the data held within the plant part of the DAISIE database, (ii) publish the basic updated information on the structure of alien flora of Europe, the first of such depth at the continental level, (iii) outline the most common naturalized aliens in Europe, and (iv) analyse large-scale geographical patterns in the level of invasion across Europe and in the composition of regional alien floras. Finally, the paper represents a state of the art in the field of plant invasions in Europe, points to research gaps and outlines avenues of further research towards documenting alien plant invasions in Europe.

DAISIE database

Definitions

We adopted an approach to the classification of alien species proposed by Richardson et al. (2000) and Pyšek et al. (2004a) and distinguished naturalized and casual species with respect to invasion status, and archaeophytes and neophytes with respect to the residence time. In order to define what constitutes a European alien in biogeographical terms, we distinguished between those species alien *to* Europe, including species with a native range entirely outside the continental boundaries described in the following section, and aliens of European origin, including species that are native in a part of Europe but alien to another part. For a small number of species, European native status remains ambiguous, and therefore we also report data on the total number of species alien *in* Europe, comprising both subgroups (see Appendix 1 for definitions).

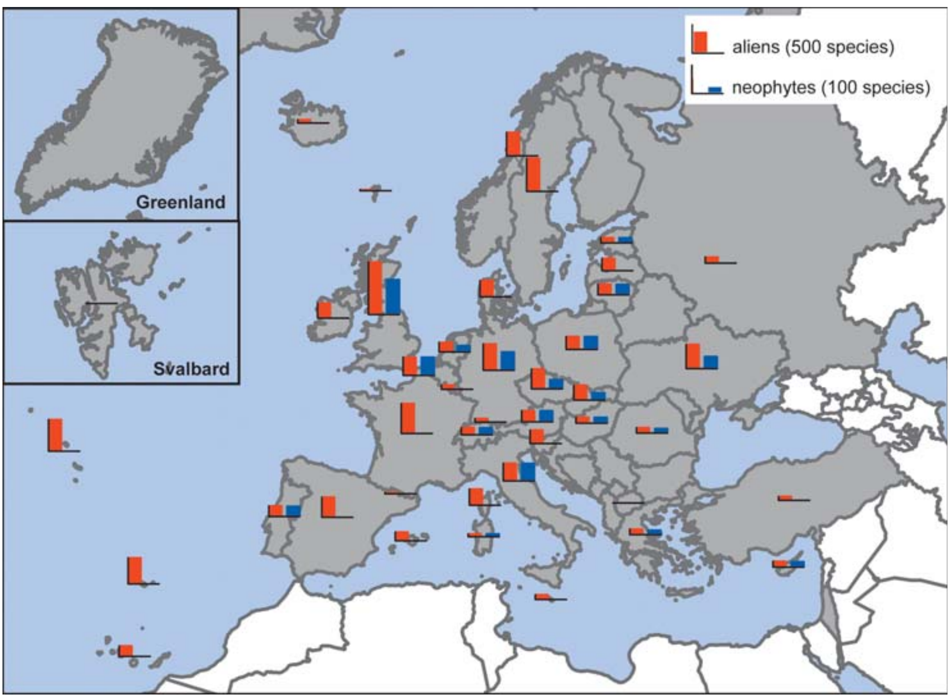

Fig. 1. – Map of Europe showing the geographical coverage of plant data within the DAISIE project (grey area) and richness of alien species in the regions covered. The height of the red bar indicates the total number of naturalized aliens in the region; blue bars indicate the total number of naturalized neophytes in regions with classification of status available, i.e. where neophytes were recorded. Grey regions without bars are those for which only information on the total number of all aliens is available. See Table 1 for species numbers.

Species coverage, taxonomy and nomenclature

The DAISIE project aimed to include the whole of Europe and "third party" nations eligible for funding under the EU Framework 6 research programme (Hulme et al. 2008c). Of these, only Israel falls wholly outside the physical boundaries of Europe. The area targeted (see Fig. 1) was partly determined by the geographical coverage of source floras, but we broadly attempted to use the limits set by Flora Europaea (Tutin et al. 1964–80) for the north and central continental boundaries (i.e., as far east as the Urals, and excluding the Caucasus). In the south-east, Turkey, the eastern Aegean islands and Cyprus were included within the database, although species native only to Anatolia were not considered as European natives. In total, 49 countries/regions were considered. For each of these "national regions", a data set was compiled from the most comprehensive literature sources available (Table 1). Where possible, regional experts were responsible for compiling and verifying the data, although for countries where we were unable to find participants, information was compiled from a recent national flora or database. Only for some of the states of the former Yugoslavia and for Albania were we unable to obtain data by either method, and in a few of the other eastern countries only a preliminary species list was available. Otherwise, reasonably detailed coverage was achieved throughout the study region.

A taxon was included in the database if it was found as an alien in at least one European country/region. In most cases the taxa were full species. However, some prominent subspecies, varieties and hybrids were also recorded, particularly if this was necessary to distinguish from native sister subtaxa (e.g., *Beta vulgaris* subsp. *vulgaris* is alien throughout much of Europe although subsp. *maritima* is widely native in coastal regions). However, for the purposes of this paper, statistics are only reported at the species level. Nominate subspecies were merged with taxa at species level (e.g., *Phalaris canariensis* and *P. canariensis* subsp. *canariensis*). In other cases, this approach creates difficulty where there are issues of sympatry between alien and native subtaxa, so all alien taxa and hybrids have been retained, regardless of whether they have indigenous subspecies (therefore, *Beta vulgaris* subsp. *vulgaris* is included as *B. vulgaris* s.l.).

The taxonomic treatment was standardized across all national checklists. Since there is not yet a global database of synonymies, we reviewed 58 different literature sources in this process, especially Flora Europaea (Tutin et al. 1964–80, 1993) and online meta-resources such as the International Plant Names Index (2006), Kerguélen (1999), the International Organization for Plant Information (2006) and the International Legume Database (Legume Web, 2006). A complete list of sources used to standardize taxonomies is available from the DAISIE Invasive Species portal (www.europe-aliens.org). We did not have the facilities to trace the true priority name for all species, but provisionally, we accepted the most widely-used name, or if this was ambiguous we preferred to follow widely-used sources or those adopted in the native range. For the most difficult genera, such as *Oenothera* and *Amaranthus*, the division of taxa into species remains somewhat subjective and our system should be considered as preliminary only. Higher taxonomic ranks (subclass, order and family) mainly follow the approach of the Angiosperm Phylogeny Group (Stevens 2001 onwards). This classification system incorporates data from molecular, chemical and morphological phylogenies in an attempt to represent the latest thinking on angiosperm evolution, and in a few lineages (e.g., *Scrophulariales*) it differs markedly from earlier treatments. For example, traditional *Callitrichaceae*, *Plantaginaceae* and *Scrophulariaceae* are almost monophyletic, but divided into two major clades which do not correspond to previous taxonomic ideas. Under this interpretation, *Callitriche* and *Plantago* are genera with very reduced floral structures and they belong in the second clade along with *Veronica*, *Hebe* and *Linaria* (Albach et al. 2005). For non-angiosperms (pteridophytes and gymnosperms), the more traditional system of Mabberley (1997) was employed, which is largely constructed from morphological evidence.

Classification of species invasion status

Status was reported as naturalized, casual or cryptogenic (see Appendix 1 for definitions), although in some cases there was insufficient information to determine the exact category and the taxon was recorded as "alien". This designation occurs most commonly in poorly-recorded countries, and was otherwise used very rarely. In countries/regions where little or no status information was available (e.g., Belarus, Israel, Croatia, Moldova), we therefore simply present the total number of species. Casuals are documented much more carefully in some countries than others (e.g., Austria, Belgium, Hungary, Czech Republic) so the level of coverage varies considerably – in many national data sets they are omitted entirely. For this reason, we base all analyses in this paper on naturalized species only, although information on the numbers of casuals is also presented in Table 1 for the sake of completeness. Since there is insufficient information to decide whether some species are naturalized or casual in some regions, an uncertainty margin remains on the final naturalized totals in these cases; these are reported as "unspecified" in Table 1, and we have avoided making subsequent judgement on their likely status. The specification is given for each statistical summary as to whether the numbers are based on all aliens or neophytes only, and on aliens *in* Europe, of European origin, or *to* Europe. In order to correctly determine European status in as many species as possible, additional effort was focused on this task after the main phase of data collection.

Each national checklist was supplemented with a range of information detailing the invasion history of the species in the given region or country. These data were recorded on standard forms according to an agreed categorization system, in order to maintain a consistent approach for the whole of Europe. Where possible, we tried to ensure that: (i) we utilized existing categorizations so that our results are comparable with other studies, (ii) the classifications were hierarchical, providing the flexibility to accommodate the different levels of detail available. For many species, information on particular aspects of invasion history could not be obtained, and the relevant analyses were therefore based on a reduced data set.

Residence time and date of introduction

Date of introduction was determined directly from available literature, or was specified to the narrowest available date range on the basis of inference (e.g., between the date that the species was described to science and the date of the first record in the given country). Dates of introduction are frequently problematic in studies of this type due to the lack of detailed historical records. The standard approach is to use minimum residence time (based on the latest possible date when the species could have arrived) as a conservative estimate (Rejmánek 2000, Pyšek & Jarošík 2005, Richardson & Pyšek 2006). Thus, we evaluated the first occurrence in Europe from the earliest recorded date in any country (or the first record as an alien for species with their native range in a part of Europe), but in cases where the introduction could only be identified to a time period, we chose the latest possible date in the range. The estimated range was within a decade for 81.3% of the species evaluated. We particularly attempted to distinguish archaeophytes from neophytes (species introduced before and after 1500 A.D.), as it has widely been found that the two groups differ in their invasion characteristics and ecology due to the contrasting regimes of selection and cultivation operating in ancient and modern societies (Kühn et al. 2003, Pyšek et al. 2004b, 2005). Archaeophytes are generally poorly-recorded and their native or alien status may be unclear. Some national data sets avoided them completely, and although we indicate the numbers recorded in Table 1, we have attempted to report neophyte totals for all subsequent analyses. All species with a native range restricted to the New World were considered to be neophytes.

Habitats

Habitat data were recorded according to the EUNIS system (Davies & Moss 2003, available at http://eunis.eea.europa.eu/habitats.jsp), which provides a physical categorization of all major European habitat types. Since habitat descriptions in most floras are relatively coarse (Chytrý et al. 2008a, b), the recording in the DAISIE database is only down to EUNIS Level 2, although in many cases only Level 1 was possible, either through low resolution or ambiguities in the source literature. The resulting classification included 10 habitat types: A. Marine habitats; B. Coastal habitats; C. Inland surface waters; D. Mires, bogs and fens; E. Grasslands; F. Heathland, scrub and tundra; G. Woodland and forest; H. Inland unvegetated or sparsely vegetated habitats; I. Arable land, gardens and parks; and J. Constructed, industrial and other artificial habitats.

Pathways of introduction

To indicate how and why a species arrived or was introduced in the given country, a three-level hierarchical system was developed (see Appendix 1 for definitions) based on the approaches of Hill et al. (2005) and Hulme et al. (2008a). The definitions in Level 2 allowed us to deal with a number of species whose status is normally ambiguous. The "unaided" category includes those which are alien in a neighbouring country and clearly should not be treated as natives, but which have subsequently spread without the aid of man.

Native ranges

Native ranges were recorded using the standardized geographical regions of the Taxonomic Database Working Group (available at http://www.bgbm.fu-berlin.de/TDWG/geo/default.htm). This system allows hierarchical recording at the continental, biogeographic regional and national levels, although due to data limitations we here present analyses for Level 1 only (continental). Generally, we excluded species where the distinction between native and introduced parts of the range was ambiguous. However, there remain a number of cosmopolitan weeds whose origins are now obscure but which are important alien pests across the world (e.g., *Cyperus esculentus*, *Setaria viridis*, *Lemna trisulca*, *Oxalis corniculata*). We felt that it would be unrepresentative to exclude these, and have attempted to give an approximation of their true native ranges, although the outcomes probably tend to be overestimated.

Species of hybrid origin include those which have arisen spontaneously in Europe through hybridization from at least one non-native parent. Although such taxa could be considered more native to Europe than anywhere else in the world, they would not have arisen without human intervention (see Pyšek et al. 2004a for discussion).

Statistical analysis

Determinants of the level of invasion

To determine why some countries harbour more alien species than others, we related the number of naturalized neophytes (Table 1) to characteristics reflecting large-scale geographical patterns in Europe and known to affect the level of invasion (McKinney 2001, 2006, Sax 2001, Pyšek et al. 2002a, Kühn et al. 2003, Taylor & Irwin 2004). For each country/region, the following variables were obtained: (i) mean annual precipitation and (ii) mean annual temperature, and (iii) difference between July and January temperature (with data at 5 minutes pixel resolution; Hijmans et al. 2005, taken from www.worldclim.org), characterizing climate; (iv) latitude, (v) longitude, and (vi) area, characterizing geography; (vii) Gross Domestic Product (GDP), (viii) human population density (number of inhabitants per square kilometre), taken from Wikipedia (www.en.wikipedia.org/wiki/Countries_of_the_world; accessed 10 December 2007), and (ix) road density (km/km^2; taken from International Road Federation 2002, www.irfnet.org/wrs.asp), characterizing economic factors. All these variables were used as explanatory variables (including the square of latitude and longitude, known as important geographical predictors from previous analyses; e.g., Legendre & Legendre 1998, Lichstein et al. 2002).

The aim of statistical analysis was to establish a minimal adequate model (MAM) for the numbers of naturalized neophytes, in which all the explanatory variables are significantly different from zero and from one another (e.g., Crawley 2002). This was achieved by backward simplifications of full models, which included all explanatory variables and their interactions (e.g., Crawley 1993: 192–197). Because, due to a limited sample size, it was impossible to start by fitting a full model for all variables, the modelling started from separate full models for variables characterizing climate, geography and economic factors. This enabled common analysis of related explanatory variables while keeping a reasonable number of the variables (Quinn & Keough 2002: 111–125). To verify whether this procedure did not omit some likely interactions, the MAMs for climate, geography and economic factors were examined for all possible two-way interactions with the explanatory variables from the other groups, which includes all the explanatory variables but not their interactions. To achieve the final multiplicative MAM, the established additive significant explanatory variables from the individual MAMs were analyzed together, re-fitted with all possible interactions among explanatory variables of this additive MAM. To verify whether this procedure did not omit some likely interactions, the residuals from the full additive model were plotted against all two-level interactions of this model, to check if any of these interactions are related to variation in the response variable of the full additive model (Quinn & Keough 2002: 132). Significant interactions between two covariates of the final established MAM were examined with simple slopes at varying values of the interacting covariates, using slopes of one variable on another to arrive at three specific values of the changing variable: mean, and mean plus and minus its sample standard deviation (Aiken & West 1991). Following Quinn & Keough (2002: 131–133), the analyses of interactions were made using centred variables, i.e., variables rescaled by subtracting their mean from each observation. The total numbers of neophytes were square-rooted (e.g., Sokal & Rohlf 1995: 415–417) and the data evaluated assuming a normal distribution of errors and identity link function. Human density and area were log-transformed prior to analyses, and all covariates standardized to zero mean and unit variance to achieve their comparable influence. Using the standardized values, collinearity was checked by calculating tolerance values among all the explanatory variables (Quinn & Keough 2002: 128). Tolerance was considered unacceptably low if its value was < 0.1; such a low value indicates a high correlation, which can negatively affect the estimates of model parameters (Quinn & Keough 2002). This was so because latitude and longitude were strongly correlated with their quadratic terms and both the coordinates strongly correlated with environmental variables. Following Quinn & Keough (2002: 129–130), the analyses were therefore repeated after exclusion of the geographical coordinates. All fitted models were checked by plotting standardized residuals against fitted values, and by normal probability plots (Crawley 1993). Calculations were made in S-Plus® v. 6.2 (Insightful Corp.).

Biogeographical patterns

In an attempt to identify biogeographical zones which display distinctive species assemblages, we performed a Detrended Correspondence Analysis (DCA) on the regional species lists, using CANOCO for Windows 4.5 (1997–2002, ter Braak & Šmilauer 2002). The starting data set was a matrix of species (columns) and countries (rows), with presence/absence of a species in each country indicated by binary scores (1 or 0). Due to indications of unimodality, the response variables were detrended by segments and rare species were down-weighted. Major environmetal determinants were passively projected into the ordination space (as supplementary variables) of the indirect gradient analysis model and the product-moment correlation between these seven supplementary environmental variables listed above and the ordination axes was estimated. To objectively classify the national regions into biogeographical groupings, an oblique cluster analysis was used (the VARCLUS procedure in SAS/STAT 9.1), based on maximizing the variance explained by the cluster averages of the unweighted standardized variables.

Structure of the European alien flora

Species richness

In total, the DAISIE database contains records of 5789 alien plant species *in* Europe, of which 2843 are alien *to* Europe, i.e., of extra-European origin. Of these 1507 and 872, respectively, are casual in all regions where they occur, and 29 and 8, respectively, cryptogenic; for 504 and 183 species, respectively, the naturalization status is uncertain. There are in total 3749 naturalized aliens recorded *in* Europe and 1780 alien *to* Europe. We do not attempt to derive the total number of naturalized neophytes since it would have to be based on a limited subset of countries with invasion and residence time status designated (n = 19), discarding naturalized neophytes from other regions where such classification is not available. This would necessarily lead to underestimation of the number of naturalized neophytes currently present in Europe.

Interestingly, the ten year old overview of the alien flora of Europe (Weber 1997) reported 1568 naturalized species *in* Europe, using our terminology, of which smaller proportion of 38% (580 species) were species alien *to* Europe. This ratio is relatively low, compared to the DAISIE data, where almost half of all aliens (47%) are of extra-European origin. Using the data analysed by Weber (1997), which were based on Flora Europaea (Tutin et al. 1964–1980), as a reference figure, it appears that the number of aliens with European origin increased drammatically (from 988 in Weber 1997 to 2671 in DAISIE), but the increase in the number of aliens *to* Europe was even more dramatic, from 580 to 2843. Although part of this increase can be attributed to a continuing influx of alien species to individual countries (Pyšek et al. 2003b) and the continent as a whole (Fig. 3), this phenomenon alone cannot explain the huge difference. The main reason is raised awareness of the issue of alien species and increasing research intensity in the last decades (Pyšek et al. 2006); specialized national checklists and databases cover alien species of extra-European origin much better than a synthetic floral work of the Flora Europaea kind.

The numbers of alien species recorded in individual countries/regions are summarized in Table 1. The highest number of all alien species, regardless of status, is reported from Belgium (1969), the United Kingdom (1779), Czech Republic (1378), France (1258), Sweden (1201) and Austria (1086); all other countries harbour less than 1000 species. High species numbers in these countries are due to the inclusion of casuals, the contribution of which is principle in the three countries with complete records of casuals, i.e., Belgium (75.5%), Austria (74.6%) and Czech Republic (64.7%), and lower in those with casuals selectively covered. In total, 18 countries/regions have a reasonably detailed classification of casuals. The highest numbers of neophytes, regardless of status, are reported from Belgium (1969), United Kingdom (1085), Austria (1070) and Czech Republic (1046) (Table 1).

The highest numbers of naturalized aliens, exceeding 500, are reported from United Kingdom (1284), Sweden (810), Azores (775), France (732), Germany (645), Madeira (640) and Ukraine (591). In terms of naturalized neophytes, United Kingdom (857), Germany (450), Belgium (447), Italy (440) are countries with the most naturalized neophytes reported (Table 1). Relating number of naturalized neophytes to area of the country, United Kingdom (159.0 species/log area), Belgium (99.6), Italy (81.5), Germany (81.0), Austria (56.0), Poland (54.6), Lithuania (53.2), Ukraine (51.4), Portugal (50.5) and Czech Republic (46.8) are the 10 countries with highest densities of naturalized neophytes.

From the continental perspective, the highest species richness of alien plants is concentrated in large industrialized north-western countries with a tradition of good botanical recording or intensive recent research (Fig. 1). High species numbers in Scandinavian countries may seem surprising given the generally negative relationship between the numbers of naturalized aliens and increasing latitude (see e.g., Sax 2001, Pyšek & Richardson 2006) and there are two main reasons for this pattern. First, the minor one, may be a rather generous approach to the acceptance of a species as naturalized within the NOBANIS project (www.nobanis.org), whether directly or deriving from Flora Scandinavica. Some species appear on the list of naturalized taxa, which might have been judged to be casuals in other countries. The main reason, however, seems to be that many species that are native south of Scandinavia occur as aliens there because they were introduced by humans. A large number of common European species, considered to be native over most of the continent, have perhaps only been able to colonize further north due to urbanization and the creation of new, more suitable habitats with warm microclimates. Examples include such widespread European species as *Stellaria media*, *Rumex crispus*, *Trifolium repens*, *Holcus lanatus* and *Ophrys insectifera*. For example, in Sweden only 27% of naturalized species are alien *to* Europe, which is a huge contrast to the average for the whole continent.

Table 1. – Summary statistics for the number of alien species recorded in 49 European countries or major islands. Alien *in* Europe refers to the number of species recorded as alien in at least one of these regions, including species which are native elsewhere in the continent. Alien *to* Europe refers to the number of species with origin outside Europe, hence alien across all regions. Data on the number of neophytes are only included where it was possible to make a comprehensive assessment of neophytic status for most species in the region. Unspecified status refers to species in which reliable information is insufficient to decide whether they are naturalized or casual in a given region. The "–" symbol indicates that data are not available for the given category. Note that parts of United Kingdom are reported separately but were not included in the analyses reported in the text. For some countries, numbers may differ from previously published accounts due to improving knowledge and also due to editorial decisions to standardize the taxonomic treatment and status evaluation across Europe; this means that some taxa may have been merged, or demoted to subspecific status.

	All aliens					Neophytes				
Country/region	Total	Naturalized	Casual	Unspecified	Cryptogenic	Total	Naturalized	Casual	Unspecified	Coverage
Alien *in* Europe (total)	5789	3749	1507	504	29	–	–	–	–	
European origin (total)	2671	1864	541	247	19					
Alien *to* Europe (total)	2843	1780	872	183	8	–	–	–	–	
Andorra	52	33	19	0	1	–	–	–	–	2, 6
Austria	1086	276	810	0	0	1086	276	810	0	1, 5
Azores	918	775	143	0	0	–	–	–	–	1, 6
Baleares	339	216	123	0	0	–	–	–	–	2, 6
Belarus	190	–	–	–	–	–	–	–	–	4, 6
Belgium	1969	447	1486	36	0	1969	447	1486	36	1
Bulgaria	708	–	–	–	–	–	–	–	–	3, 6
Canary Islands	258	258	–	–	0	–	–	–	–	1, 6
Corse	500	397	26	77	7	–	–	–	–	2, 6
Croatia	157	–	–	–	–	–	–	–	–	4, 6
Cyprus	209	143	50	16	19	199	133	50	16	1
Czech Republic	1378	487	891	0	0	1046	229	817	0	1
Denmark	978	399	59	520	0	–	–	–	–	2, 6
England	1630	–	–	–	–	–	–	–	–	2, 6
Estonia	416	125	291	0	0	412	125	287	0	1, 5
Finland	918	–	–	–	0	–	–	–	–	2, 6
Faroe Islands	62	27	32	3	0	–	–	–	–	2, 6
France	1258	732	171	355	11	–	–	–	–	2, 6
Germany	851	645	206	0	0	630	450	180	0	2
Greece	315	134	46	135	19	112	112	–	–	2, 6
Greenland	111	–	–	–	–	–	–	–	–	2, 6
Hungary	711	145	566	0	0	709	145	564	0	2, 5
Iceland	80	80	–	–	0	–	–	–	–	3, 6
Israel	187	–	–	–	–	–	–	–	–	3
Italy	557	440	117	0	0	557	440	117	0	2
Latvia	886	303	360	223	0	–	–	–	–	1, 6
Liechtenstein	189	89	39	61	5	–	–	–	–	2, 6
Lithuania	827	258	256	313	0	509	256	253	0	1, 5
Luxembourg	105	105	–	–	0	–	–	–	–	3, 6
F.Y.R.O. Macedonia	25	5	2	18	0	–	–	–	–	4, 6
Madeira	659	640	14	5	1	–	–	–	–	2, 6
Malta	183	117	65	1	9	–	–	–	–	1, 6
Moldova	176	–	–	–	–	–	–	–	–	3, 6
Netherlands	232	232	–	–	0	154	154	–	–	3
Northern Ireland	550	–	–	–	–	–	–	–	–	2, 6

Country/region	All aliens					Neophytes				
	Total	Naturalized	Casual	Unspecified	Cryptogenic	Total	Naturalized	Casual	Unspecified	Coverage
Norway	873	576	97	200	0	–	–	–	–	2, 6
Poland	300	300	–	–	0	300	300	–	–	2
Portugal	547	261	177	109	0	537	250	173	114	1
Republic of Ireland	734	364	246	124	53	–	–	–	–	2, 6
Romania	435	131	304	0	0	384	113	271	0	1
Sardinia	122	70	52	0	0	122	70	52	0	1, 5
Scotland	1185	–	–	–	–	–	–	–	–	2, 6
Slovakia	741	367	374	0	0	545	182	363	0	1
Slovenia	750	330	338	82	0	–	–	–	–	1, 6
Spain	933	495	362	76	0	–	–	–	–	1, 6
Svalbard	44	6	38	0	0	–	–	–	–	1, 6
Sweden	1201	810	188	203	0	–	–	–	–	2, 6
Switzerland	313	175	138	0	0	287	170	117	0	1
Turkey	220	95	115	10	3	–	–	–	–	2, 6
Ukraine	803	591	211	1	0	666	297	179	190	2
United Kingdom	1779	1284	395	100	0	1085	857	216	12	2
Wales	1043	–	–	–	–	–	–	–	–	2, 6

Coverage notes: 1 Comprehensive data set including a large number of casuals; 2 Data set limited to naturalized species and common casuals; 3 Data set includes naturalized species only; 4 Data set limited to an incomplete species list; 5 Archaeophytes omitted; 6 Insufficient data to determine archaeophyte/neophyte status for many species

Note: The DAISIE database also includes the first estimate of the alien flora of the European part of Russia. In total, 371 aliens were recorded, of which 149 are naturalized, 195 casual and 27 of unspecified status. The vast majority of species are neophytes, the date of introduction is known for 209 species. As these data need additional verification, they were not included in calculations of summary statistical figures.

Data sources (see Electronic Appendix 1 for full references):
Andorra: Bolós et al. 2005; **Austria**: Essl & Rabitsch 2002; **Azores:** Schäfer 2002, 2003; **Baleares**: Moragues Botey & Rita Larrucea 2005; **Belarus**: Herbarium of CBG NASB MSKH 2006; **Belgium**: Verloove 2006; **Bulgaria**: Vladimirov V. (unpublished data, 2006); **Canary Is**.: Izquierdo et al. 2001, Sanz-Elorza et al. 2004b; **Corse**: Coste 1990, Fournier 1977, Guinochet & de Vilmorin 1973, Jauzein 1995, Jeanmonod & Natali 1996, Kerguélen 1987, Muller 2004, Tutin et al. 1964–1980; **Croatia**: Starmühler W. (unpublished document, 2006); **Cyprus**: Akkelidou et al. 2004, Alziar 1999, Barbéro & Quézel 1979, Chilton 2005, Christodoulou 2003, Chrtek & Slavík 1981, 1994, 2000, Delipetrou 2006, Della & Latrou 1995, Géhu et al. 1990, Georgiades 1987, 1994, Georgiades & Yannitsaros 2000, Greuter et al. 1984–1989, Hadjikyriakou 2008, Hadjikyriakou & Hadjisterkotis 2002, Hadjikyriakou et al. 2004, Hand 2000, 2001–2006, Holmboe 1914, Meikle 1977, 1985, Pantelas et al. 1997, Strid & Tan 2002, Tsintides et al. 2002; **Czech Republic**: Pyšek et al. 2002b; **Denmark**: Hansen 1964, 1988, Hartvig et al. 1992, Svart & Lyck 1991, Weidema 2000 (see www.nobanis.org for complete sources); **England**: Preston et al. 2002; **Estonia**: Kukk 1999; **Finland**: Hämet-Ahti et al. 1992, 1998, Kurtto & Helynranta 1998, Lohammar 1955, Weidema 2000 (see www.nobanis.org for complete sources); **Faroe Islands**: Hansen 1966, 1988, Svart & Lyck 1991, Tømmerås 1994; **France**: Pradalie & Blot 2003, Coste 1990, Fournier 1977, Global Invasive Species Programme 2006, Guinochet & de Vilmorin 1973, Jauzein 1995, 2001, Kerguélen 1987, Muller 2004, Tutin et al. 1964–1980; **Germany**: Klotz et al. 2002; **Greece**: Akeroyd & Preston 1981, 1987, Arampatzis 1998, 2001, Athanasiadis & Drossos 1990, Authier 1989, 1998, 2001a, b, 2002a, b, Babalonas 1977, 1981, Babalonas et al. 2001, Bergmeier et al. 1997, 2001, Biel 2002, Böhling 1997, Böhling & Scholz 2003, Boratyński & Browicz 1993, 1996, Boratyński et al. 1983, 1988, Browicz 1993, 1998, 2000, Burton 1999, Carlström 1986, Chilton & Turland 1997, 2004, Christodoulakis 1986, 1996, Chronopoulos & Christodoulakis 1996, 2000, Constantinidis 1997, Constantinidis & Yannitsaros 1993, Cullen et al. 2000, Damanakis & Yannitsaros A. 1986, Davis 1965–2002, Economidou 1969, Georgiadis 1983, Georgiou 1988, Greuter 1973, 1976, 1979, 1980, Greuter & Raus 1982–2006, Greuter et al. 1983, 1984–1989, 1984a, b, 1985, Güner et al. 2000, Hanelt 2001, Hansen 1980, 1982, Hansen & Nielsen 1993, Hofmann 1968, Jalas & Suominen 1976–1994, Jalas et al. 1999, Kavvadas 1956, Krigas & Kokkini 2004, Krigas et al. 1999, Panitsa et al. 2003, Pavlides 1985, Phitos & Damboldt 1985,

Pignatti 1982, Raus 1996a, b, Raus & Raabe 2002, Rechinger 1939, 1943, 1961, Sarika 1999, Sarika et al. 2005, Sideris & Yannitsaros 1983, Snogerup & Snogerup 1991, 1993, 2000, Snogerup et al. 2001, Strid & Tan 1997, 2002, Trigas & Iatrou 2000, Tsiotsiou & Christodoulakis 2004, Turland et al. 1993, Tutin et al. 1964–1980, 1993, Vladimirov et al. 2006, Walters et al. 1986, 1989, Yannitsaros 1969, 1979, 1982, 1986, 1990, 1991, 1992, 1997, 1998, 2004, Yannitsaros & Bazos 2000, Yannitsaros & Damanakis 1983, Yannitsaros & Economidou 1974, Yannitsaros & Protopapadakis 1989, 1995; **Greenland**: Bay 1993, Pedersen 1972, Porsild 1932, Weidema 2000; **Hungary**: Balogh et al. 2004; **Iceland**: Babington 1871, Davidsson 1967, Einarsson 2006, Gronlund 1881, Weidema 2000 (see www.nobanis.org for complete sources); **Israel**: Danin 2004, Dufour-Dror 2005, Kutiel et al. 2007; **Italy**: Celesti-Grapow et al. 2008a[1], b; **Latvia**: Kabuce 2007; **Liechtenstein**: Waldburger et al. 2003; **Lithuania**: Gudžinskas 1997–2005, 2005; **Luxembourg**: Colling 2005; **F.Y.R.O. Macedonia**: Kostadinovski M. (unpublished data, 2005); **Madeira**: Vieira 2002; **Malta:** Haslam et al. 1977; **Moldova**: Sîrbu C. (unpublished data, 2006); **Netherlands**: Tamis et al. 2004; **Northern Ireland:** Preston et al. 2002; **Norway**: Fremstad & Elven 1997, Lid & Lid 1994, Tømmerås 1994, Weidema 2000; **Poland**: Anon. 2006, Mirek et al. 2002, Tokarska-Guzik 2005; **Portugal**: Almeida 1999, Almeida & Freitas 2006, Marchante et al. 2005; **Republic of Ireland**: Preston et al. 2002, Reynolds 2002, Scannel & Synnott 1972; **Romania:** Anastasiu & Negrean 2005a, 2005b, Sîrbu 2004; **Sardinia**: Brundu et al. 2003, Camarda 1998, 2001, Viegi 1993; **Scotland:** Preston et al. 2002; **Slovakia**: Gojdičová et al. 2002, Halada 1997; **Slovenia**: Jogan N. (unpublished data, 2006), Starmühler W. (unpublished data, 2006); **Spain**: Alcázar 1984, Bolós et al. 2005, Campos & Herrera 1997, Carretero 1989, Casasayas 1989, Castroviejo et al. 1986–2005, Fernández 1991, González 1988, Greuter et al. 1984–1989, Izquierdo et al. 2001, Masalles et al. 1996, Sanz-Elorza et al. 2004a, b, Tutin et al. 1964–1980, Valdés et al. 1987; **Svalbard**: Liška & Soldán 2004; **Sweden**: Berg & Nilsson 1997, Karlsson 1998, Mossberg & Stenberg 2003, Weidema 2000 (see www.nobanis.org for complete sources); **Switzerland:** Wittenberg 2005; **Turkey**: Davis 1965–2002; **Ukraine:** Mosyakin & Yavorska 2003, Protopopova 1991, Protopopova et al. 2006; **United Kingdom:** Preston et al. 2002, Hill et al. 2005; **Wales:** Preston et al. 2002.

Table 2. – The 150 most widespread alien plant species *in* Europe, which occur in more than 25 regions considered. Number of occurrences in the regions considered (n = 49) as naturalized or casual is shown. Unspecified occurrences refer to regions where the species is definitely alien but classification as to whether it is casual or naturalized is not available. Occurrence as neophyte or archaeophyte is not distinguished but given the focus of DAISIE (see section DAISIE database), most relate to neophyte status. Species are ranked according to the decreasing number of total occurrences in Europe as aliens.

Species	Family	Naturalized	Casual	Unspecified	Total
Conyza canadensis	*Asteraceae*	33	1	13	47
Datura stramonium	*Solanaceae*	25	7	13	45
Amaranthus retroflexus	*Amaranthaceae*	30	4	10	44
Galinsoga parviflora	*Asteraceae*	27	2	15	44
Helianthus tuberosus	*Asteraceae*	26	5	12	43
Xanthium strumarium	*Asteraceae*	22	5	16	43
Lepidium virginicum	*Brassicaceae*	16	11	15	42
Oenothera biennis	*Onagraceae*	28	2	12	42
Robinia pseudoacacia	*Fabaceae* (*Faboideae*)	32	2	8	42
Galinsoga quadriradiata	*Asteraceae*	25	1	15	41
Matricaria discoidea	*Asteraceae*	23	3	15	41
Panicum miliaceum	*Poaceae*	16	20	5	41
Veronica persica	*Plantaginaceae*	27	0	14	41
Ailanthus altissima	*Simaroubaceae*	30	1	9	40
Amaranthus albus	*Amaranthaceae*	24	5	11	40
Erigeron annuus	*Asteraceae*	27	3	10	40
Fallopia japonica	*Polygonaceae*	29	1	10	40
Medicago sativa	*Fabaceae* (*Faboideae*)	23	4	13	40
Amaranthus blitoides	*Amaranthaceae*	24	6	9	39

[1] Refers to complete alien flora of Italy, including 1023 alien vascular plants of which 920 are neophytes (including casuals) and 103 archaeophytes. At the time of publication of the present paper only data on neophytes (mostly naturalized) were included into DAISIE database.

Species	Family	Naturalized	Casual	Unspecified	Total
Lepidium sativum	*Brassicaceae*	10	21	8	39
Papaver somniferum	*Papaveraceae*	12	17	10	39
Solidago canadensis	*Asteraceae*	28	0	11	39
Acer negundo	*Sapindaceae*	26	3	9	38
Chenopodium ambrosioides	*Amaranthaceae*	22	6	10	38
Elodea canadensis	*Hydrocharitaceae*	26	0	12	38
Juncus tenuis	*Juncaceae*	26	0	12	38
Panicum capillare	*Poaceae*	17	16	5	38
Phalaris canariensis	*Poaceae*	10	15	13	38
Vicia sativa	*Fabaceae* (*Faboideae*)	15	13	10	38
Cymbalaria muralis	*Plantaginaceae*	23	3	11	37
Helianthus annuus	*Asteraceae*	10	16	11	37
Nicandra physalodes	*Solanaceae*	10	13	14	37
Oxalis stricta	*Oxalidaceae*	22	2	13	37
Amaranthus deflexus	*Amaranthaceae*	20	5	11	36
Ambrosia artemisiifolia	*Asteraceae*	17	8	11	36
Brassica napus	*Brassicaceae*	15	11	10	36
Kochia scoparia	*Amaranthaceae*	16	9	11	36
Lycopersicon esculentum	*Solanaceae*	12	13	11	36
Mentha spicata	*Lamiaceae*	18	6	12	36
Oxalis corniculata	*Oxalidaceae*	17	6	13	36
Xanthium spinosum	*Asteraceae*	19	7	10	36
Cuscuta campestris	*Convolvulaceae*	20	7	8	35
Impatiens glandulifera	*Balsaminaceae*	25	2	8	35
Solidago gigantea	*Asteraceae*	25	2	8	35
Amaranthus cruentus	*Amaranthaceae*	8	22	4	34
Amaranthus hybridus	*Amaranthaceae*	19	5	10	34
Bidens frondosa	*Asteraceae*	24	2	8	34
Brassica rapa	*Brassicaceae*	13	11	10	34
Chamaesyce maculata	*Euphorbiaceae*	20	3	11	34
Eleusine indica	*Poaceae*	15	13	6	34
Impatiens parviflora	*Balsaminaceae*	25	1	8	34
Phacelia tanacetifolia	*Hydrophyllaceae*	8	16	10	34
Prunus cerasus	*Rosaceae*	20	6	8	34
Quercus rubra	*Fagaceae*	19	5	10	34
Rosa rugosa	*Rosaceae*	19	6	9	34
Lolium multiflorum	*Poaceae*	19	4	10	33
Lycium barbarum	*Solanaceae*	23	4	6	33
Tanacetum parthenium	*Asteraceae*	21	5	7	33
Trifolium incarnatum	*Fabaceae* (*Faboideae*)	11	14	8	33
Veronica filiformis	*Plantaginaceae*	22	1	10	33
Amaranthus crispus	*Amaranthaceae*	16	11	5	32
Aster novi-belgii	*Asteraceae*	20	2	10	32
Coriandrum sativum	*Apiaceae*	9	12	11	32
Fallopia sachalinensis	*Polygonaceae*	23	3	6	32
Hordeum jubatum	*Poaceae*	15	7	10	32
Lunaria annua	*Brassicaceae*	15	9	8	32
Petroselinum crispum	*Apiaceae*	12	11	9	32
Portulaca oleracea	*Portulacaceae*	18	7	7	32
Ricinus communis	*Euphorbiaceae*	13	15	4	32
Sedum spurium	*Crassulaceae*	17	5	10	32
Sinapis alba	*Brassicaceae*	11	11	10	32
Veronica peregrina	*Plantaginaceae*	15	4	13	32
Abutilon theophrasti	*Malvaceae*	12	13	6	31
Acorus calamus	*Acoraceae*	21	1	9	31
Aster lanceolatus	*Asteraceae*	19	4	8	31

Species	Family	Naturalized	Casual	Unspecified	Total
Coronopus didymus	*Brassicaceae*	17	6	8	31
Fallopia baldschuanica	*Polygonaceae*	15	7	9	31
Iris germanica	*Iridaceae*	17	4	10	31
Lupinus polyphyllus	*Fabaceae* (*Faboideae*)	19	4	8	31
Mimulus guttatus	*Phrymaceae*	19	2	10	31
Oenothera glazioviana	*Onagraceae*	18	4	9	31
Prunus domestica	*Rosaceae*	17	4	10	31
Sorghum halepense	*Poaceae*	16	6	9	31
Aesculus hippocastanum	*Sapindaceae*	16	4	10	30
Alcea rosea	*Malvaceae*	12	10	8	30
Aster × *salignus* hyb.	*Asteraceae*	19	5	6	30
Cardaria draba	*Brassicaceae*	17	2	11	30
Hesperis matronalis	*Brassicaceae*	15	7	8	30
Hordeum murinum	*Poaceae*	10	10	10	30
Lepidium densiflorum	*Brassicaceae*	17	6	7	30
Prunus cerasifera	*Rosaceae*	15	5	10	30
Pyrus communis	*Rosaceae*	14	4	12	30
Syringa vulgaris	*Oleaceae*	18	4	8	30
Tropaeolum majus	*Tropaeolaceae*	14	13	3	30
Artemisia verlotiorum	*Asteraceae*	15	3	11	29
Azolla filiculoides	*Azollaceae*	18	3	8	29
Bromus catharticus	*Poaceae*	13	9	7	29
Bunias orientalis	*Brassicaceae*	18	1	10	29
Calendula officinalis	*Asteraceae*	9	12	8	29
Camelina sativa	*Brassicaceae*	9	10	10	29
Conyza sumatrensis	*Asteraceae*	17	4	8	29
Epilobium ciliatum	*Onagraceae*	21	1	7	29
Ipomoea purpurea	*Convolvulaceae*	14	11	4	29
Malus domestica	*Rosaceae*	21	7	1	29
Pisum sativum	*Fabaceae* (*Faboideae*)	7	16	6	29
Rudbeckia laciniata	*Asteraceae*	16	6	7	29
Trifolium hybridum	*Fabaceae* (*Faboideae*)	14	6	9	29
Anthriscus cerefolium	*Apiaceae*	8	11	9	28
Artemisia annua	*Asteraceae*	15	9	4	28
Buddleja davidii	*Scrophulariaceae*	16	4	8	28
Centranthus ruber	*Valerianaceae*	17	4	7	28
Chrysanthemum segetum	*Asteraceae*	9	7	12	28
Eschscholzia californica	*Papaveraceae*	8	12	8	28
Inula helenium	*Asteraceae*	16	2	10	28
Mahonia aquifolium	*Berberidaceae*	16	5	7	28
Malva sylvestris	*Malvaceae*	9	8	11	28
Paspalum distichum	*Poaceae*	18	2	8	28
Physocarpus opulifolius	*Rosaceae*	16	6	6	28
Phytolacca americana	*Phytolaccaceae*	18	4	6	28
Senecio inaequidens	*Asteraceae*	16	3	9	28
Sisymbrium altissimum	*Brassicaceae*	15	3	10	28
Armoracia rusticana	*Brassicaceae*	16	2	9	27
Conyza bonariensis	*Asteraceae*	18	2	7	27
Heracleum mantegazzianum	*Apiaceae*	20	1	6	27
Lens culinaris	*Fabaceae* (*Faboideae*)	8	16	3	27
Linum usitatissimum	*Linaceae*	8	12	7	27
Melissa officinalis	*Lamiaceae*	12	7	8	27
Parthenocissus quinquefolia	*Vitaceae*	15	3	9	27
Rapistrum rugosum	*Brassicaceae*	10	8	9	27
Setaria verticillata	*Poaceae*	10	10	7	27
Symphoricarpos albus	*Caprifoliaceae*	17	3	7	27

Species	Family	Naturalized	Casual	Unspecified	Total
Centaurea cyanus	*Asteraceae*	15	2	9	26
Chenopodium album	*Amaranthaceae*	11	10	5	26
Digitaria sanguinalis	*Poaceae*	10	5	11	26
Geranium pyrenaicum	*Geraniaceae*	15	2	9	26
Hirschfeldia incana	*Brassicaceae*	9	8	9	26
Isatis tinctoria	*Brassicaceae*	12	5	9	26
Juglans regia	*Juglandaceae*	16	2	8	26
Lobularia maritima	*Brassicaceae*	9	8	9	26
Lonicera japonica	*Caprifoliaceae*	14	3	9	26
Narcissus pseudonarcissus	*Amaryllidaceae*	11	5	10	26
Populus × canadensis hyb.	*Salicaceae*	15	4	7	26
Sisymbrium loeselii	*Brassicaceae*	17	3	6	26
Vicia villosa	*Fabaceae* (*Faboideae*)	14	5	7	26
Vitis vinifera	*Vitaceae*	8	11	7	26

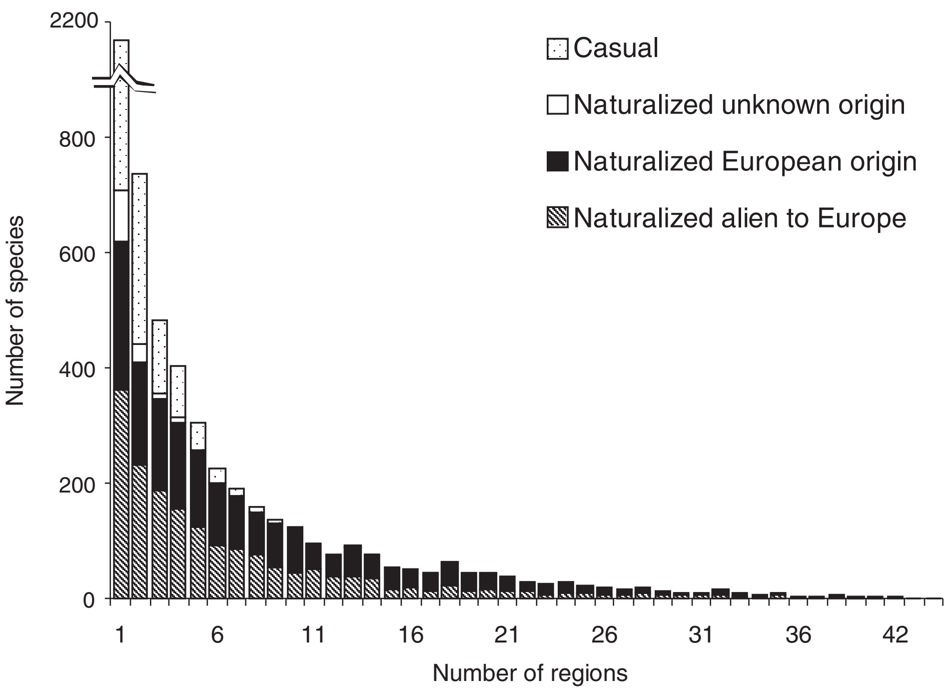

Fig 2. – Frequency distribution of range sizes of European alien plant species. Each bar represents the number of (i) casual species, (ii) naturalized species of unknown origin, (iii) naturalized species of European origin, and (iv) naturalized species from outside Europe, that are recorded from a given number of regions.

In addition, species that occur as archaeophytes in other parts of Europe may be classified as neophytes in Scandinavia since they have reached this region later due to the effect of distance from the source area and a colder climate in the north (Pyšek et al. 2005). Therefore, we believe that the high diversity of alien species in Scandinavia is reality rather than an artefact of research approaches.

There are 128 species recorded from more than a half of the countries considered (Table 2). The most common European alien species is *Conyza canadensis*, native to North America, occurring in 47 countries/regions (95.9%). Other species occurring in more than 80% of regions are *Helianthus tuberosus*, *Robinia pseudoacacia* (native to North America), *Amaranthus retroflexus*, *Datura stramonium*, *Lepidium virginicum* (North and Central America), *Galinsoga quadriradiata* (Central and South America), *Galinsoga parviflora*, *Matricaria discoidea* (South America), *Xanthium strumarium* (Eurasia), *Panicum miliaceum*, *Veronica persica* (Asia) and *Oenothera biennis* (probably originating somewhere in Europe but considered as an alien in most national checklists). These widely distributed aliens are naturalized in the vast majority of regions from which the information on invasion status is available, and the same is likely to be true for those where such assessment is missing (unspecified occurrences in Table 2). Notably, almost all of them are aliens *to* Europe, mostly originating from North and South America. In addition to *Oenothera biennis* (as described above), *Cymbalaria muralis*, *Medicago sativa* and *Lycium barbarum* (all 23 regions) are the most common species native to Europe. Most alien species have a relatively restricted European distribution at present (Fig. 2). Half of all naturalized species occur in four or fewer countries/regions, whereas 70% of non-naturalized species occur in only one region. The figures are biased by the inclusion of a moderate proportion of European natives, which, by definition, can only be alien in part of the continent. However, in many cases, these represent regional endemics which were not able to disperse away from their native ranges unaided due to geographical barriers (e.g., they include many Aegean and Alpine species now cultivated ornamentally), and therefore their native ranges tend to be small. The fact that so many aliens remain local may indicate that their distributions are strongly constrained by climatic and environmental factors, and evidence that the flora has a regional character, which may be influenced by climate to a limited extent, is presented below. Alternatively, for many (especially urban, agricultural or nitrophilic) species, there may yet be considerable opportunity for expansion. The distribution of range size is strongly log-normal, and 20 species are thus far recorded from at least 40 regions in total. Although the homogenization effect of alien species has been repeatedly suggested (McKinney 2004, Olden et al. 2004), this distribution pattern, with most of the species found only in a few countries (e.g., due to climatic or other environmental variables which govern biogeographic patterns), suggests that recruitment of alien species has increased floristic differentiation; such a differentiating effect of alien species was found for counties in Florida and California (Qian et al. 2008). On the contrary, increased spread in Europe seems to be inevitable and if the rare species become more abundant this could lead to floristic homogenization in the future. It is therefore difficult to predict what the effect of alien species on the floristic similarity of European regions will be and the scale must be considered in this assessment because alien species tend to have a more homogenizing (or less differentiating) effect with increasing distances between the administrative units compared (Qian et al. 2008).

Taxonomic affiliation

In terms of taxonomy, the European list is dominated by large global plant families which have a weedy tendency and have undergone major radiations in temperate regions. Therefore, in descending order, the highest diversities are found in the *Asteraceae*, *Poaceae*, *Rosaceae*, *Fabaceae* (subfamily *Faboideae*) and the *Brassicaceae* (Table 3). The *Rosaceae* is an obvious exception to the general rule since the majority of species introduced to Europe are boreo-temperate woody shrubs and trees. The only other predominantly woody family ranked in the top 20 is the *Pinaceae*. In total, alien species are from 213 families, almost twice as many as reported by Weber (1997).

At higher taxonomic levels, important alien family clusters are present in the orders *Asparagales*, *Ranunculales*, *Caryophyllales*, *Lamiales* and *Solanales*. At least in the Mediterranean alien flora, invasiveness is not directly related to phylogeny in a way consistent with inheritance at the evolutionary level (Lambdon 2008a). The patterns are often related to clades with high diversification rates (Magallón & Sanderson 2001) which is clearer under the systematic treatment of the Angiosperm Phylogeny Group than in some traditional taxonomies, since this treatment splits some major alien clades such as the *Liliales* and *Lamiales*, giving a truer representation of diversity. However, in some cases success may to be linked to frequent introduction. Certain family characteristics make the species valuable for human uses (e.g., the *Rosaceae* as fruit crops, the *Pinaceae* for timber and the *Lamiaceae* as herbs and ornamental plants). Also, families originating in distant regions (especially the New World) are likely to be later introductions and to be influenced by more recent import fashions. Those families which have diversified in Europe tend to have correspondingly greater numbers that are aliens of European origin.

There are 1567 genera which have alien members in European countries. As with the representation at higher taxonomic levels, the commonest genera (Table 4) tend to be globally-diverse ones comprising mainly urban and agricultural weeds (e.g., *Amaranthus*, *Chenopodium* and *Solanum*). However, the largest, *Cotoneaster*, comprises a variety of berry-producing shrubs predominantly from temperate Asia and almost exclusively introduced for ornamental purposes. Few naturalized *Cotoneaster* species are very abundant in Europe. The second ranked genus, *Oenothera*, is the most critically-difficult of all European taxa due to its almost complete inter-fertility (Mihulka & Pyšek 2001, Mihulka et al. 2006). Any two populations coming into contact rapidly give rise to a hybrid swarm, but the genotype tends to become true breeding after a few generations of isolation. Therefore, the number of species recognized is highly subjective.

Since genera are low-ranking taxonomic units, they are more likely to radiate within continents, and therefore there tends to be greater disparity between the number of species alien *to* Europe and alien *in* Europe. Only a few large genera which have successfully invaded (e.g., *Oxalis*, *Panicum*, *Helianthus*) are predominantly non-European, and Table 4 shows a considerable bias towards aliens native to part of the continent. This is particularly true because taxa with high diversification rates and which are transported efficiently by man tend to be annual weeds. A high proportion of the global weed flora originated in Europe, especially in the Mediterranean region, where agriculture has existed for many centuries, and from where it has been widely exported by human colonists (Guillerm 1991).

Table 3. – Taxonomic composition of the alien flora of Europe, according to the Angiosperm Phylogeny Group (Stevens 2001 onwards) and Mabberley (1997). Three sets of statistics are given: (1) the total number of alien species recorded; (2) the number of species naturalized within the continent (Natlzd); (3) the number of species known to be both naturalized and neophytes within the continent (Neoph). These are presented separately for all alien species *in* Europe and two subgroups distinguished: aliens of European origin and aliens *to* Europe; note that the native distribution status could not be assigned to a small number of species, therefore the total number of aliens in Europe is in some cases higher than the sum of the two subgroups. Note that the rows can be read like a phylogenetic tree, and the evolutionary clusters with concentrations of alien species become obvious. Clades which display high incidences of aliens are highlighted in bold and shaded.

Class/Order	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
LYCOPSIDA										
Lycopodiales	*Selaginellaceae*	2	2	1	0	0	0	1	1	1
Pteridopsida										
Ophioglossales	*Ophioglossaceae*	1	0	0	0	0	0	0	0	0
Osmundales	*Osmundaceae*	1	0	0	1	0	0	0	0	0
Filicales	*Aspleniaceae*	3	1	0	3	1	0	0	0	0
	Athyriaceae	1	1	1	0	0	0	1	1	1
	Blechnaceae	5	4	2	1	1	0	4	3	2
	Cytheaceae	1	1	1	0	0	0	0	0	0
	Davalliaceae	2	1	1	0	0	0	0	0	0
	Dennstaedtiaceae	2	2	0	0	0	0	0	0	0
	Dicksoniaceae	1	1	1	0	0	0	1	1	1
	Hypolepidaceae	1	0	0	1	0	0	0	0	0
	Polypodiaceae	4	3	0	0	0	0	4	3	0
	Pteridaceae	7	7	3	2	2	2	5	5	1
	Thelypteridaceae	1	1	0	0	0	0	1	1	0
	Woodsiaceae	3	3	2	1	1	1	2	2	1
	Dryopteridaceae	9	8	2	4	4	0	5	4	2
	Adiantaceae	5	4	3	1	0	0	4	4	3
Salviniales	*Azollaceae*	2	2	2	0	0	0	2	2	2
	Salviniaceae	3	2	2	0	0	0	3	2	2
EQUISETOPSIDA										
Equisetales	*Equisetaceae*	4	3	1	4	3	1	0	0	0
CYCADOPSIDA										
Cycadales	*Zamiaceae*	2	2	0	0	0	0	2	2	0
	Cycadaceae	2	2	0	0	0	0	2	2	0
GINGKOPSIDA										
Gingkoales	*Ginkgoaceae*	1	0	0	0	0	0	1	0	0
GYMNOSPERMOPSIDA										
Pinales	*Taxaceae*	3	3	0	1	1	0	2	2	0
	Cephalotaxaceae	1	0	0	0	0	0	1	0	0
	Cupressaceae	**19**	**13**	**11**	2	1	1	**17**	**12**	**10**
	Pinaceae	**53**	**42**	**28**	**19**	**17**	**13**	**34**	**25**	**15**
	Taxodiaceae	4	1	0	0	0	0	4	1	0
	Araucariaceae	4	4	0	0	0	0	4	4	0
GNETOPSIDA										
Gnetales	*Ephedraceae*	2	1	0	1	0	0	1	1	0
PRO-DICOTYLEDONAE										
Nymphaeales	*Nymphaeaceae*	7	3	1	3	2	1	4	1	0
	Cabombaceae	1	1	1	0	0	0	1	1	1
Ceratophyllales	*Ceratophyllaceae*	3	1	1	2	1	1	1	0	0
Magnoliales	*Magnoliaceae*	4	1	0	0	0	0	4	1	0
Laurales	*Lauraceae*	5	5	2	2	2	0	3	3	2
	Calycanthaceae	2	0	0	0	0	0	2	0	0
Canellales	*Winteraceae*	1	0	0	0	0	0	1	0	0

Class/Order	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
Piperales	*Aristolochiaceae*	5	3	2	4	3	2	1	0	0
	Saururaceae	1	1	1	0	0	0	1	1	1
MONOCOTYLEDONAE										
Acorales	*Acoraceae*	2	2	2	0	0	0	2	2	2
Alismatales	*Juncaginaceae*	2	2	2	0	0	0	2	2	2
	Potamogetonaceae	5	2	1	5	2	1	0	0	0
	Alismataceae	11	6	5	5	2	1	6	4	4
	Aponogetonaceae	1	1	1	0	0	0	1	1	1
	Araceae	26	22	14	9	8	3	17	14	11
	Butomaceae	1	0	0	1	0	0	0	0	0
	Hydrocharitaceae	18	15	10	6	4	2	12	11	8
Dioscoreales	*Dioscoreaceae*	1	1	0	1	1	0	0	0	0
Liliales	*Smilacaceae*	3	2	1	3	2	1	0	0	0
	Melanthiaceae	1	0	0	1	0	0	0	0	0
	Liliaceae	21	18	14	13	11	7	8	7	7
	Colchicaceae	1	1	1	1	1	1	0	0	0
	Alstroemeriaceae	2	2	1	0	0	0	2	2	1
Orchidales	*Orchidaceae*	9	4	1	5	1	1	4	3	0
Asparagales	***Agavaceae***	**23**	**17**	**9**	0	0	0	**23**	**17**	**9**
	Ruscaceae	**15**	**10**	**3**	**8**	**6**	**3**	**7**	**4**	**0**
	Iridaceae	**92**	**77**	**32**	**36**	**32**	**13**	**56**	**45**	**19**
	Alliaceae	**34**	**27**	**13**	**22**	**18**	**10**	**12**	**9**	**3**
	Amaryllidaceae	**37**	**30**	**15**	**27**	**22**	**10**	**10**	**8**	**5**
	Asphodelaceae	**14**	**8**	**3**	**2**	**0**	**0**	**12**	**8**	**3**
	Hyacinthaceae	**35**	**32**	**21**	**29**	**28**	**20**	6	4	1
	Asparagaceae	4	4	2	1	1	0	3	3	2
	Agapanthaceae	1	1	1	0	0	0	1	1	1
	Hemerocallidaceae	3	2	2	2	1	1	1	1	1
Arecales	*Arecaceae*	14	11	4	1	1	0	13	10	4
Poales	***Cyperaceae***	**84**	**51**	**20**	**31**	**18**	**5**	**52**	**33**	**15**
	Poaceae	**597**	**295**	**192**	**257**	**159**	**99**	**340**	**136**	**93**
	Juncaceae	**29**	**20**	**10**	**17**	**13**	**5**	**12**	**7**	**5**
	Bromeliaceae	3	3	1	0	0	0	3	3	1
	Typhaceae	3	2	1	2	1	1	1	1	0
Commelinales	*Commelinaceae*	15	12	7	0	0	0	15	12	7
	Pontederiaceae	9	8	6	0	0	0	9	8	6
Zingiberales	*Musaceae*	2	1	0	0	0	0	2	1	0
	Zingiberaceae	3	3	1	0	0	0	3	3	1
	Cannaceae	4	2	1	0	0	0	4	2	1
EU-DICOTYLEDONAE										
Ranunculales	*Lardizabalaceae*	1	1	0	0	0	0	1	1	0
	Papaveraceae	**29**	**18**	**8**	**17**	**12**	**5**	**12**	**6**	**3**
	Ranunculaceae	**85**	**65**	**38**	**65**	**52**	**32**	**20**	**13**	**6**
	Fumariaceae	**29**	**22**	**7**	**21**	**16**	**5**	8	6	2
	Berberidaceae	16	12	6	2	1	1	14	11	5
Proteales	*Proteaceae*	5	5	3	0	0	0	5	5	3
	Platanaceae	3	3	2	1	1	1	2	2	1
	Nelumbonaceae	1	1	1	0	0	0	1	1	1
Buxales	*Buxaceae*	2	2	2	1	1	1	1	1	1
Gunnerales	*Gunneraceae*	2	2	1	0	0	0	2	2	1
Caryophyllales	*Droseraceae*	2	1	0	0	0	0	2	1	0
	Polygonaceae	**106**	**63**	**36**	**46**	**28**	**16**	**45**	**30**	**18**
	Plumbaginaceae	10	8	3	7	6	2	3	2	1
	Phytolaccaceae	8	8	6	0	0	0	8	8	6

Class/Order	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
	Nyctaginaceae	8	4	2	0	0	0	8	4	2
	Molluginaceae	2	2	1	1	1	0	1	1	1
	Frankeniaceae	2	1	0	2	1	0	0	0	0
	Caryophyllaceae	**156**	**80**	**39**	**141**	**74**	**37**	**13**	**5**	**2**
	Amaranthaceae	**185**	**91**	**72**	**56**	**40**	**27**	**128**	**51**	**45**
	Cactaceae	**28**	**23**	**14**	0	0	0	**28**	**23**	**14**
	Aizoaceae	**28**	**22**	**10**	2	2	1	**26**	**20**	**9**
	Basellaceae	2	1	1	0	0	0	2	1	1
	Portulacaceae	10	6	3	2	1	0	8	5	3
	Tetragoniaceae	1	1	1	0	0	0	1	1	1
	Simmondsiaceae	1	0	0	0	0	0	1	0	0
	Tamaricaceae	9	3	2	7	3	2	2	0	0
Santalales	*Santalaceae*	2	1	1	1	1	1	1	0	0
Saxifragales	*Hamamelidaceae*	2	1	1	0	0	0	2	1	1
	Crassulaceae	**74**	**57**	**36**	**31**	**28**	**19**	**35**	**23**	**15**
	Saxifragaceae	**31**	**24**	**14**	**12**	**12**	**8**	**17**	**12**	**6**
	Grossulariaceae	12	12	8	5	5	5	6	6	3
	Haloragaceae	3	3	2	0	0	0	3	3	2
	Paeoniaceae	2	2	1	2	2	1	0	0	0
Vitales	*Vitaceae*	11	9	5	1	1	0	10	8	5
Crossosmatales	*Staphyleaceae*	1	1	1	1	1	1	0	0	0
Geraniales	***Geraniaceae***	**66**	**43**	**25**	**30**	**21**	**15**	**34**	**21**	**10**
Myrtales	***Onagraceae***	**112**	**68**	**43**	**10**	**8**	**4**	**80**	**45**	**36**
	Myrtaceae	**25**	**23**	**11**	1	1	0	**24**	**22**	**11**
	Lythraceae	**25**	**14**	**5**	6	3	2	**14**	**8**	**2**
	Melastomataceae	1	1	1	0	0	0	1	1	1
	Combretaceae	1	1	0	0	0	0	1	1	0
	Punicaceae	1	1	1	0	0	0	1	1	1
Zygophyllales	*Zygophyllaceae*	3	3	2	2	2	2	0	0	0
Celastrales	*Celastraceae*	9	7	4	3	3	1	5	4	3
Malpighiales	***Hypericaceae***	**20**	**16**	**7**	**12**	**10**	**4**	**6**	**6**	**3**
	Euphorbiaceae	**70**	**50**	**29**	**34**	**27**	**16**	**26**	**20**	**12**
	Salicaceae	**54**	**42**	**18**	**24**	**21**	**6**	**22**	**17**	**11**
	Violaceae	**22**	**12**	**2**	7	4	1	**15**	**8**	**1**
	Linaceae	9	6	5	7	5	4	2	1	1
	Ochnaceae	2	2	1	0	0	0	2	2	1
	Passifloraceae	7	5	4	0	0	0	7	5	4
	Elatinaceae	5	3	1	1	0	0	2	2	1
Oxalidales	***Oxalidaceae***	**20**	**16**	**10**	1	1	1	**16**	**13**	**9**
Fabales	*Fabaceae*: *Cercideae*	0	0	0	1	1	1	0	0	0
	Fabaceae*: *Caesalpinioideae	**30**	**21**	**6**	1	1	1	**28**	**19**	**4**
	Fabaceae*: *Mimosoideae	**29**	**21**	**16**	0	0	0	**29**	**21**	**16**
	Fabaceae*: *Faboideae	**323**	**181**	**124**	**233**	**138**	**101**	**82**	**40**	**22**
	Polygalaceae	2	2	1	0	0	0	2	2	1
Rosales	*Urticaceae*	19	12	5	12	10	4	5	2	1
	Elaeagnaceae	8	7	5	2	2	2	5	4	2
	Moraceae	14	9	4	1	1	0	13	8	4
	Ulmaceae	9	6	5	6	5	4	3	1	1
	Cannabaceae	5	4	2	0	0	0	5	4	2
	Rhamnaceae	4	3	1	2	2	1	2	1	0

Class/Order	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
	Rosaceae	**363**	**274**	**120**	**134**	**93**	**44**	**212**	**176**	**76**
Cucurbitales	*Cucurbitaceae*	23	16	13	5	4	4	18	12	9
	Begoniaceae	3	2	0	0	0	0	3	2	0
	Datiscaceae	1	0	0	0	0	0	1	0	0
	Coriariaceae	1	0	0	1	0	0	0	0	0
	Corynocarpaceae	1	1	0	0	0	0	1	1	0
Fagales	*Myricaceae*	3	3	1	0	0	0	2	2	1
	Betulaceae	16	12	6	12	11	6	3	1	0
	Casuarinaceae	2	1	1	0	0	0	2	1	1
	Juglandaceae	9	8	5	2	2	1	7	6	4
	Nothofagaceae	3	2	0	0	0	0	3	2	0
	Fagaceae	17	14	6	11	10	4	6	4	2
Brassicales	*Tropaeolaceae*	4	3	1	0	0	0	4	3	1
	Resedaceae	8	6	4	6	5	3	0	0	0
	Caricaceae	1	1	0	0	0	0	1	1	0
	Capparaceae	7	2	1	2	1	1	4	1	0
	Brassicaceae	**247**	**146**	**102**	**174**	**127**	**87**	**50**	**17**	**14**
Malvales	*Thymelaeaceae*	4	3	1	3	2	0	1	1	1
	Malvaceae	**69**	**41**	**20**	**25**	**17**	**12**	**39**	**21**	**8**
	Cistaceae	9	7	3	6	4	2	0	0	0
	Tiliaceae	7	3	2	3	2	2	3	1	0
Sapindales	*Anacardiaceae*	10	7	6	1	1	1	9	6	5
	Meliaceae	1	1	1	0	0	0	1	1	1
	Rutaceae	17	12	4	2	2	1	12	7	3
	Sapindaceae	23	15	14	7	6	6	15	9	8
	Simaroubaceae	1	1	1	0	0	0	1	1	1
Cornales	*Cornaceae*	7	5	3	2	2	1	5	3	2
	Hydrangeaceae	8	4	3	1	1	1	7	3	2
	Loasaceae	2	0	0	0	0	0	2	0	0
Ericales	*Myrsinaceae*	1	1	0	0	0	0	1	1	0
	Sarraceniaceae	1	1	0	0	0	0	1	1	0
	Ebenaceae	3	2	1	0	0	0	3	2	1
	Styracaceae	1	1	1	1	1	1	0	0	0
	Sapotaceae	1	1	0	0	0	0	1	1	0
	Polemoniaceae	10	5	5	1	1	1	9	4	4
	Primulaceae	**29**	**18**	**8**	**18**	**11**	**5**	**9**	**7**	**3**
	Ericaceae	**42**	**36**	**17**	**20**	**17**	**11**	**20**	**18**	**6**
	Balsaminaceae	9	6	6	1	0	0	8	6	6
	Actinidiaceae	2	1	0	0	0	0	2	1	0
	Theaceae	2	1	0	0	0	0	2	1	0
	Clethraceae	2	2	2	0	0	0	2	2	2
Gentianales	***Apocynaceae***	**20**	**16**	**10**	8	7	4	**12**	**9**	**6**
	Rubiaceae	**39**	**21**	**10**	**27**	**16**	**8**	5	3	2
	Gentianaceae	11	8	2	8	6	2	2	2	0
Lamiales	*Gesneriaceae*	1	0	0	1	0	0	0	0	0
	Bignoniaceae	**15**	**15**	**6**	0	0	0	**15**	**15**	**6**
	Verbenaceae	**25**	**14**	**7**	3	2	1	**22**	**12**	**6**
	Boraginaceae	**105**	**69**	**41**	**63**	**47**	**30**	**26**	**18**	**10**
	Lamiaceae	**165**	**102**	**52**	**97**	**69**	**34**	**55**	**29**	**17**
	Plantaginaceae	**132**	**84**	**31**	**82**	**58**	**23**	**38**	**21**	**7**
	Scrophulariaceae	**45**	**26**	**16**	**24**	**14**	**10**	**14**	**10**	**5**
	Orobanchaceae	**34**	**24**	**7**	**26**	**18**	**5**	5	5	2
	Phrymaceae	12	10	4	0	0	0	11	10	4
	Pedaliaceae	1	1	1	0	0	0	1	1	1

Class/Order	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
	Oleaceae	25	20	15	6	5	5	19	15	10
	Martyniaceae	2	1	1	0	0	0	2	1	1
	Linderniaceae	3	2	1	1	0	0	2	2	1
	Hydrophyllaceae	8	2	2	0	0	0	8	2	2
	Calceolariaceae	3	1	1	0	0	0	3	1	1
	Acanthaceae	12	9	4	2	2	1	10	7	3
	Lentibulariaceae	4	1	0	4	1	0	0	0	0
Solanales	***Solanaceae***	**107**	**66**	**45**	**12**	**11**	**6**	**88**	**53**	**39**
	Convolvulaceae	**45**	**29**	**18**	**16**	**13**	**7**	**24**	**14**	**11**
Aquifoliales	*Aquifoliaceae*	2	1	0	1	0	0	1	1	0
Apiales	***Apiaceae***	**143**	**87**	**44**	**103**	**64**	**33**	**31**	**20**	**10**
	Araliaceae	9	9	5	3	3	2	6	6	3
	Pittosporaceae	6	6	4	0	0	0	6	6	4
Asterales	*Menyanthaceae*	1	1	1	1	1	1	0	0	0
	Asteraceae	**692**	**424**	**283**	**334**	**225**	**144**	**334**	**193**	**138**
	Campanulaceae	**41**	**31**	**23**	**30**	**26**	**20**	9	5	3
Dipsacales	*Adoxaceae*	1	0	0	1	0	0	0	0	0
	Valerianaceae	**17**	**12**	**4**	**15**	**11**	**4**	1	0	0
	Caprifoliaceae	**35**	**29**	**23**	**14**	**14**	**10**	**20**	**15**	**13**
	Dipsacaceae	**21**	**12**	**9**	**15**	**10**	**8**	2	1	1

Table 4. – Most represented genera in the alien flora of Europe. Genera with at least 10 species are shown, listed alphabetically. Three sets of statistics are given: (1) the total number of alien species recorded; (2) the number of species naturalized within the continent (Natlzd); (3) the number of species known to be both naturalized and neophytes within the continent (Neoph). These are presented separately for all alien species *in* Europe and two subgroups distinguished: aliens of European origin and aliens *to* Europe; note that the native distribution status could not be assigned to a small number of species, therefore the total number of aliens in Europe is in some cases higher than the sum of the two subgroups.

Genus	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
Abies	*Pinaceae*	13	10	6	4	3	3	9	7	3
Acacia	*Fabaceae* (*Mimosoideae*)	20	15	13	0	0	0	20	15	13
Acer	*Sapindaceae*	12	8	8	6	5	5	5	3	3
Achillea	*Asteraceae*	17	8	7	15	7	6	1	1	1
Aegilops	*Poaceae*	10	3	3	7	3	3	3	0	0
Agrostis	*Poaceae*	15	7	4	8	5	2	7	2	2
Alchemilla	*Rosaceae*	24	15	4	22	14	4	2	1	0
Allium	*Alliaceae*	29	23	11	21	17	10	8	6	1
Aloë	*Asphodelaceae*	10	6	3	0	0	0	10	6	3
Alyssum	*Brassicaceae*	15	5	3	10	4	3	3	1	0
Amaranthus	*Amaranthaceae*	39	21	21	2	2	2	37	19	19
Anchusa	*Boraginaceae*	11	6	4	7	5	3	0	0	0
Anemone	*Ranunculaceae*	10	8	4	7	7	3	3	1	1
Anthemis	*Asteraceae*	10	6	3	9	5	2	1	1	1
Artemisia	*Asteraceae*	30	18	12	14	11	6	14	7	6
Aster	*Asteraceae*	24	15	13	3	2	2	21	13	11
Astragalus	*Fabaceae* (*Mimosoideae*)	16	4	3	10	4	3	5	0	0
Atriplex	*Amaranthaceae*	31	13	9	7	7	4	24	6	5
Avena	*Poaceae*	12	8	6	11	7	5	1	1	1
Berberis	*Berberidaceae*	10	9	4	1	1	1	9	8	3
Bidens	*Asteraceae*	11	9	8	1	1	1	10	8	7
Brassica	*Brassicaceae*	11	7	5	7	6	4	3	1	1

Genus	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
Bromus	*Poaceae*	37	22	11	24	15	8	13	7	3
Bupleurum	*Apiaceae*	11	5	2	9	4	2	1	0	0
Campanula	*Campanulaceae*	22	18	16	20	18	16	2	0	0
Cardamine	*Brassicaceae*	11	9	3	7	6	1	4	3	2
Carduus	*Asteraceae*	16	7	4	8	4	4	6	2	0
Carex	*Cyperaceae*	25	17	4	13	9	1	12	8	3
Centaurea	*Asteraceae*	51	25	20	42	22	18	7	3	2
Cerastium	*Caryophyllaceae*	14	9	6	13	8	6	1	1	0
Chenopodium	*Amaranthaceae*	52	27	19	22	17	9	29	10	10
Cirsium	*Asteraceae*	24	9	2	9	7	2	14	2	0
Conyza	*Asteraceae*	11	8	6	0	0	0	11	8	6
Cotoneaster	*Rosaceae*	75	65	17	4	3	1	70	62	16
Crassula	*Crassulaceae*	15	12	8	3	3	2	9	6	4
Crataegus	*Rosaceae*	19	16	7	9	7	3	9	8	4
Crepis	*Asteraceae*	17	14	9	15	12	7	2	2	2
Crocus	*Iridaceae*	18	16	3	16	14	2	2	2	1
Cuscuta	*Convolvulaceae*	12	10	6	7	5	4	4	4	2
Cyperus	*Cyperaceae*	35	20	9	9	4	3	26	16	6
Dianthus	*Caryophyllaceae*	22	10	7	21	10	7	1	0	0
Elymus	*Poaceae*	10	3	2	5	3	2	5	0	0
Epilobium	*Onagraceae*	30	13	4	6	5	1	20	8	3
Eragrostis	*Poaceae*	45	10	9	7	5	5	38	5	4
Erica	*Ericaceae*	10	8	4	9	7	4	1	1	0
Erodium	*Geraniaceae*	19	5	1	10	2	1	7	2	0
Erysimum	*Brassicaceae*	12	7	5	9	7	5	3	0	0
Eucalyptus	*Myrtaceae*	11	9	5	0	0	0	11	9	5
Euphorbia	*Euphorbiaceae*	47	33	17	29	23	14	10	7	2
Festuca	*Poaceae*	10	9	5	10	9	5	0	0	0
Fumaria	*Fumariaceae*	19	14	3	16	11	3	3	3	0
Galanthus	*Amaryllidaceae*	10	6	3	9	6	3	1	0	0
Galium	*Rubiaceae*	21	11	2	15	9	2	0	0	0
Genista	*Fabaceae* (*Mimosoideae*)	10	7	2	8	6	2	1	0	0
Geranium	*Geraniaceae*	32	29	18	20	19	14	12	10	4
Gypsophila	*Caryophyllaceae*	11	6	6	8	5	5	3	1	1
Helianthus	*Asteraceae*	16	9	9	0	0	0	16	9	9
Hieracium	*Asteraceae*	18	11	5	14	11	5	1	0	0
Hordeum	*Poaceae*	12	6	5	4	3	2	8	3	3
Hypericum	*Hypericaceae*	20	16	7	12	10	4	6	6	3
Ipomoea	*Convolvulaceae*	16	7	6	0	0	0	16	7	6
Iris	*Iridaceae*	23	20	10	12	11	7	11	9	3
Juncus	*Juncaceae*	22	14	9	11	8	4	11	6	5
Lathyrus	*Fabaceae* (*Mimosoideae*)	26	17	13	23	14	10	3	3	3
Lepidium	*Brassicaceae*	19	12	8	8	8	4	7	4	4
Linaria	*Plantaginaceae*	21	11	5	13	7	5	2	2	0
Lonicera	*Caprifoliaceae*	17	14	11	8	8	6	8	6	5
Lotus	*Fabaceae* (*Mimosoideae*)	11	10	6	9	9	5	1	0	0
Lupinus	*Fabaceae* (*Mimosoideae*)	13	9	5	5	3	3	7	5	2
Malva	*Malvaceae*	12	8	4	10	8	4	2	0	0
Medicago	*Fabaceae* (*Mimosoideae*)	32	13	11	27	11	10	4	2	1
Melilotus	*Fabaceae* (*Mimosoideae*)	14	10	7	13	10	7	1	0	0
Mentha	*Lamiaceae*	17	15	9	10	9	7	6	5	1
Myosotis	*Boraginaceae*	12	8	5	10	8	5	2	0	0
Narcissus	*Amaryllidaceae*	16	14	7	14	12	5	2	2	2
Nicotiana	*Solanaceae*	12	4	3	0	0	0	12	4	3

Genus	Family	Aliens *in* Europe			Aliens of European origin			Aliens *to* Europe		
		Total	Natlzd	Neoph	Total	Natlzd	Neoph	Total	Natlzd	Neoph
Oenothera	*Onagraceae*	64	49	33	3	2	2	43	32	28
Opuntia	*Cactaceae*	22	17	10	0	0	0	22	17	10
Orobanche	*Orobanchaceae*	16	10	3	10	6	2	4	4	1
Oxalis	*Oxalidaceae*	20	16	10	1	1	1	16	13	9
Panicum	*Poaceae*	22	9	5	1	1	0	21	8	5
Papaver	*Papaveraceae*	14	8	2	10	8	2	4	0	0
Paspalum	*Poaceae*	10	7	4	0	0	0	10	7	4
Pelargonium	*Geraniaceae*	13	9	6	0	0	0	13	9	6
Persicaria	*Polygonaceae*	24	19	8	7	4	1	16	14	7
Phleum	*Poaceae*	10	4	3	10	4	3	0	0	0
Physalis	*Solanaceae*	14	4	4	1	1	1	13	3	3
Pinus	*Pinaceae*	18	15	12	10	9	8	8	6	4
Plantago	*Plantaginaceae*	22	12	9	13	9	6	7	2	2
Poa	*Poaceae*	17	9	4	14	9	4	3	0	0
Polygonum	*Polygonaceae*	18	9	3	9	4	1	4	2	0
Populus	*Salicaceae*	21	16	10	5	4	3	16	12	7
Potentilla	*Rosaceae*	25	16	11	20	15	10	4	1	1
Prunus	*Rosaceae*	24	21	9	11	10	5	11	11	4
Quercus	*Fagaceae*	14	11	5	9	8	3	5	3	2
Ranunculus	*Ranunculaceae*	23	18	8	22	17	8	1	1	0
Rhododendron	*Ericaceae*	10	8	3	3	3	3	5	4	0
Ribes	*Grossulariaceae*	10	10	8	5	5	5	4	4	3
Rorippa	*Brassicaceae*	11	4	4	9	4	4	1	0	0
Rosa	*Rosaceae*	34	24	17	17	11	8	14	12	9
Rubus	*Rosaceae*	35	27	11	10	7	2	21	18	9
Rumex	*Polygonaceae*	45	20	14	26	16	12	11	3	2
Salix	*Salicaceae*	33	26	8	19	17	3	6	5	4
Salvia	*Lamiaceae*	27	14	12	16	8	8	9	5	4
Saxifraga	*Saxifragaceae*	16	15	9	12	12	8	3	3	1
Sedum	*Crassulaceae*	36	29	18	18	18	12	15	10	6
Senecio	*Asteraceae*	44	27	16	15	11	8	22	14	7
Senna	*Fabaceae* (*Caesalpinioideae*)	10	6	2	0	0	0	9	5	1
Setaria	*Poaceae*	13	9	5	3	3	1	10	6	4
Silene	*Caryophyllaceae*	47	21	9	40	18	8	5	2	1
Sisymbrium	*Brassicaceae*	17	10	8	13	9	7	2	1	1
Solanum	*Solanaceae*	45	29	20	3	2	1	35	25	19
Sorbus	*Rosaceae*	14	9	4	12	7	3	2	2	1
Spiraea	*Rosaceae*	21	18	12	5	5	3	16	13	9
Sporobolus	*Poaceae*	11	6	5	0	0	0	11	6	5
Stachys	*Lamiaceae*	11	7	1	8	6	1	2	1	0
Stipa	*Poaceae*	15	4	0	7	2	0	8	2	0
Symphytum	*Boraginaceae*	12	12	5	8	8	4	3	3	1
Trifolium	*Fabaceae* (*Faboideae*)	49	29	17	42	25	15	7	4	2
Trigonella	*Fabaceae* (*Faboideae*)	17	3	3	8	2	2	9	1	1
Triticum	*Poaceae*	10	5	5	6	4	4	4	1	1
Valerianella	*Valerianaceae*	10	8	2	9	7	2	0	0	0
Verbascum	*Scrophulariaceae*	27	13	8	19	11	7	1	0	0
Verbena	*Verbenaceae*	13	6	4	2	2	1	11	4	3
Veronica	*Plantaginaceae*	35	25	9	25	19	5	8	5	4
Vicia	*Fabaceae* (*Faboideae*)	33	20	13	29	19	13	3	1	0
Viola	*Violaceae*	22	12	2	7	4	1	15	8	1
Vulpia	*Poaceae*	11	6	3	7	5	3	4	1	0

Temporal trends

Using the minimum residence time approach, we obtained approximate European introduction dates for 1883 naturalized neophyte species, of which 954 were of European origin and 929 were alien *to* Europe. When the cumulative number of alien arrivals was plotted against time, the trend suggests a strongly exponential increase in the rate at which species capable of naturalization are being imported (Fig. 3). Of the naturalized neophytes alien to Europe, 50% arrived after 1899, 25% arrived after 1962 and 10% arrived after 1989. At present, approximately 6.2 such species are arriving each year. Aliens of European origin tended to start their spread historically earlier but the overall slope is very similar. In this case, 50% had first been detected in a non-native European country by 1876, and the most recent 10% had started to appear by 1969. Today there are approximately 5.3 European species, capable of naturalization, newly found in parts of the continent outside their native range each year. The slopes of the curves are likely to be exaggerated by the methodology's inherent tendency to underestimate true first appearances. This effect is likely to be greatest if the initial import was to a region where we have no records. Even al-

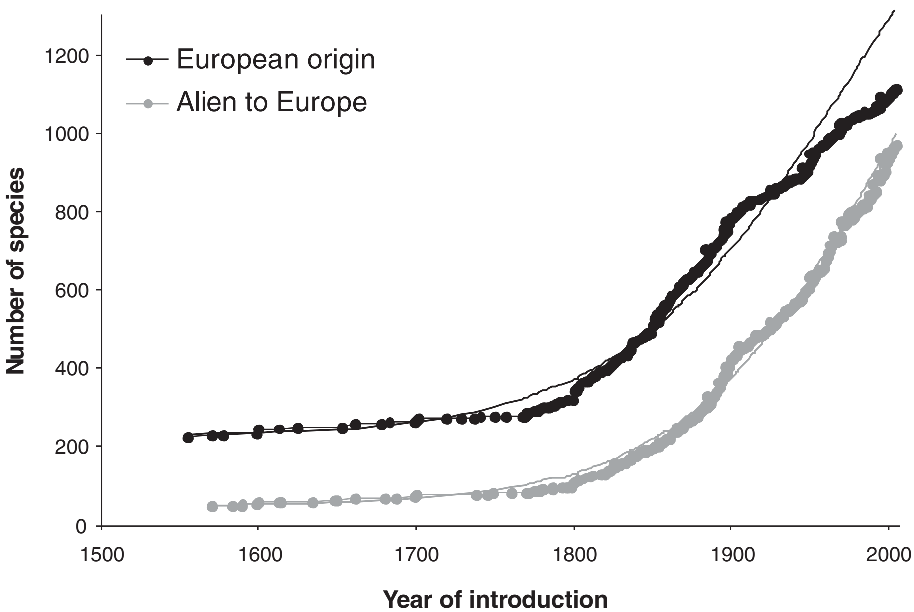

Fig. 3. – The number of species recorded as alien to at least one European country, in relation to their introduction date. Introduction dates are estimated from the minimum residence time, and species where this could not be evaluated with a reasonable degree of accuracy were excluded. Cumulative data are shown separately for species with native distribution area outside Europe: $T(p) = 0.0134y - 26.9$, $r^2 = 0.97$, $n = 929$; and those of European origin, but occurring as alien in other parts of the continent: $T(p) = 0.0113y - 22.40$, $r^2 = 0.95$, $n = 954$. Both relationships are approximately hyperbolic, and the following semi-logit transformation was applied to linearize the data: $T(p) = -\ln(p/(2-p))$, where p is the proportion of the total number of species introduced since 1500 AD and y is the year.

lowing for bias, it seems that the rate of new import has increased sharply throughout the two past centuries and is showing little sign of slowing down. This type of increase is consistent with the rate of accumulation of alien species in national floras, as documented by the pattern of arrival of neophytes to the Czech Republic (Pyšek et al. 2003b) and the United Kingdom (Walker 2007).

Distribution of alien species in European habitats

Information on habitat affinities is available for 30 countries/regions, although in some of them only a small proportion of naturalized aliens has been assigned to particular habitats. For Europe as a whole, 56.6% of recorded naturalized aliens *in* Europe and 57.7% *to* Europe, representing 2122 and 1027 species, respectively, were classified with respect to the occurrence in habitats. This provides a solid basis for evaluating distributions of alien plants in European habitats.

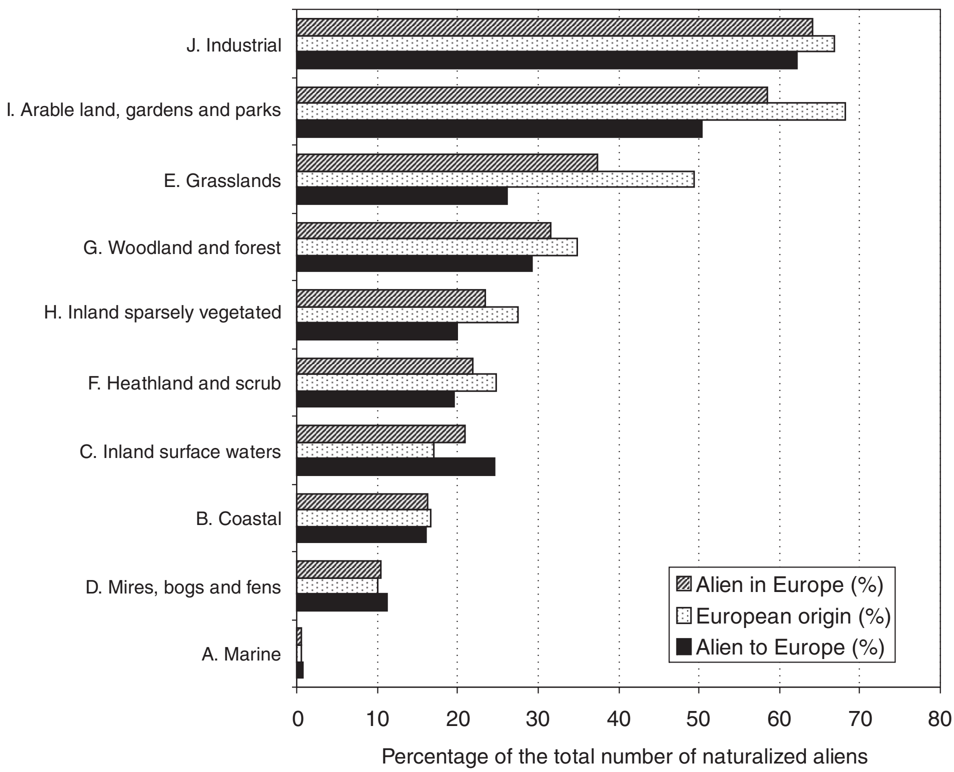

Fig. 4. – Distribution of European naturalized aliens in EUNIS habitats (see text for details on habitat classification). Aliens *to* Europe (n = 1059) are those originating outside Europe, aliens of European origin (n = 1027) are species native to some parts of the continent but alien to others, and aliens *in* Europe (n = 2122) comprises both categories, including those of undetermined provenance. See Table 5 for species numbers in habitats in individual regions. The sums of percentages across habitats do not equal 100% because some species were assigned to more than one habitat type. Habitats are ranked according to the percentage of the total number of naturalized aliens in Europe they harbour.

Table 5. – Distribution of naturalized alien plant species in European regions in EUNIS habitats (see text for details on habitat classification). Number of species for which habitat affinity was assigned and their percentage contribution to the total number of naturalized aliens is shown. Habitats not present in a country are indicated (-). Note that sums of species across habitats exceed the total number of species because some species were assigned to more than one habitat type.

Region	Number of species classified	% classified of the total	A. Marine	B. Coastal	C. Inland surface waters	D. Mires, bogs and fens	E. Grasslands	F. Heathland and scrub	G. woodland and forest	H. Inland sparsely vegetated	I. Arable land, gardens and parks	J. Industrial
Alien *in* Europe (total)	2122	56.6	12	343	444	220	793	462	668	497	1241	1361
European origin (total)	1027	56.8	5	171	174	102	508	254	357	283	701	686
Alien *to* Europe (total)	1059	57.7	7	170	260	118	276	206	310	211	533	658
Andorra	31	93.9	0	2	0	0	1	1	1	3	6	17
Austria	67	100.0	–	–	16	3	20	0	20	3	9	37
Azores	138	17.8	1	14	13	1	40	3	15	8	45	62
Baleares	59	27.3	0	3	0	3	2	0	2	6	5	68
Canary Islands	58	87.9	0	6	0	2	1	2	4	5	6	33
Cyprus	138	96.5	3	18	43	4	10	26	100	3	134	153
Czech Republic	387	82.5	–	–	122	93	743	158	464	227	174	0
Denmark	148	37.1	0	53	13	32	73	49	84	25	191	130
Estonia	125	100.0	0	15	11	7	28	0	42	0	125	114
Finland	38	32.2	0	18	1	10	19	15	21	5	56	34
Germany	587	91.0	0	6	89	7	423	1	86	21	236	233
Greece	124	92.5	6	68	46	1	46	30	58	14	83	157
Iceland	2	6.3	0	0	1	1	1	2	0	0	1	1
Italy	433	99.8	0	20	127	21	13	9	43	13	127	253
Latvia	195	64.4	0	8	40	6	15	34	37	0	333	201
Liechtenstein	84	94.4	–	–	0	2	13	26	23	17	19	53
Lithuania	257	99.6	0	46	25	18	80	0	146	109	249	235
Luxembourg	105	100.0	–	–	20	2	2	0	17	7	57	54
Madeira	368	57.5	0	22	23	3	23	5	18	28	175	158
Malta	61	52.1	0	2	0	0	0	2	0	22	33	24
Norway	157	27.3	0	61	22	32	82	64	86	25	203	140
Poland	131	48.0	0	3	0	2	40	43	27	40	54	77
Portugal	245	93.9	6	57	47	23	11	75	29	35	128	156
Republic of Ireland	352	96.7	3	48	28	14	41	123	85	18	89	192
Romania	108	99.1	0	1	6	3	11	0	4	7	18	67
Spain	441	89.1	0	30	13	42	7	4	26	38	95	327
Sweden	265	32.7	3	83	30	49	117	85	128	48	323	232
Switzerland	98	100.0	–	–	21	11	18	4	26	22	9	46
Turkey	73	76.8	0	10	9	0	5	5	9	21	34	38
United Kingdom	420	32.7	4	54	40	2	37	91	79	49	284	213

All European regions display fairly consistent patterns of habitat occupancy (Table 5.). Human made habitats (industrial habitats and arable land, parks and gardens) harbour most alien species, which accords with available national and continental analyses of the representation of alien species in vegetation (Chytrý et al. 2005, 2008a, b, Sádlo et al. 2007). Of all naturalized aliens present *in* Europe, 64.1% occur in industrial habitats and 58.5% on arable land and in parks and gardens. Grasslands and woodlands are also highly invaded, with 37.4 and 31.5%, respectively, of all naturalized aliens *in* Europe present in these habitats. Mires, bogs and fens are least invaded of terrestrial habitats; only approximately 10% of aliens *in* Europe occur there. In marine habitats, only 12 vascular plant species were recorded (7 of them alien *to* Europe), representing 0.5% of all species (Fig. 4), the only truly marine species being *Halophila stipulacea*; others are saltmarsh species with only three of these specialized to the habitat (*Spartina anglica*, *S.* ×*townsendii*, *Cochlearia officinalis*).

Aliens *in* Europe on average occur in more habitat types than aliens *to* Europe, as indicated by taller bars on Fig. 4. The mean number of habitat types for aliens which have part of their native range in Europe is 2.4 (± 1.6 standard error), compared with 2.1 (± 1.7 standard error) for those which are alien *to* Europe. This difference is significant, P = 0.03, based on a generalized linear model (procedure Genmod, SAS Institute inc.), which assumed a Poisson distribution (log link function), and where European native status (native or non-native) was nested within country/region to control for artefacts caused by range size. It has been shown that widespread species tend to occur in more habitats because they are (by definition) exposed to a greater variety of environments (Kühn et al. 2004, Lambdon 2008b), but since our analysis only looked for an effect operating within individual regions, this mechanistic bias is much reduced. The small effect of origin on the number of habitats may therefore be better interpreted in terms of greater preadaptation of aliens originating in other parts of Europe to a wider range of European habitats – these species seem to profit from a better habitat match compared to extra-European aliens, which need to adapt to the character of European habitats during the invasion process. Earlier invasion, and hence longer residence times of species with native distribution in Europe (Pyšek et al. 2003b) is also likely to have contributed to this pattern since species with longer residence times tend to be more widespread (Rejmánek 2000, Pyšek & Jarošík 2005).

Pathways of introduction of alien plants to Europe

Intentional introductions to Europe (68.2% of the total number of naturalized aliens) prevail over unintentional (37.2%) and both groups of aliens, *in* Europe and *to* Europe do not differ in their proportional contribution of individual pathways (Table 6). Ornamental and horticultural introductions escaped from cultivation account for the highest number of species, 52.2% of the total. Ornamentals constitute by far the largest and most diverse group of plant species entering Europe (Lambdon & Hulme 2006; P. Lambdon, unpublished) and elsewhere (Bell et al. 2003), so it is unlikely that they represent a greater risk "per import" than species introduced via other pathways. However, this does not reduce the importance of the management issues raised by the sheer number of naturalized species involved. Interestingly, contaminants on ornamental plants also constitute the most important pathway of entry to Europe for alien terrestrial invertebrates (Roques et al. 2008) and mosses and liverworts (Essl & Lambdon 2008). Only 11 species can, with certainty, be attributed to intentional releases in the wild. Among unintentional introductions in

Table 6. – Pathways of introduction for naturalized alien flora of Europe (see Appendix 1 for delimitation of the categories of aliens and definition of pathways). Note that summary numbers exceed the sums of individual pathways since some species are introduced by more than one pathway. Based on the classification system of Hulme et al. (2008a).

Pathway	Alien *in* Europe	European origin	Alien *to* Europe
Forestry	80	39	38
Amenity	248	119	119
Ornamental	1661	668	946
Agricultural	488	318	156
Horticultural	1018	589	415
Total escaped	**2371**	**1140**	**1211**
Released	**23**	**12**	**11**
TOTAL INTENTIONAL	2407	1160	1232
Seed contaminant	675	454	215
Mineral contaminant	129	83	43
Other commodity contaminant	287	151	145
Stowaway	363	118	235
Total transported	**1082**	**644**	**433**
Unaided	**157**	**107**	**45**
TOTAL UNINTENTIONAL	1425	846	565

Europe, contaminants of seed, mineral materials and other commodities are responsible for 1091 alien species introductions (76.6% of all species introduced unintentionally) and 363 species are assumed to have arrived as stowaways (directly associated with human transport but arriving independently of commodity, see Hulme et al. 2008a). It should be noted that the number of stowaways might be underestimated, because systematic recording is technically more difficult than inspecting commodities, such as seed admixtures (Mack 2000). Underestimation of the species number is likely to be even more pronounced in unaided species, which are assumed to arrive by means independent of man from a neighbouring region where they are not native (Hulme et al. 2008a); this group was poorly-recorded in most national datasets, but is likely to be a reasonably important source of colonization at a national level, except in island regions.

Native ranges of European aliens

Data on native ranges are based on the subset of 2271 naturalized species alien *in* Europe from the limited number of nine countries/regions with most reliable information. To get reasonable coverage of as many species as possible these countries were selected so as to cover the latitudinal gradient, including both northern (Austria, Estonia, Czech Republic, Poland, UK) and southern European countries/regions (Cyprus, France, Corsica, Greece). For 177 species (7.8%) the origin is obscure (i.e., truly wild populations have never been found), and the statistics are therefore based on 2094 species. These are somewhat biased towards species with a native range in part of Europe – 28.6% of all donor region records (attributing species that originate from more than one region to each of these regions) are from another part of Europe (Fig. 5). In terms of species numbers, this contribution is much higher (1113 species of the 2094 assessed in total, or 53.2%), because many species

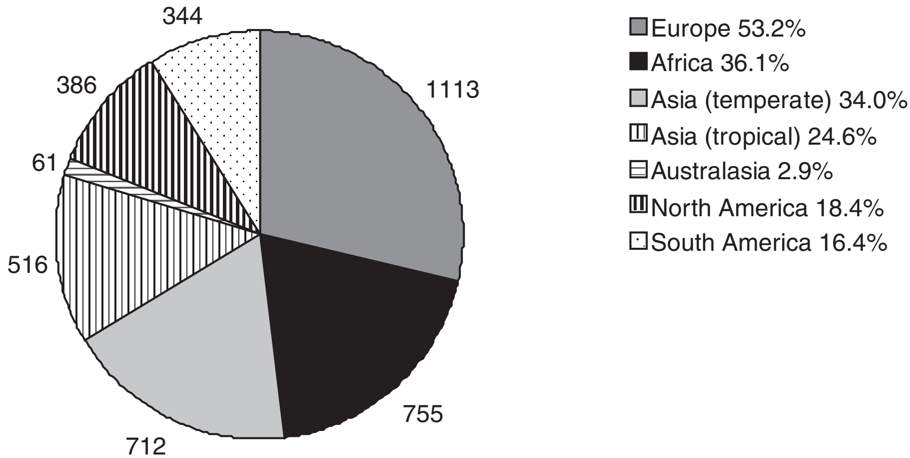

Fig. 5. – Donor regions of the alien flora of Europe. Based on 2271 naturalized aliens for which the region of origin was classified, including aliens with region of origin in Europe but alien to other parts of the continent. Species numbers are given in the pie-chart (those with native distribution in more than one continent were assigned to each of the continents), percentage contributions of regions to the total number of species follow their names.

originate in more than one continent. This is very much true for species of European origin: 648 of this group are trans-continental (i.e., also native to other major global regions). They mostly overlap their range with adjacent territories and especially the Eurasian super-continent: 65.2% are also native to Asia, 46.5% to Africa, only 3.9% to the Americas and 4.9% elsewhere. Considering aliens *to* Europe separately, 45.8% originate from North and South America, 45.9% are of Asian origin, 20.7% African and 5.3% are from Australasia. Therefore, long-distance human movements have lead to considerable increase in the representation of southern hemisphere species to Europe. This influx is particularly important because aliens with remote origins are more likely to interact differently with native communities. They are more likely to be taxonomically distant, share few specialist herbivores or pathogens and to have evolved new competitive strategies. The data are fairly consistent with the distribution of origins found previously in national floras: among aliens of the Czech Republic, 43.1% arrived from other parts of Europe, and 30.0% from Asia, although there is some regional variation as only 17.7% were from the Americas (Pyšek et al. 2002b).

One hundred and forty two aliens *in* Europe are a product of spontaneous hybridization involving one or both alien parents. This proportion is lower than recorded in thoroughly studied national floras; available data indicate hybrid origin in 184 taxa (13.3% of all aliens) in the flora of the Czech Republic, of which 15% are assumed to have immigrated but the majority (156 taxa) to have originated through hybridization in the country (Pyšek et al. 2002b). Stace (1991) reports the following numbers for the flora of British Isles: 69 crosses of alien species with native and 21 between two aliens (out of 1779 species covered). In a similar vein, 14.8% of the alien species (including archaeophytes and casual neophytes) of Germany are considered having evolved in Germany under human influence, many of them being hybrids (Kühn & Klotz 2003); considering naturalized neophytes only, the proportion would be higher.

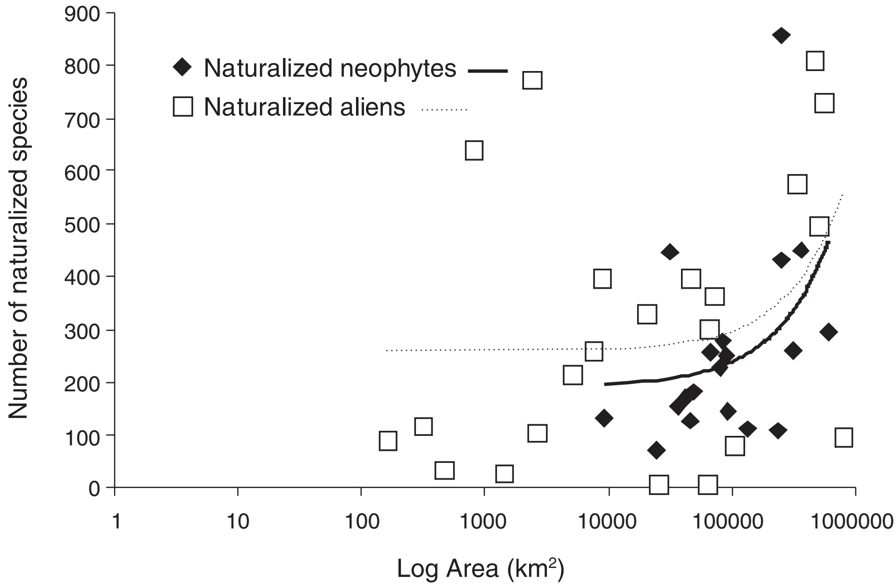

Fig. 6. – Species-area relationship for alien plants in Europe. Data for countries where the information on the number of naturalized neophytes is available (n = 19) are plotted separately from those where current state of knowledge precludes from reliable distinguishing from the total number of naturalized aliens (n = 22). Number of naturalized aliens = –203.9 5.1 + 1262.73 log(Area); F = 64.94; df = 1, 4339; P = 0.012; $r^2 = 0.14$. Based on the total numbers of aliens *in* Europe (see Methods). Note the semilog scale; numbers are square rooted for the statistical analysis but back transformed for the figure. See Table 1 for species numbers and data coverage.

Determinants of the level of invasion

The species-area relationship for naturalized alien plants *in* Europe indicates a linear increase of species numbers with increasing log area (Fig. 6), with no statistical difference between naturalized neophytes and all naturalized aliens (deletion test on common slope and intercept for square rooted numbers: F = 10.05; df = 2, 4339; P = 0.3646). This confirms that the effect of area needs to be held constant when comparing the effects of large-scale determinants of the level of invasion in countries/regions.

To obtain an insight into robust major factors determining the numbers of alien species in Europe, we analysed the effect of major geographical, climatic and economic factors on the number of naturalized neophytes in countries/regions. The minimal adequate model for naturalized neophytes explained 79.5% of the variability. There was a strong, direct positive effect of increasing precipitation on the number of naturalized aliens, and a weaker one of increasing area. In addition, the effect of precipitation significantly interacted with temperature, and the same held for area (Table 7). The effect of the interaction of precipitation with temperature was strongest at high mean annual temperature, weaker at intermediate and non-significant at low temperature. The effect of the interaction of area with temperature appeared significant only at the moderate annual temperature (Table 8). The numbers of naturalized neophytes thus appeared significantly affected by climatic and geographic, but not by economic factors. How temperature interacts with area is difficult to interpret, but the more important of the two interactions involving temperature, the one with precipitation, indicates that precipitation limits invasions by alien neophytes in warm regions.

Table 7. – Factors determining the number of naturalized neophytes in European regions. Minimal adequate model with standardized estimates, their standard errors (SE), t-tests (t), and significances (P) for the number of all naturalized neophytes (F = 10.06; df = 5, 13; P = 0.0004; R^2 = 0.79) is presented. Alien species numbers are square root transformed, latitude and longitude centered, and area and human population density log transformed. The groups of factors are in bold.

	Estimate	SE	t	P
Intercept	15.76	0.67	23.39	0.0000
Climatic factors:				
Precipitation	6.34	1.10	5.78	0.0001
Temperature	–1.18	0.85	–1.39	0.2
Temperature difference July–January	–	–	–	–
Geographical factors:				
Area	1.78	0.76	2.34	0.04
Latitude	–	–	–	–
$Latitude^2$	–	–	–	–
Longitude	–	–	–	–
$Longitude^2$	–	–	–	–
Economic factors:				
Human density	–	–	–	–
GPD	–	–	–	–
Road density	–	–	–	–
Interactions:				
Precipitation ×Temperature	4.58	1.09	4.21	0.001
Area × Temperature	–4.30	0.97	–4.45	0.0007

Table 8. – Factors determining the number of naturalized neophytes in European regions, interacting with mean annual temperature (°C). Simple slopes (estimates, standard errors SE, t-tests t and significances P) of the number of all naturalized neophytes on mean annual precipitation (mm) and area of region/country (km^2) for different values of temperature (mean, and mean plus and minus its sample standard deviation). Neophytes are square root, and area log transformed. All calculations are on centered values.

Interacting	Mean temperature 5.9 °C				Mean temperature 9.5 °C				Mean temperature 13.1 °C			
variable	Estimate	SE	t	P	Estimate	SE	t	P	Estimate	SE	t	P
Precipitation	0.0058	0.0056	1.04	0.30	0.017	0.0062	2.68	0.02	0.028	0.010	2.68	0.02
Area	6.79	4.12	1.65	0.12	6.51	2.31	2.82	0.01	3.75	3.14	1.19	0.25

Although repeatedly reported that alien species richness varies with geographical latitude or longitude (e.g., Sax 2001), the geographical coordinates did not play a role in determining the richness of neophytes. However, the geographical coordinates, which represent surrogates for environmental variables, are not particularly useful for explaining the observed patterns. Although many biological patterns are geographically structured, this is not because they are responding to geographical position but to environmental factors, which are themselves geographically structured. Therefore, including latitude and longitude in models introduces potential source of error: if they are highly correlated with some ecologically important environmental variables, as was the case in our study, they can corrupt the influence of environmental variables due to collinearity in the model. However, the presence of geographical variables did not affect our models, as the geographical coor-

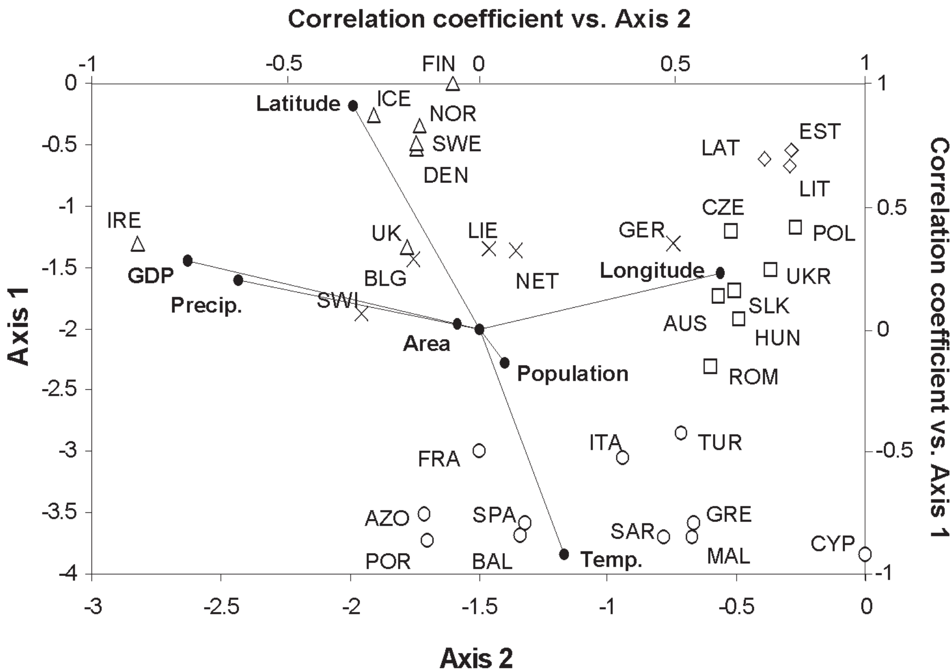

Fig. 7. – Results of a DCA to describe the major component of variation in the naturalized species assemblages of European regions. Centroids of the regions are plotted in relation to the first 2 ordination axes. Correlations between the axis scores and 6 major passive environmental variables are also represented (r coefficients). Region codes are as follows: △ Group 1 (north-western): DEN = Denmark, FIN = Finland, ICE = Iceland, IRE = Ireland, NOR = Norway, SWE = Sweden, UK = United Kingdom; × Group 2 (west-central): BLG = Belgium, GER = Germany, LIE = Liechtenstein, NET = Netherlands, SWI = Switzerland; ◇ Group 3 (Baltic) = EST = Estonia, LAT = Latvia, LIT = Lithuania; □ Group 4 (east-central): AUS = Austria, CZE = Czech Republic, HUN = Hungary, POL = Poland, ROM = Romania, SLK = Slovakia, UKR = Ukraine; ○ Group 5 (southern): AZO = Azores, BAL = Balearics, CYP = Cyprus, GRE = Greece, FRA = France, ITA = Italy, MAL = Malta, POR = Portugal, SAR = Sardinia, SPA = Spain, TUR = Turkey (European part).

dinates did not appear in the final MAM. Surprisingly, unlike in other studies (e.g., Vilà & Pujadas 2001, Pyšek et al. 2002a, Taylor & Irwin 2004), economic factors did not contribute to the explained variation.

Geographical distribution patterns of alien plant species in Europe

A DCA on the species assemblages showed only limited consistency between the national regions. The first ordination axis explained 11.7% of the total data set variance and the second explained 6.1%. All subsequent axes explained < 3.5% of the variance and were not given further consideration. However, although the joint variation component was relatively modest, it displayed a strong relationship with several basic variables (Fig. 7). Alien floras exhibited clear spatial trends, correlating strongly with both latitude and longitude

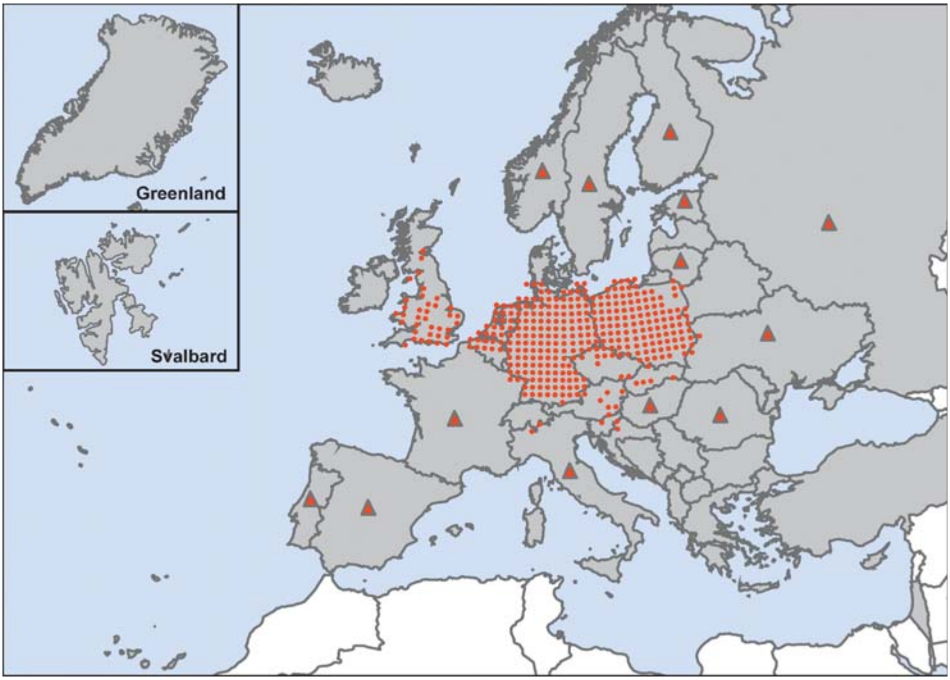

Fig. 8. – Distribution of *Prunus serotina* in Europe (example of the north-western distribution type, see text for the delimitation). The distribution is mapped using Common European Chorological Grid Reference System (CGRS) with the size of the mapping grid ca 50 × 50 km. Triangles indicate regions where the species is present but exact distribution data are not available. Based on distribution data collected by DAISIE (www.europe-aliens.org, DAISIE 2008).

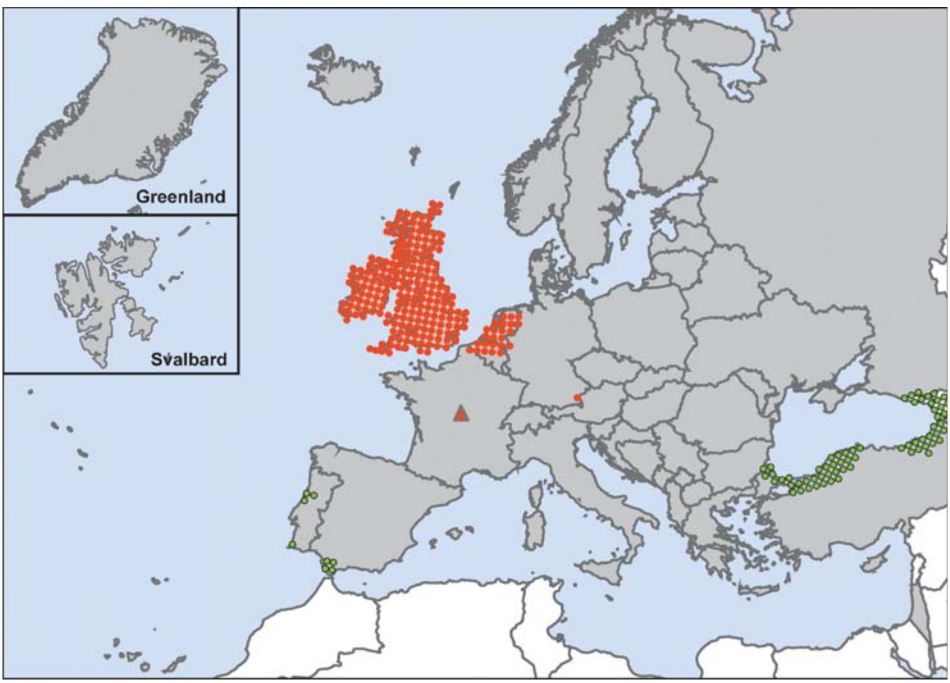

Fig. 9. – Distribution of *Rhododendron ponticum* in Europe, with western distribution type. The distribution is mapped using Common European Chorological Grid Reference System (CGRS) with the size of the mapping grid ca 50 × 50 km. Triangles indicate regions where the species is present but exact distribution data are not available. Native distribution in the east is in green. Based on distribution data collected by DAISIE (www.europe-aliens.org, DAISIE 2008).

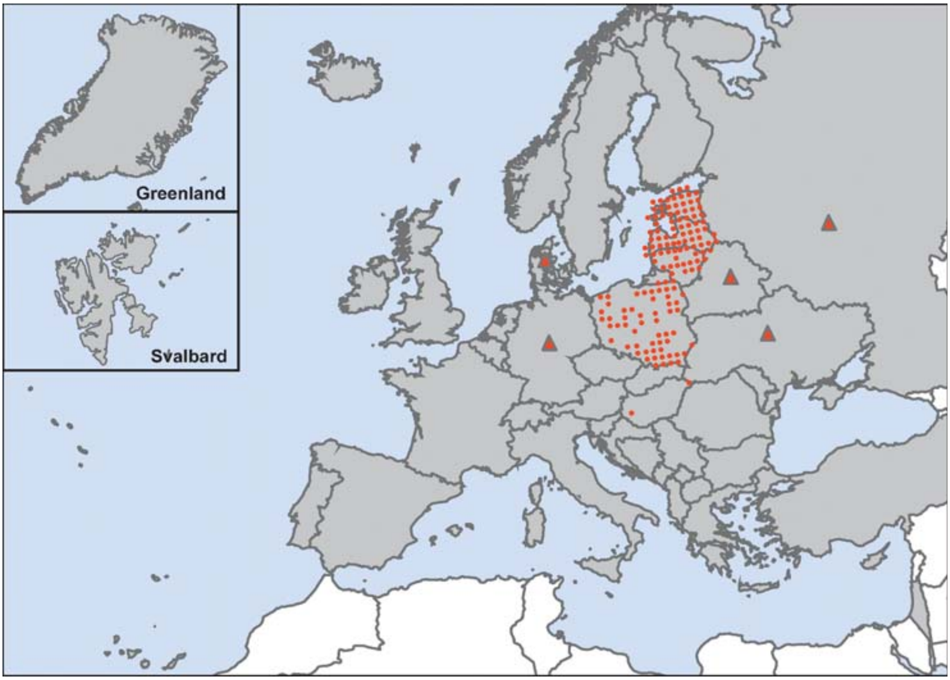

Fig. 10. – Distribution of *Heracleum sosnowskyi* in Europe (example of the Baltic distribution type, see text for the delimitation). The distribution is mapped using Common European Chorological Grid Reference System (CGRS) with the size of the mapping grid ca 50 × 50 km. Triangles indicate regions where the species is present but exact distribution data are not available. Based on data from Jahodová et al. 2007.

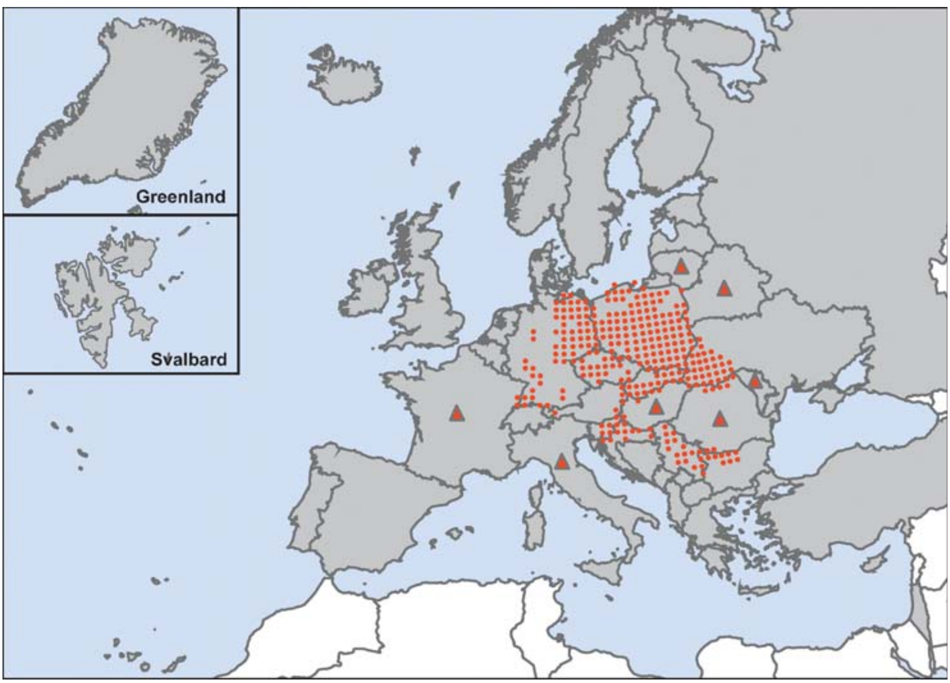

Fig. 11. – Distribution of *Echinocystis lobata* in Europe (example of the east-central distribution type, see text for the delimitation). The distribution is mapped using Common European Chorological Grid Reference System (CGRS) with the size of the mapping grid ca 50 × 50 km. Triangles indicate regions where the species is present but exact distribution data are not available. Native distribution is in green. Based on distribution data collected by DAISIE (www.europe-aliens.org, DAISIE 2008).

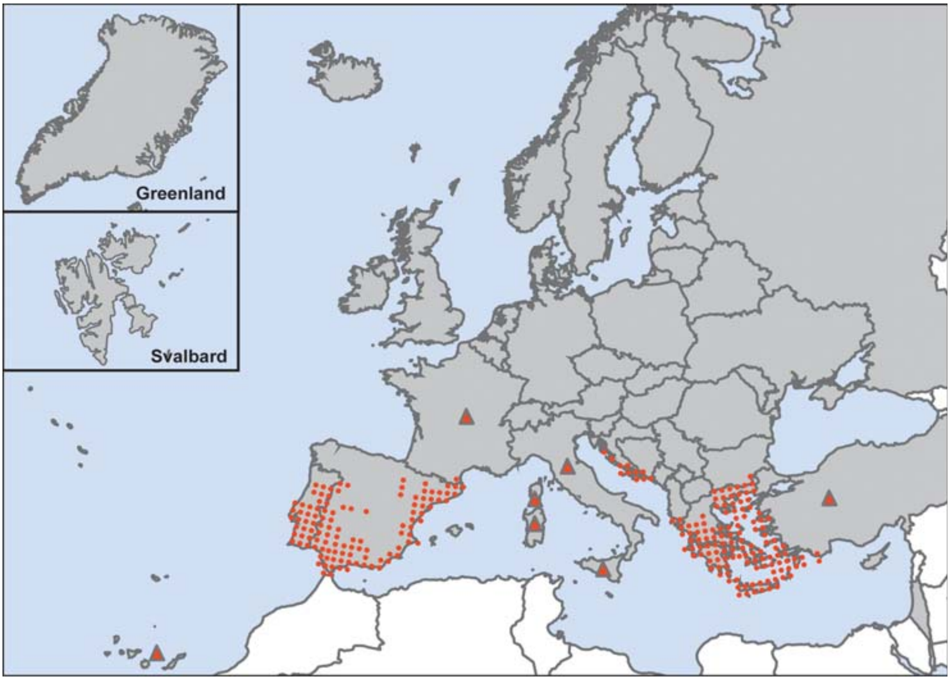

Fig. 12. – Distribution of *Opuntia ficus-indica* in Europe (example of the southern distribution type, see text for the delimitation). The distribution is mapped using Common European Chorological Grid Reference System (CGRS) with the size of the mapping grid ca 50 × 50 km. Triangles indicate regions where the species is present but exact distribution data are not available. Native distribution is in green. Based on distribution data collected by DAISIE (www.europe-aliens.org, DAISIE 2008).

($r > 0.9$) so that the plotted centroids were remarkably similar to the relative map positions of the countries. Using a cluster analysis to classify the assemblages, five major groups were identified, accounting for 40% of the explainable variation. These can be characterized as (1) north-western, comprising Scandinavia and the UK; (2) west-central, extending from Belgium and the Netherlands to Germany and Switzerland; (3) Baltic, including only the former Soviet Baltic states; (4) east-central, comprising the remainder of central and eastern Europe; (5) southern, covering the entire Mediterranean region. Some prominent European alien invaders can be used to illustrate the outlined biogeographical zones: *Prunus serotina* as a representative of the north-western (Fig. 8), *Rhododendron ponticum* of its western part (Fig. 9), *Heracleum sosnowskyi* of the Baltic (Fig. 10), *Echinocystis lobata* of the east-central (Fig. 11) and *Opuntia ficus-indica* of the southern distribution type (Fig. 12).

The main drivers behind this biogeographical segregation are less easy to unravel. It is likely that the patterns arise partly for scientific reasons, due to regional differences in the approach to botanical recording, but there are almost certainly strong cultural and climatic influences. GDP, and mean annual rainfall and temperature were also correlated strongly with one of the ordination axes ($r > 0.6$), but each of these factors is highly confounded with either latitudinal or longitudinal gradients. Country area and human population had poor ex-

Table 9. The ten largest alien genera in each of five biogeographic zones identified by cluster analysis of the regional species assemblages. The number of alien species present is indicated in parentheses.

Rank	North-western	West-central	Baltic	East-central	Southern
1	*Oenothera* (64)	*Chenopodium* (39)	*Chenopodium* (17)	*Cotoneaster* (66)	*Oenothera* (23)
2	*Eragrostis* (48)	*Oenothera* (36)	*Atriplex* (15)	*Salix* (27)	*Solanum* (21)
3	*Chenopodium* (56)	*Amaranthus* (32)	*Bromus* (14)	*Senecio* (25)	*Amaranthus* (20)
4	*Amaranthus* (49)	*Rumex* (24)	*Artemisia* (13)	*Chenopodium* (25)	*Acacia* (14)
5	*Trifolium* (57)	*Bromus* (23)	*Vicia* (12)	*Bromus* (22)	*Opuntia* (13)
6	*Centaurea* (55)	*Solanum* (23)	*Silene* (11)	*Rumex* (20)	*Silene* (12)
7	*Bromus* (41)	*Centaurea* (22)	*Amaranthus* (11)	*Allium* (18)	*Cyperus* (12)
8	*Geranium* (34)	*Silene* (22)	*Potentilla* (11)	*Amaranthus* (17)	*Persicaria* (11)
9	*Vicia* (45)	*Euphorbia* (21)	*Sedum* (10)	*Epilobium* (17)	*Trifolium* (11)
10	*Silene* (52)	*Trifolium* (21)	*Salvia* (10)	*Euphorbia* (16)	*Aster* (10)

planatory power, suggesting that factors associated with population density (e.g., urbanization) are minor determinants. Bioclimatic constraints, dictating the suitability of species to the physical environment, may be of primary importance. The clustering patterns cut across some European bioclimatic zones such as those identified by European Topic Centre on Biological Diversity (http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=839), although this is partly because our level of detail is restricted to national boundaries. Cultural factors such as regional trade links and traditional local preferences for crop, forestry and ornamental species, may also be important by influencing the introduced species pool.

Despite these regional differences, it is perhaps more striking to note the high level of uniformity across the alien floras of the continent. More detailed analyses show few distinctions between the alien species assemblages of the five biogeographical zones. For all five assemblages, the dominant families and geographical regions of origin were not substantially different from those displayed for the whole of Europe. The dominant genera were also similar across the zones (Table 9), although the southern assemblage was most distinct. It contained lower numbers of species in the temperate weedy genera such as *Chenopodium* and a stronger representation of genera with a tropical or New World bias (e.g., *Acacia*, *Opuntia*). This assemblage coincides with the Mediterranean region, which has a particularly contrasting climate compared with the rest of Europe, showing an inverted stress period (summer drought rather than winter frost and snow) and is generally warmer and/or drier than elsewhere (Blondel & Aronson 1999). Many of the common weeds alien within Europe are also native to the Mediterranean, and therefore are excluded from the alien assemblage. The east-central zone was most influenced by temperate genera (e.g., *Cotoneaster*, *Salix*), whilst the remaining three assemblages were very similar in taxonomic composition.

This uniformity implies either a high degree of homogeneity (the same species represented everywhere) or idiosyncracy (entirely different species represented everywhere). Floristic homogenization is a trend increasing globally, prompting widespread concerns over degradation of regional distinctiveness and threats to local biodiversity (McKinney 2004, Olden et al. 2004, Kühn & Klotz 2006, Castro et al. 2007). So, to what extent is the European alien flora affected by homogenization? Formally, the distribution patterns of alien species in Europe can be classified into four groups: (1) widespread: naturalized across much of the continent; (2) regionally-common: naturalized consistently across a major biogeographical zone; (3) sporadic: occurring rarely and inconsistently across several biogeographic zones; (4) local: naturalized in only a small part of Europe. A more detailed level of regional distribution data would be required to correctly assign species to these, although some approximate statistics can be inferred. Given that some countries and species were excluded from the ordination analysis due to insufficient information on status, the total number of naturalized taxa assessed was 2636. Of these, only 196 approximate to the "regionally-common" category (on the basis that they were naturalized in at least 5 countries but restricted to no more than two zones). Most of them (142 species) were associated with the southern biogeographical zone, with many fewer (30–60 species) associated with the other zones. Approximately 448 species could be considered "widespread" (occurring in at least 3 zones and 5 countries), with 76 occurring in all 5 biogeographical zones. This indicates that the homogeneous component represents a minority, albeit a substantial one. The remainder, and the considerable majority, are therefore "sporadic" or "local", and largely represent idiosyncratic occurrences, thus promoting differentiation (see Qian et al. 2008).

State of the art: the role of DAISIE project

Flora Europaea (Tutin et al. 1964–1980), the last published continental treatment of the flora of Europe, considered alien species but the data for individual countries were biased by a high degree of imprecision. The major discrepancies concern the invasion status of aliens in individual countries where more than 50% of species can be incorrectly classified as shown for the Czech Republic (Pyšek 2003). Therefore, Flora Europaea could be, with careful interpretation, used for identifying robust patterns based on species numbers, but not for in-depth analyses of invasion patterns across Europe, namely for studies on the naturalization success in different parts of the continent, since the data it contains are highly unreliable in terms of evaluating species invasion status. An urgent need to include the issue of alien species in integrated European projects, articulated in the above mentioned analysis (Pyšek 2003) has been met by the DAISIE project.

The data gathered by DAISIE make it possible to evaluate the progress towards a pan-European inventory of alien plant species attributable to the project. This can be done by comparing numbers of naturalized alien species yielded by DAISIE with those reported for individual regions by Flora Europaea (Note that Flora Europaea considers only naturalized species that had been established in a single station for at least 25 years, or were reported as naturalized in a number of widely separated locations; Tutin et al. 1964–1980). Due to the changes in national political boundaries in the last decades, such comparison can only be based on a limited number of countries (Fig. 13). These changes affected the area of former Yugoslavia, the area of the former USSR (including the Baltic countries, Kaliningrad, Ukraine and Belorussia). Turkey is fully included in DAISIE and not only its European part as it is in the Flora Europaea (Tutin et al. 1964–1980). The eastern boundaries of the geographical scope of Flora Europaea (Tutin et al. 1964–1980) are slightly different to the regions included in DAISIE (Fig. 1), due to different borders along the Ural and Caucasus mountain ranges. The deviation of countries/regions from the unity line on Fig. 13 is a result

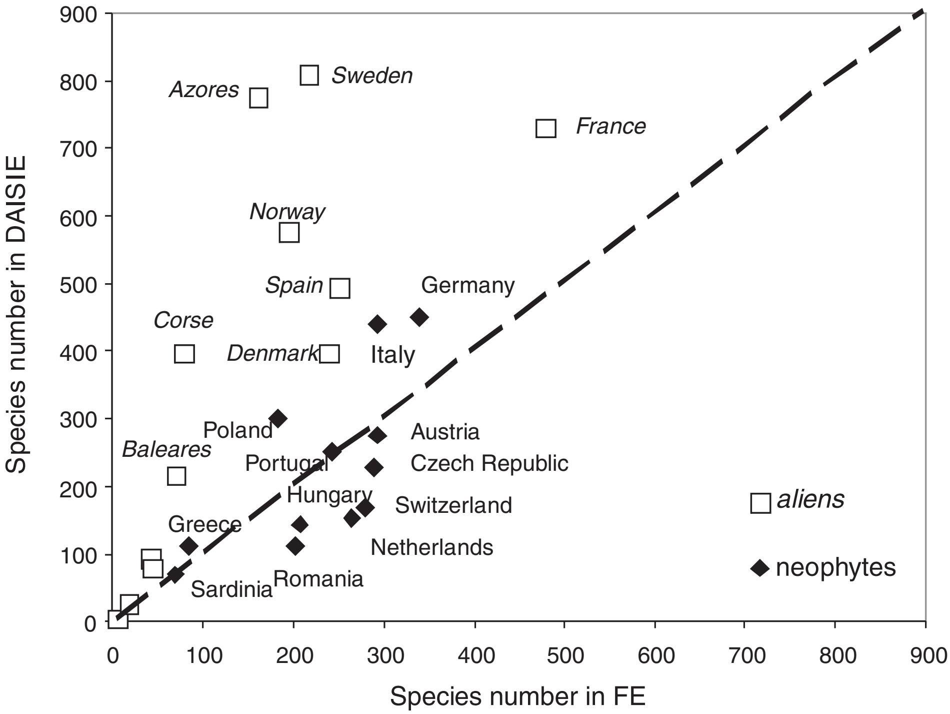

Fig. 13. – Relationship between numbers of alien species in Europe recorded during the DAISIE project (this study) and those reported in Flora Europaea (FE; Tutin et al. 1964–1980, reported by Weber 1997). Data sets from regions covered by DAISIE, with data on all naturalized aliens (squares, region names in italics) and naturalized neophytes (diamonds) are shown separately. Position of a country/region appearing above the unity line indicates that research carried out by DAISIE lead to an increase in the number of alien plant species known to occur there, and vice versa. See text for discussion on validity and reliability of data in FE.

of two factors, which cannot be separated based on the current data. First, the number of alien species in European regions has been increasing since the publication of Flora Europaea (Pyšek et al. 2003a, b) and the two data sets are separated by at least 30 years. Second, the position of countries/regions reflects an increase in research intensity over the last three decades. A high research intensity is indicated for countries that appear above and far from the unity line. This is the case of Nordic countries in particular (e.g., Sweden 810 species vs. 217 in Flora Europaea; Norway 576 vs. 194) where the knowledge of alien plants largely profited from the NOBANIS project (www.nobanis.org), which used extensive regional literature (see Table 1 for sources and Weidema 2000 for overview), but also, e.g., France (732 vs. 479), Azores (775 vs. 161) and Corse (474 vs. 80) seem to have been very poorly covered in Flora Europaea (Fig. 13). It needs to be noted that recent data for these regions include all aliens, as the classification into neophytes and archaeophytes is not available, but the bias due to inclusion of limited numbers of archaeophytes is relatively minor, given the character of data gathering in the DAISIE project (see the section DAISIE database). Therefore, it can be safely concluded that the pattern presented on Fig. 13 reflects, more than anything else, an increase in the intensity of research or publication of thorough compendia (e.g., Preston et al. 2002 for UK, Schäfer 2002, 2003 for Azores).

The comparison involving only naturalized neophytes (Fig. 13) is less biased, since Flora Europaea does not consistently mark archaeophytes as aliens, though it is not explicitly stated there that it restricts alien status to neophytes (Pyšek 2003). Also within this group, the position of countries above the unity line can be related to a systematic long-term research of specialized teams, which resulted in the publication of compendia, release of databases or establishing internet pages dealing with alien species (Germany: Klotz et al. 2002, www.biolflor.de; Italy: Celesti-Grapow et al. 2008; Poland: http://www.iop.krakow.pl/ias). For some countries, the number of species given in Flora Europaea is higher than the actual number yielded by DAISIE. This reflects errors in reporting total numbers of naturalized species in Flora Europaea. The Czech Republic can be used to support this statement: of 290 species labelled as naturalized for this country, only 118 do have this status, while the remaining 172 are casuals (Pyšek 2003). There is no reason to assume that the treatment was different for other countries with numbers of naturalized neophytes over-estimated by the Flora Europaea, e.g., Switzerland, Hungary, Netherlands or Romania (Fig. 13). The risk of over-estimation stems partly from the large number of synonyms currently in use, and accepted names may differ substantially between countries or even between local floras. The DAISIE database currently holds over 14,600 name variations (accepted or formerly accepted somewhere in Europe) for the taxa covered, and rationalizing this confusing situation remains a major challenge for global floristic research.

Research gaps and future prospects

Before DAISIE, there was no pan-European mechanism to link databases on invasive alien species across jurisdictional lines or to ensure that the information is accurate for a potentially problematic species. For some countries/regions, DAISIE collected the first comprehensive checklists of alien species, based on primary data (e.g., Cyprus, Greece, F. Y. R. O. Macedonia, Slovenia, Ukraine) or provided first summarized preliminary information on the composition of alien floras (e.g., Bulgaria, Belarus, Israel, Moldova, Russia). Existing information resources were also limited taxonomically and geographically. DAISIE represents the first Europe-wide coordinated effort for collaboration on biological invasions as part of an interconnected network for global cooperation and information exchange needed to support the objectives of the Biodiversity Convention.

The overview of the alien flora of Europe, as presented in this paper, highlights the state of the art of research in this field. The database produced by the DAISIE project, publically available at the web portal (www.europe-aliens.org), provides the first estimate of the composition and structure of alien plants in European continent. Even the provisional data that are available at the moment provide a robust overview of the species diversity, the structure of alien flora and large-scale biogeographical patterns. However, checklists from many countries need to be further assessed with respect to the invasion status and residence time of the species included. For future in-depth analyses of the dataset it is crucial that especially the naturalized/casual status is evaluated; so far, this information is available comprehensively for only for 19 countries/regions of 49 considered. This needs to be done at the national level and incorporated into the database. A more rigorous approach is also needed at the national level, in terms of recording of habitat (Chytrý et al. 2008b) and abundance data, and according to recognized standards which are comparable across the continent.

The current database lacks information on basic species traits for the majority of species, or the information is unequally distributed among countries. Populating the database with information on species traits is planned for the next period of DAISIE. Of the issues not reported in this paper, the database includes assessments of impact for a limited number of species in well-researched countries (e.g., Germany, Czech Republic); this does not allow a balanced picture to be drawn for the whole of Europe, the summary statistics would be rather biased towards these countries. In fact, data on impacts is currently the most severely lacking in DAISIE database, although this information is probably amongst the most important.

However, the completion of the database is closely associated with the future of DAISIE. The European Environment Agency (EEA), responsible for environmental information exchange and dissemination and closely collaborating with the European Topic Centre on Nature Protection and Biodiversity, could be possible hosts of the database after DAISIE. The infrastructure established by DAISIE would fit well with the aims of both the EEA and the Topic Centre. In the future, the inventory may move away from a single database to the integration of national databases across the same infrastructure. This would make the updating process efficient and cost-effective. There will certainly be political and logistic challenges in updating and delivering updated and concise information on alien species in Europe. DAISIE has a potential to contribute to meeting this challenge (Hulme et al. 2008c).

See www.preslia.cz for Electronic Appendix 1.

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Souhrn

Práce přináší přehled zavlečených rostlin vyskytujících se na území Evropy; je výsledkem projektu DAISIE (2004–2008), financovaného 6. rámcovým programem Evropské unie. Na základě přehledů zavlečených rostlin 49 evropských zemí/regionů a Izraele byla vytvořena databáze, která představuje první ucelenou informaci o nepůvodní flóře Evropy; pro některé oblasti (např. Řecko, Kypr, Makedonie, Slovinsko, Ukrajina) jde o vůbec první souhrnné přehledy. Databáze obsahuje údaje o 5789 zavlečených rostlinách, zjištěných na území Evropy (včetně druhů, které jsou v určité části kontinentu původní, ale byly zavlečeny do jiných částí Evropy); z tohoto počtu je 2843 druhů mimoevropského původu. Výzkum v rámci projektu se soustředil na naturalizované druhy; těch je registrováno celkem 3749, z toho 1780 mimoevropského původu. To představuje značné zvýšení počtu oproti 1568 naturalizovaným druhů udávaným v předchozí analýze nepůvodní flóry Evropy, založené na Flora Europaea (1964–1980). Přechodně zavlečené druhy byly evidovány pouze okrajově; v databázi je jich 1507, z toho 872 mimoevropského původu. Nejvíce nepůvodních druhů (bez ohledu na statut) je udáváno ze zemí s rozvinutým průmyslem a dobrou tradicí botanického výzkumu: Belgie (1969), Spojené království (1779) a Česká republika (1378). Spojené království (857 druhů), Německo (450), Belgie (447) a Itálie (440) jsou země s nejvyšším počtem naturalizovaných neofytů. Počet naturalizovaných neofytů v evropských zemích je určován interakcí teploty a srážek; stoupá se vzrůstajícím úhrnem srážek, avšak pouze v klimaticky teplejších oblastech. Polovina z celkového počtu dnes známých naturalizovaných neofytů byla do Evropy zavlečena po roce 1899, 25 % po roce 1962 a 10 % po roce 1989. V současné době se do Evropy dostává ročně 6,2 druhu schopných naturalizace. Většina druhů má poměrně omezené rozšíření; polovina naturalizovaných druhů se vyskytuje v méně než pěti zemích. V zavlečené flóře Evropy se vyskytují druhy z 213 čeledí (převládají *Asteraceae*, *Poaceae*, *Rosaceae*, *Fabaceae* a *Brassicaceae*) a 1567 rodů; nejpočetněji zastoupené jsou rody s velkým zastoupením plevelných druhů (*Amaranthus*, *Chenopodium* a *Solanum*) a druhů často pěstovaných pro okrasné účely (*Cotoneaster*). Mezi úspěšnými rody je pouze několik, mezi jejichž zástupci převládají mimoevropské druhy (např. *Oenothera*, *Oxalis*, *Panicum*, *Helianthus*). *Conyza canadensis*, *Helianthus tuberosus* a *Robinia pseudoacacia* jsou nejrozšířenější druhy, vyskytující se v nejvíce zemích či regionech. Celkem 64,1 % druhů se vyskytuje na městských a průmyslových ruderálních stanovištích, 58,5 % na orné půdě, v parcích a zahradách. Mnoho zavlečených druhů se vyskytuje také v travinných a lesních společenstvech (37,4 % a 31,5 % z celkového počtu); nejméně invadovaná jsou rašeliniště a vrchoviště se zhruba jen 10 % z celkového počtu druhů. 62,8 % druhů bylo introdukováno úmyslně, 37,2 % neúmyslně; mezi úmyslně introdukovanými největší podíl (53,1 %) připadá na okrasné a ostatní zahradní druhy. Mezi neúmyslně zavlečenými druhy převládají kontaminace semenářských produktů, minerálních materiálů a ostatních komodit – tímto způsobem se do Evropy dostalo 1091 druhů (76,6 % ze všech zavlečených), dalších 363 druhů spadá na vrub neúmyslnému zavlékání bez souvislosti s komoditami. Z druhů mimoevropského původu jsou nejčastější severoamerické a jihoamerické (45,8 %), 45,9 % zasahuje alespoň částí svého původního rozšíření do Asie, 20,7 % do Afriky; 5,3 % druhů je původem z Austrálie. Na základě druhového složení a vzájemné podobnosti mezi zavlečenými flórami regionů bylo vymezeno pět základních distribučních typů: (1) severozápadní (Skandinávie a UK); (2) středozápadní (od Belgie a Nizozemska po Německo a Švýcarsko); (3) pobaltský, zahrnující státy na pobřeží Baltského moře; (4) středovýchodní (zbývající státy střední a východní Evropy) a (5) jižní, zahrnující Středozemí. Vymezení je dáno především biogeografickými a kulturně-historickými faktory. Článek na závěr shrnuje stav výzkumu rostlinných invazí v Evropě, vymezuje mezery a nastiňuje, jakými cestami by se měl ubírat budoucí výzkum.

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Appendix 1. – Terms related to the invasion status, origin status (based on Pyšek et al. 2004a, Richardson et al. 2000) and classification of pathways as used in the present paper.

ORIGIN AND INVASION STATUS

Native plants (indigenous) are taxa that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention of humans from an area in which they are native. The definition excludes products of hybridization involving alien taxa since human involvement in this case includes the introduction of an alien parent.

Alien plants (exotic, introduced, non-native, non-indigenous plants) are taxa in a given area whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien. Taxa can be alien to any definable area, e.g. continents, islands, bio- or ecoregions, or any political entity (e.g., countries, states, provinces). In the present paper we distinguish plant taxa

- **alien *to* Europe**: this group includes taxa whose native distribution is outside Europe
- **alien *in* Europe**: this group includes taxa that are alien to at least one European region, regardless of whether their origin is outside Europe or in another part of the continent; the group therefore includes all aliens *to* Europe plus species with native distribution area in a part of Europe

Casual alien plants are taxa that may reproduce occasionally outside cultivation in an area, but that eventually die out because they do not form self-replacing populations, and rely on repeated introductions for their persistence.

Naturalized alien plants are taxa that sustain self-replacing populations for a period of time long enough to experience extreme climatic events in the area, and reproduce without direct intervention by people (or in spite of human intervention) by recruitment from seed or vegetative parts capable of independent growth.

Invasive alien plants are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and thus have the potential to spread over a large area. The definition is not bound to a type of habitat, hence a species may be invasive in natural or human-made habitats.

Cryptogenic species are those in which it cannot be with certainty decided whether they are native or alien to a region (Carlton 1996).

RESIDENCE TIME STATUS

Archaeophytes are alien species introduced to the region during the period since the beginning of Neolithic agriculture and the end of Medieaval (discovery of Americas, approximately the year 1500 A.D.).

Neophytes are alien species introduced to the region after the year 1500 A.D..

PATHWAYS

Intentional introductions have been introduced deliberately by humans, for commercial or recreational reasons.
- **Released** species have been released deliberately into the wild (e.g., for the enrichment of the native flora, landscaping, etc.).
- **Escaped** species have escaped into the wild from cultivation.
  - **Forestry** species are cultivated for timber on a large-scale, or as part of re-/aforestation programmes.
  - **Amenity** species are cultivated on a large to moderate scale in public places for landscaping purposes (e.g., for soil stabilization or aesthetic enhancement).
  - **Ornamental** species are cultivated for ornament on a small scale (especially in private gardens).
  - **Agricultural** species are cultivated on a field scale as commercial non-timber crops.
  - **Horticultural** species are cultivated for edible or other useful products on a small-scale (e.g., in private gardens).

Unintentional introductions have arrived as a result of human actions but have not been introduced deliberately.
- **Unaided** species have spread via natural (spontaneous) means from introduced populations elsewhere in non-native range (Hulme et al. 2008a).
- **Transported** species have been introduced accidentally via shipping, air, road or rail freight, directly by humans or with domestic animals.
  - **Seed contaminant**s have been introduced as a contaminant of crop seed or propagules.
  - **Mineral contaminants** have been introduced during the deliberate movement of soil or other minerals.
  - **Commodity contaminants** have been introduced as contaminants of non-seed crop commodities (e.g., wool, organic refuse).
  - **Stowaway** have been introduced accidentally but are not known to be associated with any particular commodity, e.g., on car tyres or in the hulls of ships (Hulme et al. 2008a).