Preslia 96: 149–182, 2024
doi: 10.23855/preslia.2024.149

Preslia

Alien plants of Europe: an overview of national and regional inventories

Veronika Kalusová[1,*], Natálie Čeplová[1,2], Jiří Danihelka[1,3], Martin Večeřa[1], Petr Pyšek[4,5], Arnaud Albert[6], Paulina Anastasiu[7], Idoia Biurrun[8], Steffen Boch[9], Cyril Cottaz[10], Franz Essl[11], Anna Kuzemko[1,12], Semir Maslo[13], Stephen Mifsud[14], Vira V. Protopopova[15,12], Myroslav Shevera[12,15], Culiţă Sîrbu[16], Jens-Christian Svenning[17], Erik Welk[18,19] & Irena Axmanová[1]

[1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, CZ-61127 Brno, Czech Republic; [2]Department of Biology, Faculty of Education, Masaryk University, Poříčí 623/7, CZ-60300 Brno, Czech Republic; [3]Czech Academy of Sciences, Institute of Botany, Department of Taxonomy, CZ-25243 Průhonice, Czech Republic; [4]Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-25243 Průhonice, Czech Republic; [5]Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Prague, Czech Republic; [6]Department of Research and Scientific Support, French Biodiversity Agency, Nantes, France; [7]Department of Botany and Microbiology, Faculty of Biology, Botanic Garden D. Brandza, University of Bucharest, Romania; [8]Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country UPV/EHU, Bilbao, Spain; [9]WSL Swiss Federal Research Institute, Birmensdorf, Switzerland; [10]Mediterranean National Botanical Conservatory, Port-Cros National Park, Hyères, France; [11]Divison of BioInvasions, Global Change & Macroecology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria; [12]M. G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine, Kyiv, Ukraine; [13]Primary School, Lundåkerskolan, Gislaved, Sweden; [14]EcoGozo Directorate, Ministry for Gozo, Victoria, Gozo, Malta; [15]Ferenc Rákóczi II Transcarpathian Hungarian College of Higher Education, Berehove, Ukraine; [16]Ion Ionescu de la Brad University of Life Sciences, Iaşi, Romania; [17]Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), Department of Biology, Aarhus University, Aarhus, Denmark; [18]Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Halle/Saale, Germany; [19]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
*corresponding author: kalusova@sci.muni.cz

Abstract: As a result of human activities, a considerable part of European vascular plants and their populations are non-native. Since the publication of previous studies summarizing the composition and structure of European alien flora, our knowledge has increased, and new alien plant inventories and updates to existing ones have been published. The aim of our work was to create an overview of currently available inventories in Europe, compare them and identify the main gaps and inconsistencies. We compiled 111 national or regional inventories published up to 2022 for 55 European territories, i.e. countries, selected regions within countries, large islands and archipelagos. Using a standardized methodological approach, we unified taxonomy, nomenclature, residence time, invasion status categories, and origin. At the level of the European species pool, we identified 7,335 alien vascular plant species, which is 1,546 more than in the previous study from 2008. Regarding residence time, 1.5% of plants were considered as archaeophytes, 77.2% as neophytes, 9.3% as archaeophytes in one part and neophytes in another part of Europe, while 12.0% of species had undistinguished alien status. Regarding

Received: 29 Dec 2023; Revised: 29 Mar 2024; Accepted: 5 Apr 2024; Published: 18 Jun 2024

invasion status, 33.3% of aliens were casual, 36.3% were naturalized, and 14.4% were invasive in at least one European territory; for 5.8% of taxa, the invasion status could not be reliably assessed. At the level of individual territories, archaeophytes and neophytes were recognized in 40.0% of the European territories with data available. Regarding the invasion status, the full categorization was available only for 43.6% of territories, while in 20.0%, only invasive species were listed. We found 114 species reported to occur in more than half of the territories. The most widespread species were *Erigeron canadensis*, *Amaranthus retroflexus*, *Galinsoga parviflora* and *Robinia pseudoacacia*. Most aliens belonged to the families *Asteraceae*, *Poaceae*, *Rosaceae* and *Fabaceae*. The highest proportions of alien species in Europe originated from temperate Asia (20.4%), temperate Europe (19.6%) and the Mediterranean region (19.0%). Invasive species originated predominantly from the American continent (22.9%) and temperate Asia (19.7%). We found gaps and significant persisting inconsistencies not only in the recognition of residence time and invasion status across territories but also in contradicting status assignments of individual species. This raises the need for a critical reassessment of species' status across Europe, most notably on the Balkan Peninsula and in north-eastern Europe. Updated and standardized national alien checklists are crucial for reliable analysis of the magnitude, mechanisms and impact of invasions, as well as for risk assessments and management across Europe.

Keywords: checklist, Europe, invasion status, non-native species, residence time, vascular plants

Introduction

Alien species are organisms introduced outside their native distribution range as a direct or indirect consequence of human activities that disrupt natural dispersal barriers (Richardson et al. 2000, Roy et al. 2023). The most species-rich group of organisms introduced to Europe are vascular plants (Hulme et al. 2009, Seebens et al. 2017), as confirmed by the most recent data presented in the IPBES report on invasive alien species (Seebens et al. 2023). The cumulative numbers of first records in Europe show a continuous increase in naturalized plant species, which has been almost linear since the beginning of the 20th century (Haubrock et al. 2023). This trend is linked to Europe's historical position as a hub of trade routes with significant long-term import of agricultural, horticultural and ornamental plants, which is still increasing (van Kleunen et al. 2018, Arianoutsou et al. 2021). The numbers of successfully established, naturalized alien plants (van Kleunen et al. 2015, Pyšek et al. 2017) and spreading, invasive plants, which cause monetary costs due to their impacts (Novoa et al. 2021, Haubrock et al. 2023), are also continuously increasing. Recent estimates of total costs associated with invasive alien species in Europe summing up damage-loss and management costs amount to €116.61 billion between 1960 and 2020, 60% of which are damage-related costs (Haubrock et al. 2021b). Moreover, the rates of introduction and accumulation of alien plants in Europe are predicted to increase further in the near future (Seebens et al. 2020).

The detailed knowledge of the composition and structure of the alien species pool in Europe thus serves as an important basis for various areas of plant invasion research and applications. Long-term gathering of information about alien plants on the continent has enabled quantification of impacts on European ecosystems and their functioning (Vilà et al. 2010, Nentwig et al. 2018, Lazzaro et al. 2020, Polce et al. 2023), economy (Cuthbert et al. 2021, Haubrock et al. 2021a, Kourantidou et al. 2021, Renault et al. 2021) and

human well-being (Schindler et al. 2015, Lazzaro et al. 2018). It has also provided tools for dealing with harmful invaders (Rumlerová et al. 2016), identifying plant invasion hotspots and predicting changes (Chytrý et al. 2009, 2012), as well as conducting risk assessments (Blackburn et al. 2014, Kumschick et al. 2015, Pergl et al. 2016, Oficialdegui et al. 2023) and developing effective strategies to mitigate negative impacts (Brundu & Richardson 2016).

The development of specialized inventories of alien floras at the national level started in the 1990s–2000s in a number of European countries, e.g. Ukraine (Protopopova 1991), UK (Clement & Foster 1994), Lithuania (Gudžinskas 1997a, b, c, d), Portugal (de Almeida 1999), Austria (Essl & Rabitsch 2002), Czech Republic (Pyšek et al. 2002), Republic of Ireland (Reynolds 2002), Spain (Sanz-Elorza et al. 2004) and Italy (Celesti-Grapow et al. 2009). The first pan-European overview of the European alien flora (Weber 1997) identified 1,568 naturalized plant species. However, it relied on Flora Europaea (Tutin et al. 1964–1980, 1993), which focused mostly on native flora and was mainly based on published records. The data were thus inherently incomplete to some extent already at the time of publication and rapidly became outdated; many naturalized alien species were either omitted or had inaccurate distribution information (Pyšek 2003).

The knowledge of the alien flora at the pan-European level significantly improved with the launching of the DAISIE database developed under the DAISIE (Delivering Alien Invasive Species Inventories for Europe) project (2004–2008; DAISIE 2009). For this database, regional data on the distribution of alien organisms were collected from 48 countries or regions. The authors identified 5,789 alien plant species occurring in Europe, of which 3,749 were considered naturalized (Lambdon et al. 2008). Subsequently, similar initiatives occurred regionally, collating and providing data on invasive species and conducting risk assessments, e.g. NOBANIS (North European and Baltic Network on Invasive Alien Species; www.nobanis.org), ESENIAS (East and South European Network for Invasive Alien Species; www.esenias.org) or INVASAQUA (Aquatic Invasive Alien Species of Freshwater and Estuarine Ecosystems: Awareness and Prevention in the Iberian Peninsula; https://lifeinvasaqua.com).

Based on the DAISIE database, Lambdon et al. (2008) made a comprehensive evaluation of European alien flora. They provided compositional, distributional and temporal analyses at both the national and pan-European levels. Where available, they assessed several categories of invasion status (casual, naturalized, unspecified and cryptogenic) and residence time categories. Data on alien species in Europe from DAISIE became a part of the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al. 2015, 2019). This database, however, compiled data for naturalized neophytes only. Based on the re-evaluated and updated records of naturalized neophytes in GloNAF, Pyšek et al. (2017) analysed recent patterns of their composition, structure and distribution in Europe, encompassing 4,139 taxa.

To collate, integrate and share information on alien species within Europe, the European Alien Species Information Network (EASIN 2020) was established by the European Commission's Joint Research Centre (Katsanevakis et al. 2012). Its primary focus is supporting policy development and management strategies in EU member states, including implementation of the EU Regulation 1143/2014 on the prevention and management of the introduction and spread of invasive alien species (EU 2014). Taxa records in the database mostly came from DAISIE, NOBANIS and 16 other national or global online

databases published up to 2019. According to the EASIN database, 6,250 plant taxa alien to Europe were identified as occurring on this continent (Arianoutsou et al. 2021). However, this pan-European assessment, based on the most extensive compilation of available data, is primarily focused on introduction pathways, countries' gateways, and temporal dynamics of pathways rather than the composition and structure of the alien flora.

In addition to the previously mentioned sources, several large databases have been developed for various purposes, including to some extent, alien plant species records for Europe. They are the Global Register of Introduced and Invasive Alien Species (GRIIS; Pagad et al. 2018), Euro+Med PlantBase (Euro+Med 2006–2024) and Plants of the World Online (POWO 2023). GRIIS focuses primarily on invasive species and stores national inventories of all taxonomic groups worldwide. Euro+Med PlantBase is an online database of European and Mediterranean vascular flora, while Plants of the World Online is an online database of worldwide vascular flora. Databases, however, often vary in alien status categorizations and differ in the quality of the distribution data, particularly for alien taxa. These inconsistencies are more pronounced in regions with less intensive research, as evidenced by examples such as Turkey (Uludağ et al. 2017).

Leaving aside differences in adopted taxonomic concepts, changes in the numbers of alien species in pan-European studies demonstrate not only temporal trends in plant introductions and spread across Europe but also an increase in data availability for alien plants. In parallel with the aforementioned large databases, national and regional inventories of alien plants are continuously emerging. The increasing levels of knowledge allow for the extension and reassessment of existing alien lists in some countries, while improved socioeconomic situations in other countries have initiated new compilations of alien floras (Pyšek et al. 2008). Inventories provide crucial information from local experts, including updates on the alien status and occurrences at the country level. This is achieved through the collation and evaluation of new data, as well as the re-evaluation of older regional and national floristic records and herbarium specimens, now easily accessible via various databases, ranging from local to global repositories.

Since 2019, new and updated inventories for many European territories have been published in various formats. These include separate checklists, e.g. in Belarus (Dubovik et al. 2020), Bosnia and Herzegovina (Maslo et al. 2020), Catalonia (Aymerich & Sáez 2019), mainland France (e.g. Cottaz 2020, CBNA & CBNMed 2021) and Lithuania (Gudžinskas & Taura 2020, Gudžinskas & Petrulaitis 2021), lists published as parts of floras, e.g. Germany (Müller et al. 2021), or updates of online checklists, e.g. Croatia (Nikolić 2022). Currently, information on alien plant species in Europe remains scattered across newly emerging and previously published inventories as well as existing databases that require retrospective updating with new records from national and regional sources. Moreover, despite Europe being one of the most explored regions regarding plant invasions (Pyšek et al. 2008, 2017, Chiu et al. 2023), and notwithstanding suggestions for harmonizing general principles for alien species lists (Pyšek et al. 2004, Blackburn et al. 2011), there are still gaps and inconsistencies among sources of alien plant data. These discrepancies relate to their completeness, data quality, taxonomy and consistency of categorizations.

In our study, we compile available national and regional inventories of alien plants for European territories published up to the year 2022, along with unpublished data contributed by our collaborators. Specifically, we aim to (i) harmonize the taxonomy and

nomenclature of alien species and categorization used in the inventories, (ii) analyse the composition and structure of the updated European alien flora, (iii) compare our results with previous studies on European alien flora, and (iv) identify the main inconsistencies and gaps persisting in the current knowledge of alien plants in Europe. Our intention is to present the state of the art of alien plant checklists, highlight inadequacies, discuss possibilities for their improvement and emphasize the need for reassessments. We consider our overview of national and regional checklists as an initial step towards establishing a comprehensive database of critically revised and updated alien plant checklists for all European countries. This database will serve as a basis for an up-to-date alien flora of Europe.

Methods

Study area

Our area of interest is Europe, including selected neighbouring countries. We distinguished 55 territories, including countries, regions within countries, large islands and archipelagos. The study area spans from Svalbard and Iceland in the north to the European part of the Mediterranean region in the south, including Turkey (European and Anatolian parts), as well as major Mediterranean islands, namely Baleares, Corsica, Crete, Malta, Sardinia and Sicily, each of which was assessed separately. The corresponding mainland countries, i.e. Italy, France, Spain and Greece, were also assessed separately, excluding the major islands mentioned earlier. In the west, the study area includes the Macaronesian archipelagos (except for Cape Verde) and extends to the Urals and Georgia in the east. European Russia was divided into seven territories following the Euro+Med division (Euro+Med 2006–2024), and each territory was assessed separately.

Source inventories for alien plants

For all territories, we gathered 111 literature or online sources, including national or regional checklists, lists of alien, naturalized or invasive plants extracted from flora monographs, online floristic databases, and unpublished alien species lists or updates of published checklists. We searched for the most comprehensive sources; however, complete national checklists of alien plants are not yet available for some European territories. To account for this limitation, we also included alien species lists covering at least a part of such territories. Thus, we collected a minimum of one and a maximum of 24 source inventories for each territory, with the exception of Liechtenstein and North Macedonia, where we did not find any suitable data source. Data sources varied in their completeness and date of publishing from 1997 to 2022 (see Supplementary Table S1 for the list of European territories with source publications and online databases). In total, we obtained data for 95% of the 44 politically defined European countries.

Taxonomy and nomenclature

To standardize the checklists, we first removed non-vascular plants, i.e. algae and bryophytes, which were included in some inventories. Then, we standardized the taxonomy and nomenclature of vascular plants; we included all species, infraspecific taxa, hybrids,

and cultivars or cultivar groups pooled across all sources in each territory. The taxonomy and nomenclature in the pooled list were based on the Euro+Med Plantbase (Euro+Med 2006–2024), while the taxonomy of the taxa not included there was adjusted based on the Plant of the World Online (POWO 2023). We removed the genus-level taxa listed for some territories. All aggregates and "sensu lato" species were included at the species level. Since cultivars are included only in some inventories, if at all, we merged all cultivars and cultivar groups that included variants of the same species cultivated as a crop into a single taxon, specifically *Allium cepa*, *Avena sativa*, *Beta vulgaris*, *Brassica napus*, *B. oleracea*, *B. rapa*, *Cichorium endivia*, *C. intybus*, *Celosia argentea*, *Cucurbita pepo*, *C. maxima*, *Hordeum vulgare*, *Raphanus sativus*, *Trifolium pratense*, *Triticum aestivum* and *T. turgidum*, and counted each of them as one taxon/species. The variants of these merged taxa are available in Supplementary Table S2. We adopted this approach to allow for better comparability of the resulting numbers of alien taxa among European territories.

Because of the different taxonomies used in the source lists, taxonomic and nomenclatural standardization resulted in several duplicate records of taxa in the unified lists for some territories. In such cases, we deleted duplicate entries within the territory and kept only one unique name. All the above-described procedures led to a decrease in the final number of alien plant species in each territory compared to the source inventories. We compiled the final list of alien plants for each territory at two taxonomic levels: (i) including all infraspecific taxa, i.e. subspecies and varieties, and (ii) merging subspecies and varieties at the species level. Subsequently, we reassessed residence time or invasion status categories when they differed between original entries merged into one taxon (see the next section for details). Finally, we assigned all taxa to families based on the APG IV taxonomy system (Angiosperm Phylogeny Group 2016 available from POWO 2023).

The geographical origin of alien plants at the level of species was assessed in the following categories: temperate Europe, the Mediterranean region (incl. Mediterranean part of Europe, Mediterranean northern Africa, and the Middle East), Macaronesia, Africa non-Medit., North America, Central America, South America, temperate Asia, tropical Asia, Australia and New Zealand, Pacific, hybrid (incl. spontaneous hybrids of at least one alien parental taxon and artificial hybrids originated in cultivation) and anecophyte (taxa with unknown native range incl. cultivars and cultivar groups). Where possible, we used data on native range distributions from POWO (2023) to match our broadly defined categories of geographical origin; if needed, the distribution was also checked with other sources, such as the Global Biodiversity Information Facility (GBIF 2023).

Unification of residence time categories

The source publications and online databases contained various systems for classifying the residence time of alien taxa. Some inventories focused only on subgroups of alien taxa, e.g. neophytes or invasive taxa. Based on the descriptions in the original publications, we unified these categories as follows: (i) archaeophytes (arch) – taxa identified as archaeophytes and taxa described as introduced before ~1500 CE; (ii) neophytes (neo) – taxa identified directly as neophytes and taxa reported as introduced after ~1500 CE, or after 1700 CE in Sweden (Karlsson 1998) and after 1750 CE in Iceland (Kristinsson 2008); (iii) undistinguished aliens (arch+neo) – taxa labelled as "alien" only or taxa for

which the authors were unable to distinguish with certainty whether they were archaeophytes or neophytes; (iv) uncertain – taxa for which the original authors could not decide with certainty whether they are native or alien in their territory; taxa marked as "doubtfully occurring" or with "deficient data." Taxa marked as "recorded by mistake" were omitted.

Inconsistencies in the residence time of a particular taxon within a given territory resulted from (i) taxonomic standardization leading to the merging of different taxa into one taxon, (ii) different residence time categories reported for the same taxon in different source publications, or (iii) merging infraspecific taxa with different residence time categories to the species level.

Also, when pooling taxa entries across all territories into a single alien plant list for Europe, we encountered numerous inconsistencies in residence time categories. To reassess such cases, we followed the decision table shown in Supplementary Table S3. First, we reassessed the residence time categories of duplicate taxa entries within European territories for the territory-based statistics; then, we reassessed the categories again in the same manner across territories for the Europe-wide statistics. The "arch+neo" category in the Europe-wide statistics thus included taxa marked as undistinguished aliens in all European territories where they were listed, but also those taxa recognized as archaeophytes in some European territories and as neophytes in others. In territories where this information was lacking due to incomplete source lists without residence time categories, we could not distinguish whether a species was an archaeophyte or neophyte.

Standardization of invasion status categories

Invasion status showed even higher variability in assigning species to the categories than residence time. We reassessed the categories used in the original papers to match them with invasion status categories developed by Richardson et al. (2000), which are based on overcoming barriers along the introduction-naturalization-invasion continuum (see also Pyšek et al. 2004, Blackburn et al. 2011). In inventories that clearly followed this concept, we accepted the original categories; others were adjusted based on the descriptions of the status in source publications. We distinguished (i) cultivated (cult) – alien taxa kept in cultivation assessed by authors as having a potential to escape and naturalize or exert a constant propagule pressure; (ii) casual (cas) – alien taxa with rare or occasional occurrence as individuals or small populations, usually characterized as "occurring temporarily and dependent on repeated propagule inputs"; (iii) casual and naturalized (cas+nat) – taxa to which neither the previous nor the next stage of invasion could be assigned, either due to a vague definition in the source list or because the only category with clear separation in the source was invasive; (iv) naturalized (nat) – taxa forming self-sustaining populations, recruiting offspring freely, whose persistence does not depend on the ongoing human-driven input of propagules; labelled as naturalized or established, mainly in human-made or semi-natural habitats; (v) naturalized and invasive (nat+inv) – taxa to which neither the previous nor the next stage of invasion could be assigned, either due to a vague definition in source lists or because the only category with a clear separation in the source was casual (described as escapes, recent escapes); (vi) invasive (inv) – a subset of naturalized taxa producing offspring in large numbers with the potential for long-distance spread, usually characterized as "well-established, spreading and occurring also in

natural habitats"; (vii) uncertain – taxa for which authors were unable to assign any of the categories used in the given inventory; (viii) not available (NA) – invasion status was not assessed in a given inventory at all. The taxa marked in source publications as "partly naturalized" or "potentially invasive" were categorized as naturalized.

During the taxonomic standardization, when merging different source inventories or merging infraspecific taxa at the species level within territories, we also encountered inconsistencies in the categories of invasion status for entries identified as the same taxon. When reassessing the status of such taxa, we prioritized the newer and more complete inventories within the same territory. We also preferred national over regional checklists or databases for the same territory. In the case of regional checklists or databases that were available for different parts of one territory (e.g. mainland France or Spain), we adopted the rule of the higher status attained. That means, if a species was assessed e.g. as casual in one part of the territory and naturalized in another, we listed it as naturalized for the whole territory.

We applied the same principle for reassessing invasion status categories for taxa across territories, i.e. for the European pooled alien list. Taxa assessed as naturalized as their highest invasion status category in at least one European territory were considered naturalized at the pan-European level, taxa assessed as invasive as their highest invasion status category in at least one territory were considered invasive, etc.

Data handling and analyses

We digitized all gathered alien inventories, partial lists and online databases into unified formats. This involved implementing the changes in taxonomic levels described above, merging the alien plant entries within and across European territories, conducting residence time and status reassessment procedures, and calculating territory-based and Europe-wide statistics using the tidyverse package (Wickham et al. 2019) in R, v. 4.1.1. (R Core Team 2021). We compiled the resulting species data from all territories into a single list of European alien flora, encompassing all species with alien status indicated by inventories in at least one European territory. This includes alien species originating both outside and within Europe. We created maps of the number of alien plant species, archaeophytes, neophytes, casuals, naturalized and invasive species. Further, we produced maps showing the availability of invasion status categorizations across European territories. These maps were generated using the R packages raster (Hijmans et al. 2021), rgdal (Bivand et al. 2020), berryFunctions (Boessenkool 2021) and classInt (Bivand 2020). Unless specified otherwise, the individual territory-based and Europe-wide statistics presented below typically contain the numbers of alien species at the species level, with infraspecific taxa aggregated to species, excluding hybrids and cultivars/cultivar groups. We adopted this approach to ensure better comparability of data among European territories, considering the varying levels of recognition of such taxa in inventories. Donor regions of alien species to Europe were assigned at the species level except for 146 species (i.e. 0.02% of the data set) with unresolved nomenclature or not included in POWO (2023) and 43 species with uncertain alien status in Europe. Because species may have origins in more than one world region, the reported proportions of taxa donated by particular world regions are not calculated from the total number of species but from the total number of assigned origins (n = 15,006).

Results

Alien plant richness in Europe

We recorded a total of 8,079 vascular plant taxa considered alien in at least some parts of Europe. When harmonized to the species level, these correspond to 6,774 species and 561 hybrids and cultivars, further referred to as 7,335 alien species in total. In the pooled list of alien plant taxa for the entire Europe, residence time categories contained 165 taxa (corresponding to 108 species) marked exclusively as archaeophytes, 735 taxa (682 species) assessed as archaeophytes in one part of Europe and neophytes in another, and 6,171 taxa (5,663 species) listed exclusively as neophytes. For 1,008 taxa (882 species), we recorded undistinguished alien status (Fig. 1A, B), and 57 taxa (43 species) were assigned uncertain status across all of Europe; each of these species was recorded in only one of the 55 distinguished territories.

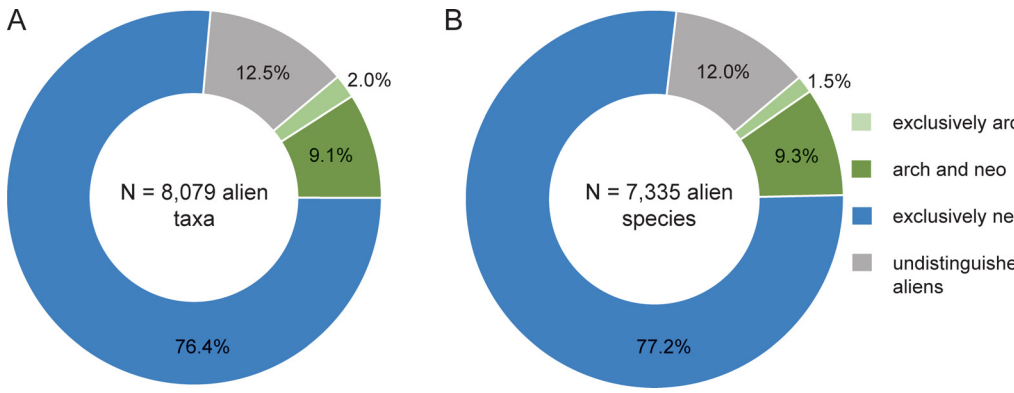

Fig. 1. Proportions of (A) alien plants (all taxa) and (B) alien plants at the species level in categories of residence time in the European alien flora. Exclusively arch – taxa or species listed exclusively as archaeophytes across Europe; arch and neo – taxa or species listed as archaeophytes for one part and as neophytes in another part of Europe; exclusively neo – taxa or species listed exclusively as neophytes in Europe; undistinguished aliens (arch+nat) – taxa or species listed as aliens without residence time indication or listed as archaeophyte or neophyte only for a part of Europe and as alien in another part. Additional 57 taxa (43 species) with uncertain alien status in Europe were excluded.

Regarding invasion status (Fig. 2A, B), we identified 2,711 casual taxa (2,445 species), 2,990 naturalized taxa (2,662 species), and 1,082 invasive taxa (1,037 species) listed in Europe. These figures are based on the highest level of invasion status that particular taxa reached in at least one European territory. Additionally, 307 alien taxa (278 species) were classified as casual+naturalized, 429 taxa (412 species) as naturalized+invasive, and 79 taxa (74 species) as being cultivated only. For 481 taxa (427 species), we could not gather reliable information about their invasion status in Europe, as they were marked as uncertain, or their invasion status was not given at all in the source inventories.

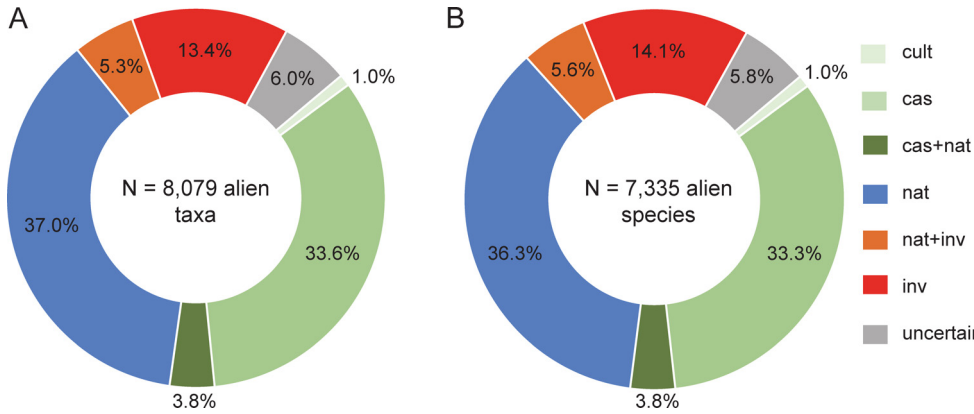

Fig. 2. Proportions of (A) alien plants (all taxa) and (B) alien plants at the species level in categories of invasion status in the European alien flora. Cult – cultivated; cas – casual; cas+nat – undistinguished casual and naturalized status; nat – naturalized; nat+inv – undistinguished naturalized and invasive; inv – invasive; uncertain+NA – invasion status not reliable or not available. Additional 57 taxa (43 species) with uncertain alien status in Europe were excluded.

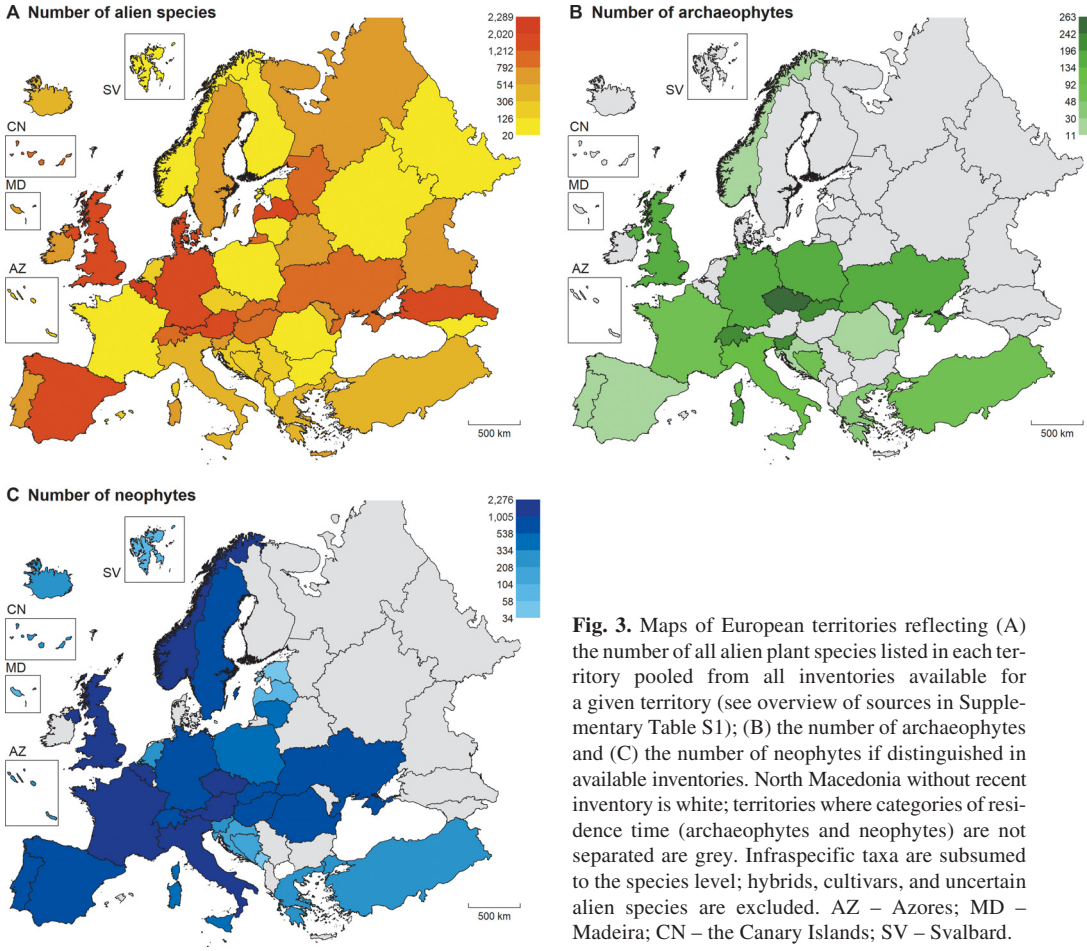

Fig. 3. Maps of European territories reflecting (A) the number of all alien plant species listed in each territory pooled from all inventories available for a given territory (see overview of sources in Supplementary Table S1); (B) the number of archaeophytes and (C) the number of neophytes if distinguished in available inventories. North Macedonia without recent inventory is white; territories where categories of residence time (archaeophytes and neophytes) are not separated are grey. Infraspecific taxa are subsumed to the species level; hybrids, cultivars, and uncertain alien species are excluded. AZ – Azores; MD – Madeira; CN – the Canary Islands; SV – Svalbard.

Alien plant richness across European territories

When comparing alien species numbers among European territories (Fig. 3A), excluding hybrids, cultivars and uncertain species regardless of their residence time, the highest numbers of alien species were reported from Belgium (2,289 species), Norway (1,750), the United Kingdom (1,663), the Czech Republic (1,561), mainland Spain (1,534), mainland France (1,492) Austria (1,410), mainland Italy (1,382), Ukraine (1,043) and Switzerland (1,038; Table 1). In all other territories, less than 1,000 alien species were recorded. This ranking reflects high proportions of casual species in inventories from those top-10 European territories. In 19 territories, inventories did not distinguish archaeophytes from neophytes (Table 1). Inventories of 10 territories clearly stated that their focus was exclusively on neophytes (Austria, Azores, Belgium, Estonia, Hungary, Iceland, Latvia, Montenegro, Svalbard and Sweden). The highest numbers of archaeophytes (Fig. 3B) were reported in the Czech Republic (263 species), Switzerland (220), Slovakia (219) and Slovenia (215); all other territories listed fewer than 200 archaeophytes. The highest numbers of neophytes (Fig. 3C) were reported in Belgium (2,289), Norway (1,722), the United Kingdom (1,469), Austria (1,410), the Czech Republic (1,264), mainland Italy (1,241) and France (1,145), while in all other territories, less than 900 neophytes have been recorded.

The full categorization of invasion status (i.e. distinguishing casual, naturalized and invasive taxa) was available for 24 (43.6%) European territories (Fig. 4a). In eight territories, including Denmark, Finland, Moldova, the Netherlands, Portugal, Slovenia, Sweden and Switzerland, invasion status of the listed taxa was not distinguished at all; only whether they were archaeophytes or neophytes was noted. In 11 other territories, including Bulgaria, Estonia, Latvia, Montenegro, and all territories within the European part of Russia, only invasive aliens were recorded. Cultivated alien taxa were only included in some of the source inventories from Croatia, the Czech Republic and the Republic of Ireland. In seven territories, namely Azores, Belarus, Canary Islands, Crete, France, Germany and Serbia, inventories did not differentiate between casual and naturalized status. In eight territories, namely Albania, Baleares, Canary Islands, Crete, Germany, Greece, Lithuania and the Republic of Ireland, the distinction between naturalized and invasive status was not made. For mainland France, the national source distinguished naturalized and invasive species, while some regional checklists used full categorization, and the rest distinguished/listed only invasive taxa.

When comparing alien species numbers (excluding hybrids, cultivars, and those with uncertain status), we observed the highest numbers of casual alien species (Fig. 4B) in Belgium (1,687 species), the Czech Republic (899), Austria (802), Norway (760), the Republic of Ireland (656), mainland Italy (625) and mainland Spain (611). In the other European territories, fewer than 600 casual alien species were recorded. Naturalized alien species were most numerous (Fig. 4C) in mainland France (1,150), the United Kingdom (877), Norway (788), Belgium (525), mainland Italy (515), Poland (444) and Ukraine (421). For the remaining territories, fewer than 400 naturalized aliens were listed. The highest numbers of invasive species (Fig 4D) were recorded in mainland Spain (279), mainland Italy (214), Norway (182), Serbia (152) and central-European Russia (150). In all other territories, fewer than 150 invasive species were listed. We excluded merged categories of casual+naturalized or naturalized+invasive status from

Table 1. The overview of 55 European territories with counts of alien species in each of the categories of residence time and invasion status, for better comparability excluding hybrids, cultivars and species with uncertain alien status in Europe (counts including previous species groups are available in the Supplementary Table S4). Arch – archaeophytes; neo – neophytes; undistinguished (arch+neo) – species listed as an alien with not-specified residence time or species subsuming infraspecific taxa with both arch and neo status in a given territory; cult – cultivated species; cas – casual; cas+nat – casual and naturalized not separated; nat+inv – naturalized and invasive not separated; nat – naturalized; inv – invasive; uncertain+NA invasion status not reliable assessed or not available at all. Territories are arranged in descending order according to the number of listed alien species.

European territory	Number of alien species	arch	neo	undistinguished aliens (arch+neo)	cult	cas	cas+nat	nat	nat+inv	inv	uncertain +NA
Belgium	2,289	–	2,289	–	–	1,687	–	525	–	58	19
Norway	1,750	20	1,722	8	–	760	–	788	–	182	20
United Kingdom	1,663	176	1,469	18	–	498	–	877	–	54	234
Czech Republic	1,561	263	1,264	34	233	899	1	372	–	56	–
Spain	1,534	21	781	732	–	611	–	631	–	279	13
France	1,492	70	1,145	277	–	217	6	1150	–	64	55
Austria	1,410	–	1,410	–	–	802	–	266	–	18	324
Italy	1,382	125	1,241	16	–	625	–	515	–	214	28
Ukraine	1,043	148	865	30	–	552	–	421	–	58	12
Switzerland	1,038	220	767	51	–	–	–	–	–	–	1,038
Germany	910	165	631	114	–	102	481	–	172	–	155
Poland	902	147	362	393	–	381	–	444	–	72	5
Canary Islands	891	–	249	642	–	91	377	117	70	144	92
Republic of Ireland	891	–	–	891	40	656	–	106	89	–	–
Slovakia	810	219	568	23	–	453	–	327	–	29	1
Netherlands	773	–	245	528	–	–	–	–	–	–	773
Romania	740	23	703	14	–	532	–	106	–	88	14
Belarus	682	–	–	682	–	–	631	–	–	51	–
Sweden	677	–	677	–	–	–	–	–	–	–	677
Hungary	675	–	675	–	–	535	–	72	–	68	–
Portugal	634	11	610	13	–	–	–	–	–	–	634
Madeira	627	–	78	549	–	177	–	381	–	69	–
Corsica	562	115	416	31	–	151	–	335	–	72	4
Sardinia	561	144	379	38	–	269	–	184	–	71	37
Lithuania	552	–	507	45	–	297	–	10	245	–	–
Slovenia	544	215	302	27	–	–	–	–	–	–	544
Malta	483	19	444	20	–	213	–	204	–	36	30
Sicily	429	69	352	8	–	196	–	193	–	14	26
Greece	413	37	275	101	–	124	1	19	203	50	16
Georgia	352	–	–	352	–	144	–	127	–	16	65
Turkey	324	59	260	5	–	105	–	219	–	–	–
Iceland	323	–	323	–	–	264	–	57	–	2	–
Baleares	290	–	–	290	–	110	–	–	173	–	7
Azores	287	–	287	–	–	68	59	136	–	24	–
Crete	262	–	–	262	–	131	3	1	126	–	1
Bosnia & Herzegovina	252	70	170	12	–	135	–	62	–	55	–
Albania	219	–	–	219	–	117	–	–	102	–	–
Moldova	203	–	–	203	–	–	–	–	–	–	203
Serbia	186	–	–	186	–	–	34	–	–	152	–
Croatia	182	17	131	34	13	–	–	22	–	63	84
Central European Russia	150	–	–	150	–	–	–	–	–	150	–
Luxembourg	116	–	–	116	–	–	–	116	–	–	–
S European Russia	102	–	–	102	–	–	–	–	–	102	–
Denmark	91	–	–	91	–	–	–	–	–	–	91
Svalbard	81	–	81	–	–	71	–	9	–	–	1
Latvia	70	–	70	–	–	–	–	–	–	13	57
NW European Russia	65	–	–	65	–	–	–	–	–	65	–
E European Russia	61	–	–	61	–	–	–	–	–	61	–

European territory	Number of alien species	arch	neo	undistinguished aliens (arch+neo)	cult	cas	cas+nat	nat	nat+inv	inv	uncertain +NA
Bulgaria	59	–	–	59	–	–	–	–	–	59	–
Finland	53	–	–	53	–	–	–	–	–	–	53
Montenegro	47	–	47	–	–	–	–	–	–	47	–
Estonia	35	–	35	–	–	–	–	–	–	35	–
Kaliningrad region	31	–	–	31	–	–	–	–	–	31	–
North Caucasus	22	–	–	22	–	–	–	–	–	22	–
N European Russia	20	–	–	20	–	–	–	–	–	20	–

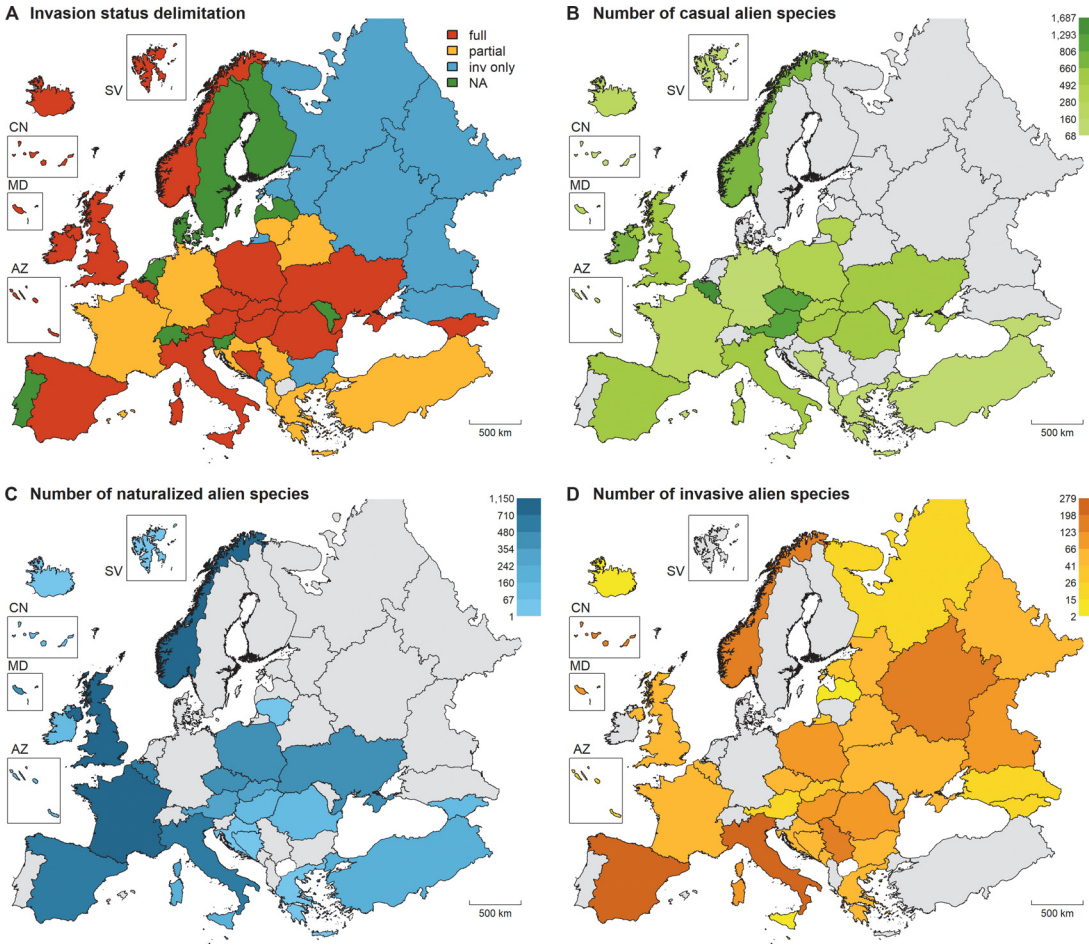

Fig. 4. Maps of European territories with (A) indication of the invasion status categories used in available inventories: full – casual, naturalized and invasive species distinguished; partial – casual and naturalized only or casual and naturalized+invasive or casual+naturalized and invasive distinguished; inv only – only invasive species lists available; NA – invasion status not assessed in available sources; (B) the number of casual alien species; (C) the number of naturalized alien species and (D) the number of invasive alien species if distinguished in available inventories. North Macedonia without recent inventory is white; territories where given categories of invasion status are not distinguished are grey. Infraspecific taxa are subsumed to the species level; hybrids, cultivars, and uncertain alien species are excluded. AZ – Azores; MD – Madeira; CN – the Canary Islands; SV – Svalbard.

these numbers. The complete overview of all European territories with all categories and corresponding counts of alien species, including hybrids, cultivars and species with uncertain alien status, is presented in Supplementary Table S4.

Most successful alien plant species

We identified 114 alien species whose occurrence is documented from more than half (i.e. ≥ 28) of the territories for which the data exist, comprising 1.6% of all alien species in Europe, including hybrids and cultivars. The great majority of alien species (72.8%) were documented in five or fewer European territories (Fig. 5). The most successful alien species, based on the number of territories from which they were reported, include (in descending order of frequency) *Erigeron canadensis*, *Amaranthus retroflexus*, *Galinsoga parviflora*, *Robinia pseudoacacia*, *Galinsoga quadriradiata*, *Helianthus tuberosus* and *Oenothera biennis*. These species are also considered invasive in many territories and categorized as neophytes across all of Europe (Table 2).

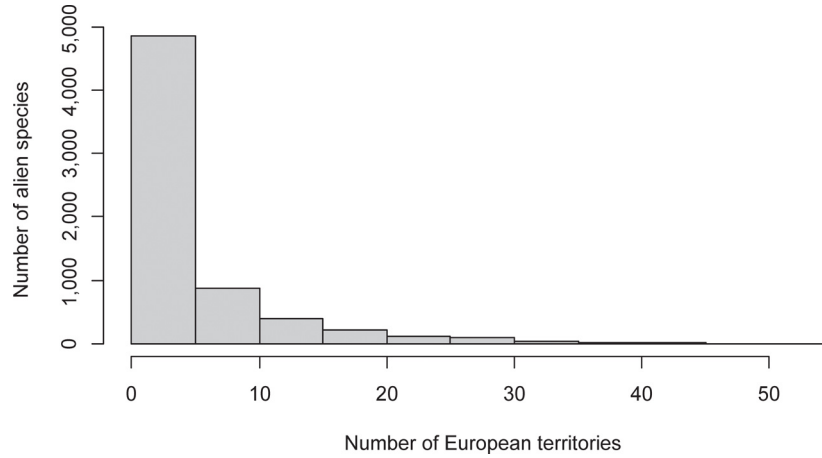

Fig. 5. Frequency of occurrence of 7,335 alien plant species in European territories (n = 55).

We found contradicting assignments to residence time categories for some of the most widespread alien species. Despite originating from outside Europe, being native to the Americas, Asia or Australia, these species were inconsistently classified as either neophytes or archaeophytes in some European territories. However, such cases only constituted rare exceptions from otherwise broadly accepted species statuses. For instance, *Veronica persica,* originating in north-western Iran, is generally regarded as a neophyte in Europe, but in the alien inventory of Corsica, it was classified as an archaeophyte. Similarly, *Amaranthus albus* and *A. blitoides*, originating in the Americas, are considered neophytes across all checklists but Turkey, where they are regarded as archaeophytes. Some widespread aliens showed contradicting residence times even in neighbouring territories. *Medicago sativa* is considered an archaeophyte in the Mediterranean part of Europe, but in Portugal, it is reported as a neophyte, and in the rest of Europe, it is listed as an undistinguished alien or neophyte. A similar case is *Sorghum halepense*, generally

Table 2. The most frequent alien plant species in European territories. For each species, we listed the numbers of European territories where it has been considered as alien, archaeophyte (arch), neophyte (neo) or undistinguished alien (arch+neo) – species subsuming infraspecific taxa with both arch and neo status or species assessed as an alien with not-specified residence time. Further, we listed numbers of European territories where a given species has been assigned to categories of invasion status, namely cas – casual; cas+nat – casual and naturalized status not separated; nat+inv – naturalized and invasive status not separated; nat – naturalized; inv – invasive; uncertain+NA – invasion status not reliable assessed or not available at all. None of the most frequent alien species has been evaluated as cultivated, thus this category was omitted. In this overview, only taxa at the species level were considered. A complete list of alien species, including hybrids, cultivars and species with uncertain alien status in Europe, is available in Supplementary Table S5. Notes: [1]incl. *Helianthus tuberosus* s.l.; [2]incl. *Datura stramonium* subsp. *stramonium* and *D. stramonium* subsp. *tatula*; [3]incl. *Erigeron annuus* subsp. *annuus* and *E. annuus* subsp. *septentrionalis*; [4]incl. *Matricaria discoidea* subsp. *discoidea* and *M. discoidea* subsp. *occidentalis*; [5]incl. *Medicago sativa* subsp. *sativa* and *M. sativa* subsp. *microcarpa*; [6]incl. *Xanthium orientale* subsp. *orientale*, *X. orientale* subsp. *californicum*, *X. orientale* subsp. *italicum* and *X. orientale* subsp. *riparium*; [7]incl. *Eleusine indica* subsp. *indica* and *E. indica* subsp. *africana*; [8]incl. *Panicum miliaceum* subsp. *miliaceum, P. miliaceum* subsp. *agricola* and *P. miliaceum* subsp. *ruderale*.

Species name	Number of European territories	arch	neo	undistinguished aliens (arch+neo)	cult	cas	cas+nat	nat	nat+inv	inv	uncertain +NA
Erigeron canadensis	53	–	32	21	–	–	2	10	5	27	9
Amaranthus retroflexus	49	–	29	20	–	2	1	11	5	21	9
Galinsoga parviflora	46	–	30	16	–	1	2	13	4	18	8
Robinia pseudoacacia	44	–	28	16	–	1	–	8	4	25	6
Galinsoga quadriradiata	43	–	27	16	–	1	2	12	3	17	8
Helianthus tuberosus[1]	43	–	26	17	–	5	–	7	3	23	5
Oenothera biennis	43	–	25	18	–	2	1	12	3	15	10
Elodea canadensis	42	–	25	17	–	–	–	7	4	22	9
Juncus tenuis	42	–	24	18	–	1	1	9	3	21	7
Datura stramonium[2]	41	–	27	14	–	2	2	14	4	12	7
Veronica persica	41	1	27	13	–	–	3	16	4	11	7
Ambrosia artemisiifolia	40	–	26	14	–	6	1	5	1	20	7
Cuscuta campestris	40	–	29	11	–	5	2	11	3	12	7
Erigeron annuus[3]	40	–	23	17	–	1	–	10	4	19	6
Matricaria discoidea[4]	39	–	28	11	–	1	1	11	4	14	8
Medicago sativa[5]	39	7	19	13	–	6	2	18	2	5	6
Xanthium spinosum	39	–	27	12	–	6	2	10	3	13	5
Amaranthus albus	38	1	24	13	–	3	3	13	4	9	6
Sorghum halepense	38	5	18	15	–	7	3	9	4	11	4
Xanthium orientale[6]	38	–	22	16	–	2	–	8	4	20	4
Acer negundo	37	–	24	13	–	3	–	2	3	25	4
Ailanthus altissima	37	–	27	10	–	–	1	2	3	27	4
Amaranthus hybridus	37	–	26	11	–	5	1	9	3	12	7
Impatiens parviflora	37	–	21	16	–	3	–	1	2	24	7
Oxalis stricta	37	–	23	14	–	2	2	9	5	10	9
Solidago canadensis	37	–	23	14	–	1	–	5	1	23	7
Amaranthus blitoides	36	1	24	11	–	4	3	12	4	8	5
Bidens frondosa	36	–	24	12	–	1	–	6	3	22	4
Eleusine indica[7]	36	–	26	10	–	8	2	8	3	10	5
Euphorbia maculata	36	–	26	10	–	3	2	11	4	11	5
Panicum miliaceum[8]	36	8	11	17	–	11	3	11	3	3	5
Impatiens glandulifera	35	–	21	14	–	–	–	2	3	24	6
Reynoutria japonica	35	–	24	11	–	3	–	1	2	22	7

Table 3. Families with the highest numbers of plant species in European alien flora (> 50 species listed, in descending order). Families were classified according to APG IV. The table shows the total number of alien species listed in inventories belonging to a given family; numbers of alien species assigned to the categories of residence time: arch –archaeophytes; neo – neophytes; undistinguished (arch+neo) – species subsuming infraspecific taxa with both arch and neo status or species assessed as an alien with not-specified residence time; and numbers of species reaching given category as the most advanced invasion status across all territories they occur: cult – cultivated; cas – casual; cas+nat –casual and naturalized not separated; nat+inv – naturalized and invasive not separated; nat – naturalized; inv – invasive; uncertain – invasion status not reliable assessed or not available at all. Hybrids, cultivars and species with uncertain alien status in Europe were omitted. A complete list of families with all species included is available in Supplementary Table S6.

Family	Number of alien species	arch	neo	undistinguished (arch+neo)	cult	cas	cas+nat	nat	nat+inv	inv	uncertain +NA
Asteraceae	889	9	693	187	4	274	33	269	40	119	150
Poaceae	653	4	498	151	1	252	31	196	23	129	21
Fabaceae	422	8	317	97	1	150	22	137	34	64	14
Rosaceae	376	5	327	44	10	105	14	140	27	57	23
Brassicaceae	268	4	192	72	3	76	13	94	20	48	14
Lamiaceae	199	–	133	66	1	73	11	74	19	14	7
Amaranthaceae	181	–	130	51	–	73	10	33	18	42	5
Caryophyllaceae	159	4	110	45	1	58	9	56	10	12	13
Apiaceae	145	3	88	54	1	47	9	50	13	18	7
Plantaginaceae	133	3	99	31	–	48	5	57	3	10	10
Solanaceae	127	–	95	32	–	48	4	38	9	25	3
Boraginaceae	123	–	92	31	1	42	1	55	4	16	4
Asparagaceae	119	–	91	28	1	42	2	50	5	14	5
Ranunculaceae	120	5	83	32	–	35	8	59	3	6	9
Onagraceae	109	–	100	9	1	26	2	44	7	25	4
Cyperaceae	103	2	81	20	–	25	5	40	5	15	13
Polygonaceae	102	1	82	19	–	26	7	43	6	19	1
Crassulaceae	92	1	76	15	1	27	2	39	8	11	4
Iridaceae	92	–	80	12	1	16	4	53	11	4	3
Malvaceae	91	1	55	35	1	37	3	29	6	11	4
Euphorbiaceae	86	–	57	29	–	25	9	28	3	15	6
Amaryllidaceae	81	–	61	20	1	21	3	35	8	9	4
Cactaceae	79	–	63	16	–	35	–	23	1	20	–
Caprifoliaceae	74	1	57	16	–	16	2	42	6	7	1
Geraniaceae	74	1	58	15	–	23	2	35	5	5	4
Papaveraceae	74	1	48	25	–	19	4	36	3	8	4
Pinaceae	62	–	53	9	3	5	1	35	4	13	1
Campanulaceae	51	–	43	8	1	17	–	25	–	3	5

considered an archaeophyte in the Mediterranean but classified as a neophyte in Portugal and Spain. Inconsistencies also exist in the evaluation of residence time of subspecies. *Panicum miliaceum*, for example, comprises three subspecies. While the type subspecies is typically considered an archaeophyte in Europe, there are exceptions, such as Austria, Belgium and Lithuania, where it is listed as a neophyte. *Panicum miliaceum* subsp. *agricola* and subsp. *ruderale* are generally regarded as neophytes in all territories except mainland Italy. Therefore, *Panicum miliaceum* usually received an unspecified residence time (arch+neo) during the reassessment at the species level, except for mainland Italy. The complete list of alien plant species, including hybrids and cultivars, along with the number of territories occupied and the frequency of their assignment to particular residence time and invasion status categories, is given in Supplementary Table S5.

Table 4. Genera with the highest numbers of plant species in the European alien flora (> 30 species listed). Genera are shown in descending order according to the total number of species. The table shows the total number of alien species listed in inventories belonging to a given genus; numbers of alien species assigned to the categories of residence time: arch –archaeophytes; neo –neophytes; undistinguished (arch+neo) – species subsuming infraspecific taxa with both, arch and neo status or species assessed as an alien with not-specified residence time; and numbers of species reaching given category as the most advanced invasion status across all territories they occur: cult – cultivated; cas – casual; cas+nat – casual and naturalized not separated; nat+inv – naturalized and invasive not separated; nat – naturalized; inv – invasive; uncertain+NA – invasion status not reliable assessed or not available at all. Hybrids, cultivars and species with uncertain alien status in Europe were omitted. A complete list of families with all species included is presented in Supplementary Table S7.

Genus	Number of alien species	arch	neo	undistinguished aliens (arch+neo)	cult	cas	cas+ nat	nat	nat+ inv	inv	uncertain +NA
Hieracium	147	1	134	12	–	6	2	14	5	–	120
Oenothera	79	–	73	6	–	13	1	38	7	16	4
Euphorbia	76	–	49	27	–	19	9	28	3	12	5
Cotoneaster	74	–	73	1	–	26	–	32	4	9	3
Trifolium	71	1	62	8	1	33	7	21	4	3	2
Centaurea	69	2	56	11	–	37	2	21	2	4	3
Solanum	56	1	39	16	–	19	3	20	1	10	3
Silene	55	1	39	15	1	24	3	22	1	3	1
Veronica	49	1	34	14	–	13	1	24	2	4	5
Allium	49	–	35	14	1	11	2	25	4	3	3
Rumex	48	1	37	10	–	7	7	24	3	7	–
Vicia	48	1	24	23	–	15	3	19	3	6	2
Opuntia	46	–	41	5	–	11	–	21	1	13	–
Rubus	46	1	42	3	–	6	–	26	3	2	9
Eragrostis	45	–	38	7	–	29	–	8	1	7	–
Amaranthus	44	–	34	10	–	13	2	6	3	18	2
Cyperus	43	1	29	13	–	11	2	14	1	11	4
Bromus	43	1	26	16	–	21	2	13	–	4	3
Rosa	40	–	32	8	1	8	8	12	3	5	3
Geranium	39	1	30	8	–	6	–	29	2	1	1
Senecio	38	–	28	10	–	8	2	20	–	7	1
Medicago	38	1	24	13	–	13	4	12	2	5	2
Artemisia	38	–	22	16	–	13	6	12	4	3	–
Salvia	37	–	30	7	–	13	3	15	4	2	–
Sedum	35	1	29	5	–	6	1	15	7	4	2
Ranunculus	34	–	20	14	–	7	4	20	–	–	3
Iris	32	–	30	2	1	4	2	20	3	–	2
Potentilla	32	–	29	3	–	10	1	11	5	3	2
Prunus	31	2	14	15	3	5	4	5	4	7	3

Most alien species-rich families and genera

The alien flora of Europe comprises species from 208 plant families (excluding hybrids, cultivars and uncertain alien species). The families richest in alien species are *Asteraceae*, *Poaceae*, *Fabaceae*, *Rosaceae* and *Brassicaceae* (Table 3). The alien species richness of plant families is mainly due to the numbers of neophytes. The families with the highest numbers of alien species also tend to have most naturalized and invasive species. The most successful genera in the European alien flora are *Hieracium*, *Oenothera*, *Euphorbia*, *Cotoneaster* and *Trifolium* (Table 4). For instance, the highest number of alien *Hieracium* species was recorded in Sweden (78% of all *Hieracium* species records), where the corresponding species were listed as neophytes without distinguishing their invasion status.

However, it is important to note that the genus *Hieracium* contains apomictic taxa, making their numbers not entirely comparable to those of other genera. The richness of alien species within a given genus typically correlates with the number of neophytes it includes. Notably, the genera with the most naturalized alien species in Europe are *Oenothera*, *Cotoneaster*, *Geranium* and *Euphorbia*, while those with the highest numbers of invasive alien species include *Amaranthus*, *Oenothera*, *Opuntia* and *Euphorbia*. In total, 1,751 genera contribute their species to the European alien flora (excluding hybrids, cultivars and uncertain alien species). The complete lists of plant families and genera contributing their species to the alien flora of Europe are presented in Supplementary Tables S6 and S7.

Geographical origin of European alien flora

In total, 317 alien plant species (i.e. 4.4% of alien species with assigned origin) are native to more than one world region. The highest proportion of species in the European alien flora originate from temperate Asia (20.4% of assigned origins), temperate Europe (19.6%), the Mediterranean region (19.0%) and the Americas (16.0%). North America donated more alien species (8.9%) than Central and South Americas combined (7.2%; Fig. 6). Most archaeophytes were considered of Mediterranean origin (24.7%) or as hybrids and anecophytes (21.5%). Neophytes originated mostly in temperate Asia (20.0%), temperate Europe (19.4%) and the Americas (19.0%). The same pattern as observed for neophytes was also evident for undistinguished aliens. Casual alien species mainly originated in temperate Asia (20.0%), the Americas (18.6%), and the Mediterranean region (18.0%). Naturalized alien species came from temperate Asia (21.8%), temperate Europe (20.8%) and the Mediterranean region (20.2%). Conversely, invasive alien species more frequently originated from the Americas (22.9%, of which North America accounted for more than half, i.e. 11.7%), followed by temperate Asia (19.7%), temperate Europe (16.0%) and the Mediterranean region (16.0%). Alien species with uncertain invasion status came mostly from temperate Europe (31.7%) and the Mediterranean region (19.0%). A complete overview of the proportions of alien species with different residence times, invasion statuses, and regions of origin is presented in Supplementary Table S8.

Discussion

Alien species richness in European flora

We compiled information on 7,335 alien plant species occurring in Europe, which is an increase compared to the previous comprehensive study of European alien flora (Lambdon et al. 2008) that was based on the DAISIE database (DAISIE 2009) and reported 5,789 species, including hybrids. We also identified more alien plant taxa, including species, subspecies and hybrids (8,079), than reported for Europe by Arianoutsou et al. (2021) based on the EASIN database (6,250 taxa). In our study, we included both groups of aliens, i.e. taxa of extra- and within-European origin, to provide a complete overview of European alien flora.

The observed increase in the total richness of alien species compared to earlier studies can have several causes. Firstly, there has been an accumulation of records of escaped and

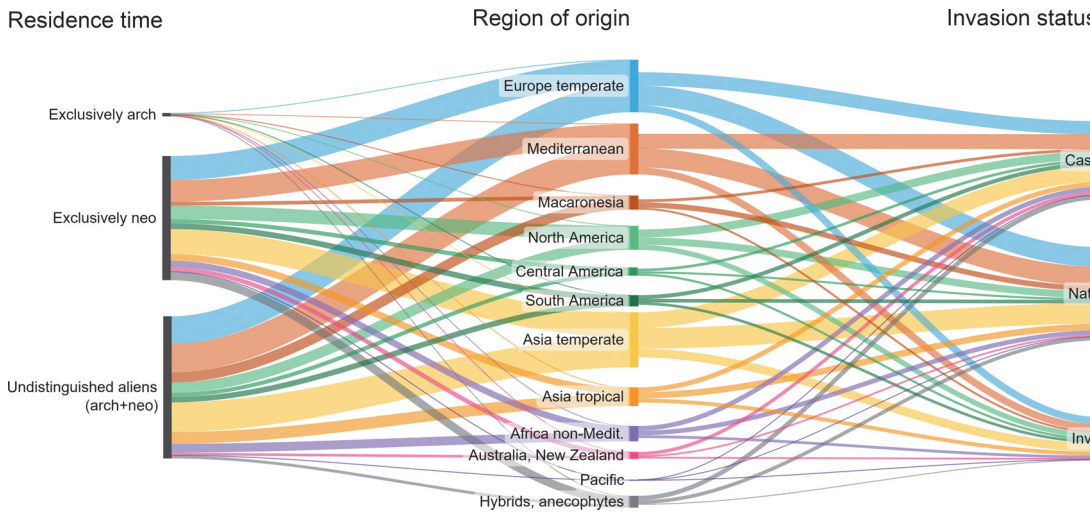

Fig. 6. Geographical origin of European alien flora. Sankey plot shows the proportions of alien species assigned to three categories of residence time and three main categories of invasion status originating in 11 world regions or being hybrids and anecophytes based on distribution data in POWO (2023). Residence time: exclusively arch – species listed exclusively as archaeophytes; exclusively neo – species listed exclusively as neophytes; undistinguished aliens (arch+neo) – species subsuming infraspecific taxa with both arch and neo status or species assessed as an alien with not-specified residence time or species having arch and neo status in different European territories; invasion status: cas – casual; nat – naturalized; inv – invasive. Please note that merged categories of invasion status (cas+nat, nat+inv and uncertain+NA) and cultivated alien species were omitted from the right part. Region of origin: temperate Europe – includes Europe except for the Mediterranean part; Mediterranean – includes Mediterranean part of Europ; Mediterranean northern Africa and the Middle East; Africa non-Medit. – includes Africa except for the Mediterranean northern part; North America; Central America; South America; temperate Asia; tropical Asia; Australia and New Zealand; Pacific; Hybrids and anecophytes – include spontaneous hybrids with at least one parental species considered alien to Europe, artificial hybrids originated from cultivation, cultivars and species without known native range. The map delimiting distinguished regions of origin based on TDWG level 3 regions is shown in Supplementary Fig. S1.

temporarily occurring alien plant taxa (i.e. casual aliens) since the earliest study (Lambdon et al. 2008). Although Haubrock et al. (2023) found that the year-to-year increase in plants newly introduced to Europe was slowing down or even started to decline in some European countries over the past thirty years, the recording of new escapes of already introduced species has been going on, especially in countries with intensive floristic research. Such records stored in floristic repositories and herbaria are more likely to appear sooner in regional and national checklists than in international databases where the data delivery can be delayed. The substantial contribution of casual alien plants to the total richness of alien flora in a given territory is illustrated in countries with comprehensive national checklists with well-distinguished and recorded casual aliens, such as the Czech Republic (Pyšek et al. 2002, 2012 with updates in Pyšek et al. 2022b and PLADIAS; Chytrý et al. 2021), Austria (Essl & Rabitsch 2002 with unpublished updates), or Belgium (Verloove 2006). Despite their smaller areas, these countries are among the top territories in terms of the total number of alien taxa recorded. Discrepancies in the recording of casual taxa among European territories likely contribute to the fact that the total number of reported casuals is lower than that of naturalized species, although casuals are

a more numerous group than naturalized species, which recruit from them (Williamson & Fitter 1996, Richardson et al. 2000, Richardson & Pyšek 2006, Pyšek et al. 2012).

Secondly, the increase in alien plant richness compared to earlier studies can also be due to increasing knowledge in European countries. Compared to Lambdon et al. (2008), who also provided territories-based statistics, we recorded more alien plants in 68.3% of 41 territories that were comparably delimited in both studies. In Hungary, Madeira and Baleares, we recorded a decline of less than 50 species; slightly lower numbers of alien plant species probably result from different taxonomic concepts and reassessments of species status in newer sources. For example, we subsumed *Amaranthus hybridus* var. *aciculatus* under *Amaranthus hybridus* and *Capsicum annuum* subsp. *frutescens* under *Capsicum annuum* in Madeira based on taxonomic concepts in the Euro+Med PlantBase (Euro+Med 2006–2024), and subsumed all subspecies and varieties of *Brassica rapa* under one taxon (i.e. *Brassica rapa* groups/cultivars) in Baleares and Hungary.

In contrast, larger differences in the number of aliens were found in the Azores, Bulgaria, Denmark, Estonia, Finland, Latvia, Slovenia, and the United Kingdom (a decline of more than 100 species). Here, it can be because Lambdon et al. (2008) based their analysis on entire floras, while in our study, we included only more recent specialized checklists that might be focused on specific categories of alien plants or are regionally restricted. In some countries, the difference can also result from erroneous status assignments in the DAISIE database (DAISIE 2009). For example, about 557 taxa native to Bulgaria were misclassified as aliens in DAISIE, including e.g. *Artemisia alba*, *Arnica montana*, *Carduus nutans* or *Chondrilla juncea* (Euro+Med 2006–2024). In Denmark, there were about 234 native taxa (Buchwald et al. 2013) misclassified as alien or neophytes, e.g. *Aegopodium podagraria*, *Myosotis sylvatica* and *Veronica spicata*. In Finland, about 249 native taxa were misclassified in the DAISIE database as aliens, including *Campanula patula*, *Geranium pratense* and *Ajuga reptans* (FinBIF 2020). Compared to Lambdon et al. (2008), we also found new alien plant inventories for additional 14 territories, including six from European Russia. Nevertheless, the increase in the total alien taxa/species richness in compared studies highlights the importance of national and regional checklists as primary sources of up-to-date information on alien plants in Europe and the need to update new records regularly into large summarizing databases.

Alien species categorization and its inconsistencies

We found large differences in the recognition of invasion status, ranging from full categorization in 43.6% of the 55 European territories analysed (i.e. casual, naturalized and invasive status assigned separately) to partly distinguished categories in 21.8% of territories and 20.0% of territories that only listed invasive species. In some other territories with otherwise complete national checklists, inventories do not provide information on invasion status and only report on residence time (14.5%, e.g. the Netherlands, Portugal, Slovenia, Sweden and Switzerland). In general, checklists with fully distinguished residence time (categories of archaeophytes and neophytes assigned unequivocally) were available for even fewer territories (40.0%) than was the case with invasion status, whereas 32.7% of territories only had neophyte lists. This suggests a persistent imbalance in the level of detail with which the alien flora of the different parts of Europe has been studied.

Regarding invasion status, we also identified a category not considered in the previous European overviews, i.e. cultivated alien plants. This category was clearly separated only in three territories: the Czech Republic (including additional data in PLADIAS; Chytrý et al. 2021), the Republic of Ireland and Croatia. However, regarding low numbers of cultivated taxa reported in particular checklists, this category represents an incomplete and subjective selection rather than complete lists of taxa that have the potential to escape or to be released because the identification of such potential depends on the available evidence of continuous propagule pressure from planted species (Pyšek et al. 2012). Although this category could help to indicate those species that may appear in the wild in the future as casual aliens, the methodological difficulties and lack of reliable information associated with selecting species belonging to this category make it a questionable part of alien species checklists. However, because of the low total number of plants in this category across checklists (~1% of alien taxa), it did not much influence the alien species richness of the European flora as reported in our study.

We identified 2,662 naturalized species or 2,990 naturalized taxa. These numbers are lower than those of naturalized taxa/species reported by Lambdon et al. (2008) and Pyšek et al. (2017). Lambdon et al. (2008) recorded 3,749 species naturalized in Europe. In the more recent overview of naturalized species of Europe based on the GloNAF database (Pyšek et al. 2017), 4,139 taxa (incl. subspecies) naturalized in Europe are listed. However, compared to the previous studies, where invasive species were presented as a subset of naturalized species, we separated them into distinct categories and displayed their numbers separately. Moreover, we also adopted a more conservative approach. We used two other categories, transient to naturalized, if source inventories did not separate naturalized plants from casual or invasive plants (20.0% of territories). When we merge clearly identified naturalized and invasive plants with the transient naturalized+invasive category, we arrive at 4,111 species or 4,501 naturalized taxa in Europe that exceed previously reported numbers. Therefore, even when using naturalized aliens as a metric, which is the most robust category because of rigorous criteria for inclusion (Richardson & Pyšek 2012), there is an evident increase attributable to a combined effect of new introductions and improved quality of data.

A general weakness of national inventories, compared to the specialized databases focused on specific groups of alien species, such as GloNAF on naturalized (Pyšek et al. 2017, van Kleunen et al. 2019), is the persistent inconsistency or incompleteness in the categorization of invasion status. Inventories currently available for many territories of south-eastern and north-eastern Europe often separate only invasive species from other reported alien plants and do not assess naturalized species as a separate category. However, for the Baltic countries, Finland, Sweden and European Russia, such information is included in the GloNAF database (Pyšek et al. 2017). In contrast, for those countries where information on naturalized alien plants is available, this category is the most represented (e.g. the United Kingdom, France, Norway, Belgium and mainland Italy), which is shown both here and in the previous European overviews (Lambdon et al. 2008, Pyšek et al. 2017). The numbers of naturalized species reported recently are even higher than those reported in Lambdon et al. (2008). This may indicate a shift of alien plants proceeding along the naturalization-invasion continuum towards forming established, self-sustaining populations and the continued introduction of plants with the potential to naturalize, as also shown in Lambdon et al. (2008).

Invasive plants were not separated from naturalized plants in the previous studies of European alien flora except for that by Pyšek et al. (2017). In their study, the classification of a species as invasive was based on impact, following the IUCN (2000) definition, and they list numbers of invasive species for 61 territories, ranging from 1 to 139 in mainland Italy (Pyšek et al. 2017). This is much less than what we found, i.e. 1,082 alien plant taxa labelled as invasive in at least one European territory; one reason is that the GloNAF database, on which that analysis was based, focused on naturalized rather than invasive plants (Pyšek et al. 2017, van Kleunen et al. 2019). The majority of alien plant inventories that we worked with used the definition of invasive species based on their population ecology, with population growth and spread being the main criteria (Richardson et al. 2000, Blackburn et al. 2011). Labelling plants as invasive based on the rate of spread estimated from floristic observations is more suitable for general agreement among botanists because the rigorous assessment of impacts has been only recently put on robust theoretical grounds (Blackburn et al. 2014, Nentwig et al. 2018). In our data set, assigning species as invasive was relatively frequent (almost 70%, i.e. 38 territories) compared to other categories of invasion status. The increasing focus on invasive species reflects that biological invasions are recognized as an important policy topic in Europe, raising public awareness (Genovesi & Shine 2004, Genovesi et al. 2014). Still, listing a species as invasive may be subjected, to some degree, to political decisions regardless of observed ecological reality, as is the case with e.g. *Robinia pseudoacacia* (Vítková et al. 2020).

Although our definition of invasiveness does not include impact, invasive plants can adversely affect biodiversity, health or economy (Pyšek et al. 2020). Therefore, identifying invasive species in inventories is essential for their early detection, mapping and monitoring their impacts. Early detection of invasive species is crucial for applying location-specific management and successful eradication (Tataridas et al. 2022). The information on the impact of invasive species is mostly not included in inventories (but see e.g. Pyšek et al. 2022b), or only the most striking examples are mentioned (e.g. Petrova et al. 2013), description of impact in species factsheets is provided (e.g. Sanz-Elorza et al. 2004, Campos & Herrera 2009), impact is indicated in the list with further details (impact yes/no, e.g. Verloove 2006, Pyšek et al. 2012) or a parallel classification system of types of impact is developed and assigned to the listed taxa (e.g. Essl & Rabitsch 2002). Subsequently, environmental and economic impact assessments are addressed in specialized studies that propose objective scoring systems based on reported detrimental effects, such as Environmental Impact Classification for Alien Taxa (EICAT), adopted by IUCN as an official tool for scoring impacts (Blackburn et al. 2014, Kumschick et al. 2015), or the Generic Impact Scoring System (GISS; Nentwig et al. 2016). Scoring systems enable comparisons among different taxa to prioritize management strategies (Nentwig et al. 2018, Yazlık et al. 2018).

Regarding residence time, archaeophytes are not distinguished in many European territories because separating them from native species is difficult and often uncertain given the incomplete knowledge of the past that depends on the availability of archaeological and palaeobotanical data (e.g. Verloove 2006, Pyšek et al. 2022b). The status of archaeophytes in a given territory therefore often remains debatable. Unlike neophytes, for which there are usually reliable historical records about the introduction and release/escape, archaeophytes also include traded crops found at archaeological sites; obtaining evidence of their historical occurrence in the wild is difficult. Species assessed as archaeophytes in

one country can be considered native or neophytes in other countries, given separation uncertainties (Ecseri & Honfi 2020). In northern Europe, there has also been a shift in the introduction time separating archaeophytes from neophytes. In some territories, it is shifted later compared to lower latitudes of Europe, e.g. in Sweden to 1700 CE (Tyler et al. 2015) or in Iceland to 1750 CE (Wasowitz et al. 2013). In the current inventory of Norway, the borderline is set to 1500 CE similar to the rest of Europe (Sandvik et al. 2019). Thus, this discrepancy also calls for further discussion on regional specifics. In invasion-level studies, the discrepancy in archaeophyte/neophyte borderline leads to an increasing share of within-European neophytes towards northern Europe, which reflects their archaeophytic or native origin in south-eastern Europe (Axmanová et al. 2021, Kalusová et al. 2023). We detected missing data on archaeophytes, especially in north-eastern Europe and some Balkans countries, but also in western Europe, including Belgium, the Netherlands and Denmark. Arianoutsou et al. (2021) identified 506 taxa as archaeophytes in Europe. A previous comparison focused on archaeophytes using specialized lists available in 15 European countries and revealed 560 taxa (Ecseri & Honfi 2020). We found 900 taxa considered archaeophytes in at least part of their European distribution range. The increasing accumulation of information about the immigration time of particular species, although difficult to obtain, has made it possible in some territories to newly distinguish residence time or reassess the status of already listed taxa in the newest inventories (e.g. in Corsica, Norway, Spain and Turkey).

In contrast, neophytes were distinguished more often in 65.5% of the European territories dealt with in our study. Arianoutsou et al. (2021) identified 4,790 taxa as neophytes; we recorded 6,906 neophyte taxa, including those that are archaeophytes in some European territories but were introduced to others after 1500 (–1750) CE. When we compared our study to the overview by Lambdon et al. (2008), the top territories regarding neophyte richness remained the same. Still, the neophyte numbers in territories increased between studies, e.g. in Belgium (1,969 species vs. 2,289 species in our study), Austria (1,070 vs. 1,410), the Czech Republic (1,046 vs. 1,264) and the United Kingdom (1,085 vs. 1,469). This increase during the last decade, mimicking trends in the total richness of alien plants, is likely related to the continued introductions of alien taxa from other territories, to the escapes of already cultivated plants, and partly to the taxonomic reassessment of earlier herbarium specimens. Compared to the study of Lambdon et al. (2008), data on neophytes became recently available in e.g. Bosnia and Herzegovina, the Canary Islands, France or Norway. However, the main gaps remain in north-eastern Europe and some countries in the Balkan Peninsula, where residence time is not assessed and only undistinguished alien status is usually available, although classifying species with clearly extra-European origins as neophytes would be straightforward.

Geographical delimitation of European studies and data gaps

Geographical delimitation of studies and, thus, the number of included countries/territories could also influence why the most recent data presented here differ in alien species richness from previous studies. Lambdon et al. (2008) collated data for 48 regions, of which Israel and Greenland were omitted in our study due to the narrower delimitation of the European continent. We focused on 55 territories and only for two of them, namely North Macedonia and Liechtenstein, we did not find any recent alien plant checklist. In

contrast, our overview covered Albania, Bosnia and Herzegovina, Crete, Georgia, European Russia, Montenegro and Serbia, which were not previously considered but where new lists of alien species have emerged over the last decade. However, most of these territories often have incomplete inventories, so they did not contribute many alien taxa to the pooled list. Thus, the difference in geographical delimitation of both studies should not significantly contribute to the increasing trends in observed total alien species richness. Unfortunately, the study of Arianoutsou et al. (2021) does not provide a territory-based overview of the richness of alien taxa, preventing such a detailed comparison. Compared to Lambdon et al. (2008), we also separated the administrative territory of Sicily from the rest of mainland Italy, which was made possible by the regional subdivision, including Sicily and surrounding archipelagos available in Galasso et al. (2018).

Our results point to main data gaps in north-eastern Europe, the Balkan Peninsula, and some countries in western Europe that did not indicate invasion status in their checklists (see examples above). Apart from revisions and updates of inventories by local ecologists and botanists, we can use records accessible in existing specialized databases that collect information on distributions of naturalized plant taxa, such as GloNAF (van Kleunen et al. 2019), or alien plant taxa generally, such as the Global Biodiversity Information Facility (GBIF 2023). Moreover, political boundaries do not determine plant dispersal boundaries. Thus, complete inventories in the surrounding territories can also suggest which taxa have a high probability of introduction and occurrence in a given area. However, a cautious approach must be taken to reassess alien categorizations across different sources.

Successful alien plant species and inconsistencies in categorization of their status

The most successful species measured by the number of European territories invaded was *Erigeron canadensis*, an annual neophyte with a large native range in North, Central and South America (POWO 2023). This species has also been indicated as Europe's most widespread alien and naturalized species in previous studies (Lambdon et al. 2008, Pyšek et al. 2022a), and it is the most widely distributed naturalized species in the temperate biome of the world (Pyšek et al. 2017). *Erigeron canadensis* is now considered invasive in 27 European territories. In its native range, it behaves as an early successional colonizer of abandoned arable land and other disturbed sites, including roadsides and native vegetation of woodlands and floodplains (Weaver 2001). The species is a habitat generalist in Europe, preferring disturbed patches in many different habitat types. Campos et al. (2013) found it was one of the alien species with the broadest ecological amplitude. It invades forests and shrublands (Wagner et al. 2017, Kalusová et al. 2023), grasslands (Axmanová et al. 2021), and arable land and urban habitats (Lososová et al. 2004, 2011); however, there is no evidence of a strong impact on native communities (but see Shah et al. 2014). *Erigeron canadensis* has also naturalized almost globally (Pyšek et al. 2017), which is consistent with the hypothesis that species with extensive native ranges are also predisposed to have extensive invaded ranges (Lavoie et al. 2013). The rapid spread of *E. canadensis* across its invaded range is facilitated by the production of large amounts of small, wind-dispersed achenes (Weaver 2001), self-compatibility and autogamy (Hao et al. 2011), resistance to diseases and herbicides (Weaver 2001) and allelopathy (Shaukat et al. 2003).

Previous studies reported the same widespread alien species as we identified in our overview among their top 10–15 rankings (Lambdon et al. 2008, Pyšek et al. 2022a). These species are often annuals or short-lived plants, except for several perennials such as the forb *Helianthus tuberosus,* the graminoid *Juncus tenuis*, and the tree *Robinia pseudoacacia*. Many share similar traits that contribute to their successful invasion, such as large production of tiny fruits, efficient dispersal, and persistent seed banks (*Amaranthus* spp.; Mohler & Callaway 1995, Burnside et al. 1996), phenotypic plasticity (*Robinia pseudoacacia*; Bouteiller et al. 2021), vegetative reproduction (*Elodea canadensis*; Thiébaut 2007), allelopathy (*Ailanthus altissima*; Kowarik & Säumel 2007) and utilizations by humans (*Helianthus tuberosus*; Kays & Nottingham 2008), to name just a few examples.

Most widespread alien plants in Europe, often considered invasive wherever reported, are mainly of North- and/or South-American origin; fewer species come from temperate Asia. One exception is *Medicago sativa*, which is assessed as an anecophyte, i.e. a species with unknown native range. This translates into a higher representation of American (mainly North-American) species among the invasive plants, while among the naturalized ones, species from temperate Asia prevail (Pyšek et al. 2022b). The invasion success of North-American species in Europe, especially trees and shrubs, is related to their native range size and subsequent climatic niche width together with long residence times (Sychrová et al. 2022) or to the escape from native enemies (Reinhart et al. 2003). The higher representation of species from temperate Asia among naturalized plants can result from the time lag in their spread due to later introductions to Europe, as shown for Asian woody species (Kowarik 1995).

Although for alien species that are widespread across Europe, one would expect a broad agreement on their categorization, particularly regarding residence time relative to the region of origin and time since introduction, we found several discrepancies between European territories. The most striking ones are *Veronica persica* considered an archaeophyte in Corsica (Puddu et al. 2016), and *Amaranthus albus* and *A. blitoides*, which are considered archaeophytes in Turkey (Uludağ et al. 2017) despite being neophytes in all other territories with reported occurrence. Both *Amaranthus* species are clearly neophytes due to their North- to South-American origin (POWO 2023) and first records in Europe in 1778 for *A. albus* and 1759 for *A. blitoides* (Arianoutsou et al. 2021). The archaeophytic occurrence of *Veronica persica* in Corsica is also a clear misclassification. *Veronica persica* is considered an allotetraploid derived from the cross *V. ceratocarpa* × *V. polita* (Fisher 1987). It is native to the Elburz Mts in north-western Iran (Fisher 1987), and the first recorded escape in Europe occurred in 1805 (Lehmann 1907). In some cases, a critical revision of the assignment of a given taxon to a specific category is necessary, especially when the taxon's origin, often in combination with assessments of surrounding territories, indicates the possibility of erroneous classification.

Conclusions and outlooks

In this study, we present an updated overview of the alien flora of Europe based on the compilation and critical revision of data collected from national and regional alien plant inventories. These inventories represent essential sources of regional expert knowledge about the introduction, establishment, and spread of alien plants, and provide valuable

insights into plant invasions to the broader scientific community. Our results illustrate a substantial increase in the richness of alien floras throughout Europe, accompanied by significant advancement in the underlying knowledge over recent decades. However, despite considerable progress in data availability in individual European territories, data gaps remain, particularly in north- and south-eastern Europe. Inventories still vary considerably in the completeness of information, especially concerning the documentation of casual taxa and the distinction of naturalized species from other stages along the introduction-naturalization-invasion continuum. Major inconsistencies are also evident in the assessments of residence time and invasion status of particular taxa across territories. We suggest that integrating information from inventories and specialized databases of alien plants, along with critical review, can enhance data accuracy in less explored territories and provide a comprehensive view of the distribution of alien plant taxa across Europe. The updated information on alien taxa can also serve as a basis for macroecological analyses of plant invasions and inform prioritization of monitoring and management efforts.

Supplementary materials

Fig. S1. Map delineating the world regions of origin of alien plant species based on TDWG level 3 regions.
Table S1. Source national and regional inventories of the European alien flora.
Table S2. Overview of the taxa with groups of cultivars and other subordinal taxa subsumed.
Table S3. Decision table for the reassessment of the residence time status.
Table S4. Overview of 55 European territories with counts of alien species in each of the categories of residence time and invasion status, with hybrids and cultivars and uncertain alien species included.
Table S5. Complete list of vascular plant species in the European alien flora.
Table S6. Complete list of vascular plant families in the European alien flora.
Table S7. Complete list of vascular plant genera in the European alien flora.
Table S8. Proportions of alien species originated in 11 regions of the world grouped by residence time and invasion status.

Supplementary materials are available at https://www.preslia.cz

Acknowledgements

The study was financially supported by the Czech Science Foundation (EXPRO grant no. 19-28491X). PP was supported by EXPRO grant no. 19-28807X (Czech Science Foundation) and together with JD also by and long-term research development project RVO 67985939 (Czech Academy of Sciences). IB was funded by the Basque Government (IT1487-22). FE appreciates funding from the Austrian Science Fund FWF (project no. I 5825-B). JCS considers this work a contribution to his VILLUM Investigator project "Biodiversity Dynamics in a Changing World", funded by VILLUM FONDEN (grant 16549), and Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by the Danish National Research Foundation (grant DNRF173).

References

Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. – Botanical Journal of the Linnean Society 181: 1–20.

Arianoutsou M., Bazos I., Christoupoulo A., Kokkoris Y., Zikos A., Zervou S., Delipetrou P., Cardoso A. C., Deriu I., Gervasini E. & Tsiamis K. (2021) Alien plants of Europe: introduction pathways, gateways and time trends. – PeerJ 9: e11270.

Axmanová I., Kalusová V., Danihelka J., Dengler J., Pergl P., Pyšek P., Večeřa M., Attore F., Biurrun I., Boch S., Conradi T., Gavilán R. G., Jimenéz-Alfaro B., Knollová I., Kuzemko A., Lenoir J., Leostrin A., Medvecká J., Moeslund J. E., Obratov-Petkovic D., Svenning J.-C., Tsiripidis I., Vassilev K. & Chytrý M. (2021) Neophyte invasions in European grasslands. – Journal of Vegetation Science 32: e12994.

Aymerich P. & Sáez L. (2019) Checklist of the vascular alien flora of Catalonia (northeastern Iberian Peninsula, Spain). – Mediterranean Botany 40: 215–242.

Bivand R. (2020) classInt: choose univariate class intervals. Version 0.4-3. – URL: https://cran.r-project.org/web/packages/classInt/index.html.

Bivand R., Keitt T., Rowlingson B., Pebesma E., Sumner M., Hijmans R., Baston D., Rouault E., Warerdam F., Ooms J. & Rundel C. (2020) rgdal: bindings for the 'geospatial' data abstraction library. Version 1.5-12. – URL: https://cran.r-project.org/web/packa ges/rJava/index.html.

Blackburn T. M., Essl F., Evans T., Hulme P. E., Jeschke J. M., Kühn I., Kumschick S., Marková Z., Mrugała A., Nentwig W., Pergl J., Pyšek P., Rabitsch W., Ricciardi A., Richardson D. M., Sendek A., Vilà M., Wilson J. R. U., Winter M., Genovesi P. & Bacher S. (2014) A unified classification of alien species based on the magnitude of their environmental impacts. – PLoS Biology 12: e1001850.

Blackburn T. M., Pyšek P., Bacher S., Carlton J. T., Duncan R. P., Jarošík V., Wilson J. R. U. & Richardson D. M. (2011) A proposed unified framework for biological invasions. – Trends in Ecology and Evolution 26: 333–339.

Boessenkool B. (2021) berryFunctions: function collection related to plotting and hydrology. Version 1.19.1. – URL: https://cran.r-project.org/web/packages/berryFunctions/index.html.

Bouteiller X. P., Moret F., Ségura R., Klisz M., Martinik A., Monty A., Pin J., van Loo M., Wojd T., Porte A. J. & Mariette S. (2021) The seeds of invasion: enhanced germination in invasive European populations of black locust (*Robinia pseudoacacia* L.) compared to native American populations. – Journal of Plant Biology 23: 1006–1017.

Brundu G. & Richardson D. M. (2016) Planted forests and invasive alien trees in Europe: a code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. – In: Daehler C. C., van Kleunen M., Pyšek P. & Richardson D. M. (eds), Proceedings of 13th International EMAPi conference, Waikoloa, Hawaii, NeoBiota 30: 5–47.

Buchwald E., Wind P., Bruun H. H., Møller P. F., Ejrnæs R. & Svart H. E. (2013) Hvilke planter er hjemmehørende i Danmark [Which plants are native to Denmark]? – Flora & Fauna 118: 73–96.

Burnside O. C., Wilson R. G., Weisberg S. & Hubbard K. (1996) Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. – Weed Science 44: 74–86.

Campos J. A., Biurrun I., García-Mijangos I., Loidi J. & Herrera M. (2013) Assessing the level of plant invasion: a multi-scale approach based on vegetation plots. – Plant Biosystems 147: 1148–1162.

Campos J. A. & Herrera M. (2009) Diagnosis de la Flora alóctona invasora de la CAPV [Description of the invasive allochthonous flora of the Basque County]. – Dirección de Biodiversidad y Participación Ambiental, Departamento de Medio Ambiente y Ordenación del Territorio, Gobierno Vasco, Bilbao.

CBNA & CBNMed (2021) Catalogue de la flore vasculaire exogène de la région Provence-Alpes-Côte d'Azur (PACA) [Catalogue of the exotic vascular flora of the Provence-Alpes-Côte d'Azur (PACA) region]. – Conservatoire botanique national méditerranéen de Porquerolles (CBNMed) et alpin (CBNA).

Celesti-Grapow L., Alessandrini A., Arrigoni P. V., Banfi E., Bernardo L., Bovio M., Brundu G., Camarda I., Carli E., Conti F., Fascetti S., Galasso G., Gubellini L., La Valva V., Lucchese F., Mazzola P., Peccenini S., Pretto F., Poldini L., Prosser F., Siniscalco C., Villani M. C., Viegi L., Wilhalm T. & Blasi C. (2009) The inventory of the non-native flora of Italy. – Plant Biosystems 143: 386–430.

Chiu J. H., Chong K. Y., Lum S. K. Y. & Wardle D. A. (2023) Trends in the direction of global plant invasion biology research over the past two decades. – Ecology and Evolution 13: e9690.

Chytrý M., Danihelka J., Kaplan Z., Wild J., Holubová D., Novotný P., Řezníčková M., Rohn M., Dřevojan P., Grulich V., Klimešová J., Lepš J., Lososová Z., Pergl J., Sádlo J., Šmarda P., Štěpánková P., Tichý L., Axmanová I., Bartušková A., Blažek P., Chrtek J. Jr., Fischer F. M., Guo W.-Y., Herben T., Janovský Z., Konečná M., Kühn I., Moravcová L., Petřík P., Pierce S., Prach K., Prokešová H., Štech M., Těšitel J., Těšitelová T., Večeřa M., Zelený D. & Pyšek P. (2021) Pladias database of the Czech flora and vegetation. – Preslia 93: 1–87.

Chytrý M., Pyšek P., Wild J., Maskell L. C., Pino J. & Vilà M. (2009) European map of alien plant invasions, based on the quantitative assessment across habitats. – Diversity and Distributions 15: 98–107.

Chytrý M., Wild J., Pyšek P., Jarošík V., Dendoncker N., Reginster I., Pino J., Maskell L., Vilà M., Pergl J., Kühn I., Spangenberg J. & Settele J. (2012) Projecting trends in plant invasions in Europe under different scenarios of future land-use change. – Global Ecology and Biogeography 21: 75–87.

Clement E. J. & Foster M. C. (1994) Alien plants of the British Isles. A provisional catalogue of vascular plants (excluding grasses). – Botanical Society of the British Isles, London.

Cottaz C. (ed.) (2020) Actualisation de la liste des espèces végétales exotiques envahissantes de la région Provence-Alpes-Côte d'Azur (PACA) [Update of the list of invasive alien plant species in the Provence-Alpes-Côte d'Azur (PACA) region]. – Conservatoire botanique national méditerranéen de Porquerolles (CBNMed).

Cuthbert R. N., Bartlett A. C., Turbelin A. J., Haubrock P. J., Diagne C., Pattison Z., Courchamp F. & Catford J. A. (2021) Economic costs of biological invasions in the United Kingdom. – NeoBiota 67: 299–328.

DAISIE (2009) Handbook of alien species in Europe. – Springer, Berlin.

de Almeida J. D. (1999) Flora exótica subespontânea de Portugal continental (plantas vasculares) [Subspontaneous exotic flora of mainland Portugal (vascular plants)]. Ed. 2. – Universidade de Coimbra, Coimbra.

Dubovik D. V., Dmitrieva S. A., Laman N. A., Lebedko V. N., Levkovich A. V., Maslovsky O. M., Parfenov V. I., Prokhorov V. N., Pugachevsky A. V., Savchuk S. S., Skuratovich A. N., Sysoy I. P., Chumakov L. S., Yakovleva I. M., Garanovich I. M., Jus M. A. & Romanyuk A. L. (2020) Chernaya kniga flory Belarusi: chuzerodnye vredonosnye rasteniya [The black book of the flora of Belarus: alien harmful plants]. – Belaruskaya navuka, Minsk.

EASIN (2020) European Commission – Joint Research Centre – European Alien Species Information Network (EASIN). – URL: https://easin.jrc.ec.europa.eu/.

Ecseri K. & Honfi P. (2020) Comparison of European archaeophyte lists in the light of distribution data. – Notulae Botanicae Horti Agrobotanici Cluj-Napoca 47: 480–491.

Essl F. & Rabitsch W. (eds) (2002) Neobiota in Österreich [Neobiota in Austria]. – Umveltbundesamt, Vienna.

EU (2014) Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. – Official Journal of the European Union L 317: 35–55.

Euro+Med (2006–2024) Euro+Med PlantBase. – URL: http://www.europlusmed.org.

FinBIF (2020) The FinBIF checklist of Finnish species 2019. – Finnish Biodiversity Information Facility, Finnish Museum of Natural History, University of Helsinki, Helsinki.

Fisher M. A. (1987) On the origin of *Veronica persica* (*Scrophulariaceae*): a contribution to the history of a neophytic weed. – Plant Systematics and Evolution 155: 105–132.

Galasso G., Conti F., Peruzzi L., Ardenghi N. M. G., Banfi E., Celesti-Grapow L., Albano A., Alessandrini A., Bacchetta G., Ballelli S., Bandini Mazzanti M., Barberis G., Bernardo L., Blasi C., Bouvet D., Bovio M., Cecchi L., Del Guacchio E., Domina G., Fascetti S., Gallo L., Gubellini L., Guiggi A., Iamonico D., Iberite M., Jiménez-Mejías P., Lattanzi E., Marchetti D., Martinetto E., Masin R. R., Medagli P., Passalacqua N. G., Peccenini S., Pennesi R., Pierini B., Podda L., Poldini L., Prosser F., Raimondo F. M., Roma-Marzio F., Rosati L., Santangelo A., Scoppola A., Scortegagna S., Selvaggi A., Selvi F., Soldano A., Stinca A., Wagensommer R. P., Wilhalm T. & Bartolucci F. (2018) An updated checklist of the vascular flora alien to Italy. – Plant Biosystems 152: 556–592.

GBIF (2023) What is GBIF? – URL: https://www.gbif.org/what-is-gbif.

Genovesi P., Carboneras C., Vilà M. & Walton P. (2014) EU adopts innovative legislation on invasive species: a step towards a global response to biological invasions? – Biological Invasions 17: 307–311.

Genovesi P. & Shine C. (2004) European strategy on invasive alien species. – Nature and Environment 137: 1–67.

Gudžinskas Z. (1997a) Conspectus of alien plant species of Lithuania. 1. *Liliopsida* (excluding *Poaceae*). – Botanica Lithuanica 3: 3–23.

Gudžinskas Z. (1997b) Conspectus of alien plant species of Lithuania. 2. *Poaceae*. – Botanica Lithuanica 3: 107–134.

Gudžinskas Z. (1997c) Conspectus of alien plant species of Lithuania. 3. *Brassicaceae*. – Botanica Lithuanica 3: 215–249.

Gudžinskas Z. (1997d) Conspectus of alien plant species of Lithuania. 4. *Asteraceae*. – Botanica Lithuanica 3: 335–366.

Gudžinskas Z. & Petrulaitis L. (2021) New alien taxa of the genus *Cornus* (*Cornaceae*) recorded in Lithuania and Latvia. – Botanica 27: 160–169.

Gudžinskas Z. & Taura L. (2020) New alien plant species recorded in South Lithuania. – Botanica 26: 170–183.

Hao J., Qiang S., Chrobock T., van Kleunen M. & Liu Q. (2011) A test of Baker's law: breeding systems of invasive species of *Asteraceae* in China. – Biological Invasions 13: 571–580.

Haubrock P. J., Balzani P., Macędo R. & Tarkan A. S. (2023) Is the number of non-native species in the European Union saturating? – Environmental Sciences Europe 35: 35–48.

Haubrock P. J., Cuthbert R. N., Sundermann A., Diagne C., Golivets M. & Courchamp F. (2021a) Economic costs of invasive species in Germany. – NeoBiota 67: 225–246.

Haubrock P. J., Turbelin A. J., Cuthbert R. N., Novoa A., Taylor N. G., Angulo E., Ballesteros-Mejia L., Bodey T. W., Capinha C., Diagne C., Essl F., Golivets M., Kirichenko N., Kourantidou M., Leroy B., Renault D., Verbrugge L. & Courchamp F. (2021b) Economic costs of invasive alien species across Europe. – NeoBiota 67: 153–190.

Hijmans R. J., van Etten J., Sumner M., Cheng J., Baston D., Bevan A., Bivan R., Busetto L., Canty M., Fasoli B., Forrest D., Ghosh A., Golicher D., Gray J., Greenberg J. A., Hiemstra P., Hingee K., Ilich A., Institute for Mathematics Applied Geosciences, Karney C., Mattiuzzi M., Mosher S., Naimi B., Nowosad J., Pebesma E., Lamigueiro O. P., Racine E. B., Rowlingson B., Shortidge A., Venables B. & Wueest R. (2021) raster: geographic data analysis and modeling. Version 3.3-13. – URL: https://cran.r-project.org/web/packages/raster/index.html.

Hulme P. E., Pyšek P., Nentwig W. & Vilà M. (2009) Will threat of biological invasions unite the European Union? – Science 324: 40–41.

IUCN (2000) Guidelines for the prevention of biodiversity loss caused by alien invasive species. – IUCN, Gland.

Kalusová V., Chytrý M., Večeřa M., Svenning J.-C., Biurrun I., Kintrová K., Agrillo E., Carli E., Ecker K., Garbolino E., Šibíková M. & Axmanová I. (2023) Neophyte invasions in European heathlands and scrub. – Biological Invasions 25: 1739–1765.

Karlsson T. (1998) Förteckning över svenska kärlväxter [List of Swedish vascular plants]. – Svensk Botanisk Tidskrift 91: 241–560.

Katsanevakis S., Bogucarskis K., Gatto F., Vandekerkhove J., Deriu I. & Cardoso A. C. (2012) Building the European Alien Species Information Network (EASIN): a novel approach for the exploration of distributed alien species data. – BioInvasions Records 1: 235–245.

Kays S. J. & Nottingham S. F. (2008) Biology and chemistry of Jerusalem artichoke: *Helianthus tuberosus* L. – CRC Press/Taylor & Francis Group, London.

Kourantidou M., Cuthbert R. N., Haubrock P. J., Novoa A., Taylor N. G., Leroy B., Capinha C., Renault D., Angulo E., Diagne C. & Courchamp F. (2021) Economic costs of invasive alien species in the Mediterranean basin. – NeoBiota 67: 427–458.

Kowarik I. (1995) Time lags in biological invasions with regard to the success and failure of alien species. – In: Pyšek P., Prach K., Rejmánek M. & Wade M. (eds), Plant invasions, general aspects and social problems, p. 15–38, SPB Academic Publishing, Amsterdam.

Kowarik I. & Säumel I. (2007) Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. – Perspectives in Plant Ecology, Evolution and Systematics 8: 207–237.

Kristinsson H. (2008) Íslenskt plöntutal: blómplöntur og byrkninga [Islandic plant checklist: flowering plants and ferns]. – Fjölrit Náttúrufræðistofnunar 51: 1–58.

Kumschick S., Bacher S., Evans T., Marková Z., Pergl J., Pyšek P., Vaes-Petignat S., van der Veer G., Vilà M. & Nentwig W. (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. – Journal of Applied Ecology 52: 552–561.

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.

Lavoie C., Shah M. A., Bergeron A. & Villeneuve P. (2013) Explaining invasiveness from the extent of native range: new insights from plant atlases and herbarium specimens. – Diversity and Distributions 19: 98–105.

Lazzaro L., Bolpagni R., Buffa G., Gentili R., Lonati M., Stinca A., Acosta A. T. R., Adorni M., Aleffi M., Allegrezza M., Angiolini C., Assini S., Bagella S., Bonari G., Bovio M., Bracco F., Brundu G., Caccianiga M., Carnevali L., Di Cecco V., Ceschin S., Ciaschetti G., Cogoni A., Foggi B., Frattaroli A. R., Genovesi P., Gigante D., Lucchese F., Mainetti A., Mariotti M., Minissale P., Paura B., Pellizzari M., Perrino E. V., Pirone G., Poggio L., Poldini L., Poponessi S., Prisco I., Prosser F., Puglisi M., Rosati L., Selvaggi A., Sottovia L., Spampinato G., Stanisci A., Venanzoni R., Viciani D., Vidali M., Villani M. & Lastrucci L. (2020) Impact of invasive alien plants on native plant communities and Natura 2000 habitats: state of the art, gap analysis and perspectives in Italy. – Journal of Environmental Management 274: e111140.

Lazzaro L., Essl F., Lugličˇ A., Padedda B. M., Pyšek P. & Brundu G. (2018) Invasive alien plant impacts on human health and well-being. – In: Mazza G. & Tricario E. (eds), Invasive species and human health, p. 16–33, CAB International Publishing, Wallingford.

Lehmann E. (1907) Wanderung und Verbreitung von *Veronica tournefortii* Gm. – Sitzungsberichte und Abhandlungen der Naturwissenschaftlichen Gesellschaft Isis in Dresden, Abhandlungen 1906: 91–107.

Lososová Z., Chytrý M., Cimalová S., Kropáč Z., Otýpková Z., Pyšek P. & Tichý L. (2004) Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. – Journal of Vegetation Science 15: 415–422.

Lososová Z., Horsák M., Chytrý M., Čejka T., Danihelka J., Fajmon K., Hájek O., Juřičková L., Kintrová K., Láníková D., Otýpková Z., Řehořek V. & Tichý L. (2011) Diversity of Central European urban biota: effects of human-made habitat types on plants and land snails. – Journal of Biogeography 38: 1152–1163.

Maslo S., Wong L. J. & Pagad S. (2020) GRIIS checklist of introduced and invasive species: Bosnia and Herzegovina. Version 1.3. – Invasive Species Specialist Group, ISSG.

Mohler C. L. & Callaway M. B. (1995) Effect of tillage and mulch on weed seed production and seed banks in sweet corn. – Journal of Applied Ecology 32: 627–639.

Müller F., Ritz C. M., Welk E. & Wesche K. (2021) Rothmaler. Exkursionsflora von Deutschland. Ed. 22. – Springer, Berlin.

Nentwig W., Bacher S., Kumschick S., Pyšek P. & Vilà M. (2018) More than "100 worst" alien species in Europe. – Biological Invasions 20: 1611–1621.

Nentwig W., Bacher S., Pyšek P., Vilà M. & Kumschick S. (2016) The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species. – Environmental Monitoring and Assessment 188: 315.

Nikolić T. (ed.) (2022) Flora Croatica database. – Department of Botany, Faculty of Science, University of Zagreb, URL: http://hirc.botanic.hr/fcd.

Novoa A., Moodley D., Catford J., Golivets M., Bufford J., Essl F., Lenzner B., Pattison Z. & Pyšek P. (2021) Global costs of plant invasions must not be underestimated. – NeoBiota 69: 75–78.

Oficialdegui F. J., Zamora-Marín J. M., Guareschi S., Anastácio P. M., García-Murillo P., Ribeiro F., Miranda R., Cobo F., Gallardo B., García-Berthou E., Boix D., Arias A., Cuesta J. A., Medina L., Almeida D., Banha F., Barca S., Biurrun I., Pilar Cabezas M. P., Calero S., Campos J. A., Capdevilla-Argüelles L., Capinha C., Casals F., Clavero M., Encarnação J., Fernández-Delgado C., Franco J., Guillén A., Hermoso V., Machordom A., Martelo J., Mellado-Díaz A., Morcillo F., Oscoz J., Perdices A., Pou-Rovira Q., Rodríguez-Merino A., Ros M., Ruiz-Navarro A., Sánchez M. I., Sánchez-Fernández D., Sánchez-González J. R., Sánchez-Gullón E., Teodósio M. A., Torralva M., Vieira-Lanero R. & Oliva-Paterna F. J. (2023) A horizon scan exercise for aquatic invasive alien species in Iberian inland waters. – Science of the Total Environment 869: 161798.

Pagad S., Genovesi P., Carnevali L., Schigel D. & McGeoch M. A. (2018) Introducing the Global Register of Introduced and Invasive Species. – Scientific Data 5: e170202.

Pergl J., Sádlo J., Petrusek A., Laštůvka Z., Musil J., Perglová I., Šanda R., Šefrová H., Šíma J., Vohralík V. & Pyšek P. (2016) Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. – NeoBiota 28: 1–37.

Petrova A., Vladimirov V. & Georgiev V. (2013) Invasive alien species of vascular plants in Bulgaria. – Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia.

Polce C., Cardoso A. C., Deriu I., Gervasini E., Tsiamis K., Vigiak O., Zulian G. & Maes J. (2023) Invasive alien species of policy concerns show widespread patterns of invasion and potential pressure across European ecosystems. – Scientific Reports 13: e 8124.

POWO (2023) Plants of the World Online. – URL: http://www.plantsoftheworldonline.org.

Protopopova V. (1991) Synantropnaya flora Ukrainy i puti yeye razvitiya [Synanthropic flora of Ukraine and ways of its development]. – Naukova dumka, Kiev.

Puddu S., Podda L., Mayoral O., Delage A., Hugot L., Petit Y. & Bacchetta G. (2016) Comparative analysis of the alien vascular flora of Sardinia and Corsica. – Notulae Botanicae Horti Agrobotanici Cluj-Napoca 44: 337–346.

Pyšek P. (2003) How reliable are data on alien species in Flora Europaea? – Flora 198: 499–507.

Pyšek P., Danihelka J., Sádlo J., Chrtek J. jr., Chytrý M., Jarošík V., Kaplan Z., Krahujec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. – Preslia 84: 155–255.

Pyšek P., Hulme P. E., Simberloff D., Bacher S., Blackburn T. M., Carlton J. T., Dawson W., Essl F., Foxcroft L. C., Genovesi P., Jeschke J. M., Kühn I., Liebhold A. M., Mandrak N. E., Meyerson L. A., Pauchard A., Pergl J., Roy H. E., Seebens H., van Kleunen M., Vilà M., Wingfield M. J. & Richardson D. M. (2020) Scientists' warning on invasive alien species. – Biological Reviews 95: 1511–1534.

Pyšek P., Pergl J., Dawson W., Essl F., Kreft H., Weigelt P., Winter M. & van Kleunen M. (2022a) European plant invasions. – In: Clements D. R., Upadhyaya M. K., Joshi S. & Shrestha A. (eds), Global plant invasions, p. 151–165, Springer Nature, Cham.

Pyšek P., Pergl J., Essl F., Lenzner B., Dawson W., Kreft H., Weigelt P., Winter M., Kartesz J., Nishino M., Antonova L. A., Barcelona J. F., Cabezas F. J., Cárdenas D., Cárdenas-Toro J., Castaño N., Chacón E., Chatelain C., Dullinger S., Ebel A. L., Figueiredo E., Fuentes N., Genovesi P., Groom Q. J., Henderson L.,

Inderjit, Kupriyanov A., Masciadri S., Maurel N., Meerman J., Morozova O., Moser D., Nickrent D., Nowak P. M., Pagad S., Patzelt A., Pelser P. B., Seebens H., Shu W., Thomas J., Velayos M., Weber E., Wieringa J. J., Baptiste M. P. & van Kleunen M. (2017) Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. – Preslia 89: 203–274.

Pyšek P., Richardson D. M., Pergl J., Jarošík V., Sixtová Z. & Weber E. (2008) Geographical and taxonomic biases in invasion ecology. – Trends in Ecology & Evolution 23: 237–244.

Pyšek P., Richardson D. M., Rejmánek M., Webster G., Williamson M. & Kirschner J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. – Taxon 53: 131–143.

Pyšek P., Sádlo J., Chrtek J. Jr., Chytrý M., Kaplan Z., Pergl J., Pokorná A., Axmanová I., Čuda J., Doležal J., Dřevojan P., Hejda M., Kočár P., Kortz A., Lososová Z., Lustyk P., Skálová H., Štajerová K., Večeřa M., Vítková M., Wild J. & Danihelka J. (2022b) Catalogue of alien plants of the Czech Republic (3rd edition): species richness, status, distributions, habitats, regional invasion levels, introduction pathways and impacts. – Preslia 94: 447–577.

Pyšek P., Sádlo J. & Mandák B. (2002) Catalogue of alien plants of the Czech Republic. – Preslia 74: 97–186.

R Core Team (2021) R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/.

Reinhart K. O., Packer A., Van der Putten W. H. & Clay K. (2003) Plant–soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. – Ecology Letters 6: 1046–1050.

Renault D., Manfrini E., Leroy B., Diagne C., Ballesteros-Mejia L., Angulo E. & Courchamp F. (2021) Biological invasions in France: alarming costs and even more alarming knowledge gaps. – NeoBiota 67: 191–224.

Reynolds S. C. P. (2002) A catalogue of alien plants in Ireland. – National Botanic Gardens, Glasnevin.

Richardson D. M. & Pyšek P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. – Progress in Physical Geography 30: 409–431.

Richardson D. M. & Pyšek P. (2012) Naturalization of introduced plants: ecological drivers of biogeographic patterns. – New Phytologist 196: 383–396

Richardson D. M., Pyšek P., Rejmánek M., Barbour M., Panetta F. D. & West C. J. (2000) Naturalization and invasion of alien plants: concepts and definition. – Diversity and Distribution 6: 93–107.

Roy H. E., Pauchard A., Stoett P. & Renard Truong T. (2023) The thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. – IPBES secretariat, Bonn, URL: https://doi.org/10.5281/zenodo.7430682.

Rumlerová Z., Vilà M., Pergl J., Nentwig W. & Pyšek P. (2016) Scoring environmental and socioeconomic impacts of alien plants invasive in Europe. – Biological Invasions 18: 3697–3711.

Sandvik H., Dolmen D., Elven R., Falkenhaug T., Forsgren E., Hansen H., Hassel K., Husa V., Kjærstad G., Ødegaard F., Pedersen H. C., Solheim H., Stokke B. G., Åsen P. A., Åström S., Brandrud T.-E., Elven H., Endrestøl A., Finstad A., Fredriksen S., Gammelmo Ø., Gjershaug J. O., Gulliksen B., Hamnes I., Hatteland B. A., Hegre H., Hesthagen T., Jelmert A., Jensen T. C., Johnsen S. I., Karlsbakk E., Magnusson C., Nedreaas K., Nordén B., Oug E., Pedersen O., Pedersen P. A., Sjøtun K., Skei J. K., Solstad H., Sundheim L., Swenson J. E., Syvertsen P. O., Talgø V., Vandvik V., Westergaard K. B., Wienerroither R., Ytrehus B., Hilmo O., Henriksen S. & Gederaas L. (2019) Alien plants, animals, fungi and algae in Norway: an inventory of neobiota. – Biological Invasions 21: 2997–3012.

Sanz-Elorza M., Dana Sánchez E. D. & Sobrino-Vesperinas E. (eds) (2004) Atlas de las plantas alóctonas invasoras en España [Atlas of invasive alien plants in Spain]. – Ministerio de Medio Ambiente, Secretaría General para el Territorio y la Biodiversidad, Dirección General para la Biodiversidad, Madrid.

Schindler S., Staska B., Adam M., Rabitsch W. & Essl F. (2015) Alien species and public health impacts in Europe: a literature review. – NeoBiota 27: 1–23.

Seebens H., Bacher S., Blackburn T. M., Capinha C., Dawson W., Dullinger S., Genovesi P., Hulme P. E., van Kleunen M., Kühn I., Jeschke J. M., Lenzner B., Liebhold A. M., Pattison Z., Pergl J., Pyšek P., Winter M. & Essl F. (2020) Projecting the continental accumulation of alien species through to 2050. – Global Change Biology 27: 970–982.

Seebens H., Blackburn T. M., Dyer E. E., Genovesi P., Hulme P. E., Jeschke J. M., Pagad S., Pyšek P., Winter M., Arianoutsou M., Bacher S., Blasius B., Brundu G., Capinha C., Celesti-Grapow L., Dawson W., Dullinger S., Fuentes N., Jäger H., Kartesz J., Kenis M., Kreft H., Kühn I., Lenzner B., Liebhold A., Mosena A., Moser D., Nishino M., Pearman D., Pergl J., Rabitsch W., Rojas-Sandoval J., Roques A., Rorke S., Rossinelli S., Roy H. E., Scalera R., Schindler S., Štajerová K., Tokarska-Guzik B., van Kleunen M., Walker K., Weigelt P., Yamanaka T. & Essl F. (2017) No saturation in the accumulation of alien species worldwide. – Nature Communications 8: e14435.

Seebens H., Meyerson L. A., Rahlao S. J., Lenzner B., Tricarico E., Aleksanyan A., Courchamp F., Keskin E., Saeedi H., Tawake A. & Pyšek P. (2023) Chapter 2: Trends and status of alien and invasive alien species. – In: Roy H. E., Pauchard A., Stoett P. & Renard Truong T. (eds), The thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES secretariat, Bonn, URL: https://doi.org/10.5281/zenodo.7430726.

Shah M. A., Callaway R. M., Shah T., Houseman G. R., Pal R. W., Xiao S., Luo W., Rosche C., Reshi Z. A., Khasa D. P. & Chen S. (2014) *Conyza canadensis* suppresses plant diversity in its nonnative ranges but not at home: a transcontinental comparison. – New Phytologist 202: 1286–1296.

Shaukat S. S., Munir N. & Sidique I. A. (2003) Allelopathic response of *Conyza canadensis* (L.) Cronquist: a cosmopolitan weed. – Asian Journal of Plant Science 14: 1034–1039.

Sychrová M., Divíšek J., Chytrý M. & Pyšek P. (2022) Niche and geographical expansions of North American trees and tall shrubs in Europe. – Journal of Biogeography 49: 1151–1161.

Tataridas A., Jabran K., Katnas P., Oliveira R. S., Freitas H. & Travlos I. (2022) Early detection, herbicide resistance screening and integrated management of invasive plant species: a review. – Pest Management Science 78: 3957–3972.

Thiébaut G. (2007) Invasion success of non-indigenous aquatic and semi-aquatic plants in their native and introduced ranges. A comparison between their invasiveness in North America and in France. – Biological Invasions 9: 1–12.

Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (eds) (1964–1980) Flora Europaea. Vols 1–5. – Cambridge University Press, Cambridge.

Tutin T. G., Heywood V. H., Burges N. A., Moore D. M., Valentine D. H., Walters S. M. & Webb D. A. (eds) (1993) Flora Europaea. Ed. 2, Vol. 1. – Cambridge University Press, Cambridge.

Tyler T., Karlsson T., Milberg P., Sahlin U. & Sundberg S. (2015) Invasive plant species in the Swedish flora: developing criteria and definitions, and assessing the invasiveness of individual taxa. – Nordic Journal of Botany 33: 300–317.

Uludağ A., Aksoy N., Yazlık A., Arslan Z. F., Yazmış E., Üremiş İ., Cossu T. A., Groom Q., Pergl J., Pyšek P. & Brundu G. (2017) Alien flora of Turkey: checklist, taxonomic composition and ecological attributes. – NeoBiota 35: 61–85.

van Kleunen M., Dawson W., Essl F., Pergl J., Winter M., Weber E., Kreft H., Weigelt P., Kartesz J., Nishino M., Antonova L. A., Barcelona J. F., Cabezas F. J., Cárdenas D., Cárdenas-Toro J., Castańo N., Chacón E., Chatelain C., Ebel A. L., Figueiredo E., Fuentes N., Groom Q. J., Henderson L., Inderjit, Kupriyanov A., Masciadri S., Meerman J., Morozova O., Moser D., Nickrent D. L., Patzelt A., Pelser P. B., Baptiste M. P., Poopath M., Schulze M., Seebens H., Shu W.-S., Thomas J., Velayos M., Wieringa J. J. & Pyšek P. (2015) Global exchange and accumulation of non-native plants. – Nature 525: 100–103.

van Kleunen M., Essl F., Pergl J., Brundu G., Carboni M., Dullinger S., Early R., González-Moreno P., Groom Q. J., Hulme P. E., Kueffer C., Kühn I., Máguas C., Maurel N., Novoa A., Parepa M., Pyšek P., Seebens H., Tanner R., Touza J., Verbrugge L., Weber E., Dawson W., Kreft H., Weigelt P., Winter M., Klonner G., Talluto M. V. & Dehnen-Schmutz K. (2018) The changing role of ornamental horticulture in alien plant invasions. – Biological Reviews 93: 1421–1437.

van Kleunen M., Pyšek P., Dawson W., Essl F., Kreft H., Pergl J., Weigelt P., Stein A., Dullinger S., Konig C., Lenzner B., Maurel N., Moser D., Seebens H., Kartesz J., Nishino M., Aleksanyan A., Ansong M., Antonova L. A., Barcelona L. A., Breckle S. W., Brundu G., Cabezas F. J., Cárdenas D., Cárdenas-Toro J., Castańo N., Chacón E., Chatelain C., Conn B., de Sá Dechoum M., Dufour-Dror J.-M., Ebel A. L., Figueiredo E., Fragman-Sapir O., Fuentes N., Groom Q. J., Henderson L., Inderjit, Jogan N., Krestov P., Kupriyanov A., Masciadri S., Meerman J., Morozova J., Nickrent D., Nowak A., Patzelt A., Pelser P. B., Shu W.-S., Thomas J., Uludağ A., Velayos M., Verkhosina A., Villaseńor J. L., Weber E., Wieringa J. J., Yazlık A., Zeddam A., Zykova E. & Winter M. (2019) The Global Naturalized Alien Flora (GloNAF) database. – Ecology 100: e02542.

Verloove F. (2006) Catalogue of neophytes in Belgium (1800–2005). – Scripta Botanica Belgica 39: 1–89.

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

Vítková M., Sádlo J., Roleček J., Petřík P., Sitzia T., Müllerová J. & Pyšek P. (2020) *Robinia pseudoacacia*-dominated vegetation types of Southern Europe: species composition, history, distribution and management. – Science of the Total Environment 707: 134857.

Wagner V., Chytrý M., Jiménez-Alfaro B., Pergl J., Hennekens S., Biurrun I., Knollová I., Berg C., Vassilev K., Rodwell J. S., Škvorc Ž., Jandt U., Ewald J., Jansen F., Tsiripidis I., Botta-Dukát Z., Casella L., Attorre F., Rašomavičius V., Ćušterevska R., Schaminée J. H. J., Brunet J., Lenoir J., Svenning J.-C., Kącki Z., Petrášová-Šibíková M., Šilc U., García-Mijangos I., Campos J. A., Fernández-González F., Wohlgemuth T., Onyshchenko V. & Pyšek P. (2017) Alien plant invasions in European woodlands. – Diversity and Distribution 23: 969–981.

Wasowitz P., Przedpelska-Wasowicz E. M. & Kristinsson H. (2013) Alien vascular plants in Iceland: diversity, spatial patterns, temporal trends, and the impact of climate change. – Flora 208: 648–673.

Weaver S. E. (2001) The biology of Canadian weeds. 115. *Conyza canadensis* – Canadian Journal of Plant Sciences 81: 867–875.

Weber E. F. (1997) The alien flora of Europe: a taxonomic and biogeographic overview. – Journal of Vegetation Science 8: 565–572.

Wickham H., Averick M., Bryan J., Chang W., McGowan L. D., François R., Grolemund G., Hayes A., Henry L., Hester J., Kuhn M., Pedersen T. L., Miller E., Bache S. M., Müller K., Ooms J., Robinson D., Seidel D. P., Spinu V., Takahashi K., Vaughan D., Wilke C., Woo K. & Yutani H. (2019) Welcome to the tidyverse. – Journal of Open Source Software 4: 1686.

Williamson M. & Fitter A. (1996) The varying success of invaders. – Ecology 77: 1661–1666.

Yazlık A., Pergl J. & Pyšek P. (2018) Impact of alien plants in Turkey assessed by the generic impact scoring system. – NeoBiota 39: 31–51.

Nepůvodní rostliny Evropy: přehled národních a regionálních seznamů

Evropská flóra je v důsledku dlouhodobého lidského vlivu obohacena velkým počtem nepůvodních cévnatých rostlin. Od roku 2008, kdy byl uveřejněn poslední přehled nepůvodní složky evropské květeny, se podařilo získat nové a upřesnit existující údaje o výskytu nepůvodních druhů v mnoha evropských zemích. Článek přináší přehled aktuálních seznamů nepůvodních cévnatých rostlin pro jednotlivé evropské země a souhrn zaznamenaných druhů. Porovnáváme jejich současné kategorizace v různých zemích i s předchozími přehledovými studiemi a upozorňujeme na různé nesrovnalosti. Celkem jsme získali a zpracovali 111 národních a regionálních seznamů nepůvodních cévnatých rostlin uveřejněných do roku 2022 pro 55 evropských regionů, tj. jednotlivých zemí, jejich částí nebo velkých ostrovů a souostroví. U nepůvodních taxonů jsme sjednotili taxonomické pojetí, nomenklaturu a kategorizaci podle doby zavlečení, invazního statusu a geografického původu. Výsledný seznam nepůvodních druhů zavlečených do Evropy nebo její části obsahuje 7335 druhů cévnatých rostlin, což je o 1546 druhů více, než obsahoval předešlý přehled z roku 2008. Podle doby, která uplynula od zavlečení, je mezi nimi 1,5 % archeofytů, 77,2 % neofytů a 9,3 % druhů, jež jsou v některých regionech Evropy považovány za archeofyty a jinde za neofyty. Pro 12,0 % druhů je uveden pouze nepůvodní status bez rozlišení na archeofyty a neofyty. Podle invazního statusu patří 33,3 % druhů mezi přechodně zavlečené/zplanělé, 36,3 % mezi zdomácnělé a 14,4 % mezi invazní alespoň v jednom evropském regionu; pro 5,8 % druhů není tato informace dostupná. Všechny tři kategorie invazního statusu jsou rozlišeny v seznamech 43,6 % regionů, archeofyty a neofyty jsou rozlišeny v seznamech 40,0 % evropských regionů, zatímco pro 20,0 % regionů jsou dostupné jen seznamy invazních druhů. Do více než poloviny regionů se rozšířilo 114 nepůvodních druhů rostlin, z nichž nejhojnější jsou *Erigeron canadensis*, *Amaranthus retroflexus*, *Galinsoga parviflora* a *Robinia pseudoacacia*. Mezi nepůvodními rostlinami evropské květeny jsou nejvíce zastoupeny druhy čeledí *Asteraceae*, *Poaceae*, *Rosaceae* a *Fabaceae*. Nejvíce nepůvodních druhů evropské květeny pochází z temperátní Asie (20,4 %), temperátní Evropy (19,6 %), evropského Středozemí spolu se severní Afrikou a Blízkým východem (19,0 %). Invazní druhy pocházejí hlavně z amerického kontinentu (22,9 %) a temperátní Asie (19,7 %). Nedostatek informací a další nesrovnalosti se projevují jak v kategorizacích druhů v jednotlivých zemích, tak v nejednotnosti statusu stejného druhu v různých regionech. Doplnění a revize údajů jsou nutné zejména na Balkánském poloostrově a v severovýchodní Evropě. Aktuální a vzájemně srovnatelné seznamy nepůvodních druhů rostlin jsou základní podmínkou pro vznik spolehlivých studií o rostlinných invazích včetně hodnocení jejich vlivu a rizik, jakož i pro efektivní management zavlečených druhů v celoevropském měřítku.

How to cite: Kalusová V., Čeplová N., Danihelka J., Večeřa M., Pyšek P., Albert A., Anastasiu P., Biurrun I., Boch S., Cottaz C., Essl F., Kuzemko A., Maslo S., Mifsud S., Protopopova V. V., Shevera M., Sîrbu C., Svenning J.-C., Welk E. & Axmanová I. (2024) Alien plants of Europe: an overview of national and regional inventories. – Preslia 96: 149–182.

Preslia, a journal of the Czech Botanical Society

https://www.preslia.cz