

Running Head: A pan-European inventory of alien species

A pan-European inventory of alien species: rationale, implementation and implications for managing biological invasions.

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Abstract

Historically the number and impact of harmful invasive alien species in Europe have been chronically underestimated, yet such data would play a pivotal role in informing policy and identifying resource priorities. The European Strategy on Invasive Alien Species encouraged the development of a pan-European inventory of invasive alien species to mobilise existing expertise for species records, include and describe alien species that have a high likelihood of introduction or spontaneous spread from neighbouring countries, and identify priority species. To achieve this objective, the European Commission funded the Strategic Targeted Research project DAISIE (Delivering Alien Invasive Species Inventories in Europe). DAISIE focused on four major areas of information gathering and dissemination: European Alien Species Expertise Registry, European Alien Species Database, European Invasive Alien Species Information System and Species Distribution Maps and Spatial Analysis. Each of these activities has been integrated together as a single internet portal for information on European alien species. The inventory, accounts, and distribution maps today provide the first qualified reference system on invasive alien species for the European region. The information presents an outstanding resource to synthesise current knowledge and trends in biological invasions in Europe. The data will help identify the scale and spatial pattern of invasive alien species in Europe, understand the environmental, social, economic and other factors involved in invasions, and can be used as a framework for considering indicators for early warning. In addition, the data will assist Member States develop and manage their National Biodiversity Action Plans as well as enable the European Union to monitor its performance towards the 2010 target.

3.1 Introduction

Biological invasions by alien (cf. non-native, non-indigenous, foreign, exotic) species are recognised as a significant component of global environmental change, often resulting in a significant loss in the economic value, biological diversity and function of invaded ecosystems (Wittenberg and Cock 2001). Numerous alien species, many introduced only in the last 200 years ago, have become successfully established over large areas of Europe (Hulme 2007). Future global biodiversity scenarios highlight potentially dramatic increases in biological invasions in European ecosystems (Sala et al. 2000). Interacting effects through rising atmospheric CO₂ concentrations, warmer temperatures, greater nitrogen deposition, altered disturbance regimes and increased habitat fragmentation may facilitate further invasions (Vilà et al. 2006). Early warning and prevention of the harmful impact of exotic species on ecosystems is a fundamental requirement of the European Biodiversity Strategy and the EU Action Plan to 2010 and Beyond (European Commission, 2006) yet, in the absence of reliable regional analyses, the European states have been unable to tackle this issue strategically (Miller *et al.* 2006; Hulme *et al.* 2007).

In the United States, the cost of biological invasions has been estimated to total \$97 billion hitherto for 79 major bioinvasions (Pimentel 2001). Although only limited monetary data are available at present for Europe, there is a similar indication that biological invasions have imposed losses on the economy. The strongest evidence is for alien pest and weeds that impact upon the agriculture, forestry, aquaculture and other sectors (Williamson, 2002). Examples of direct economic impacts include the damage caused by Japanese knotweed (*Fallopia japonica*) to flood defences and the impact of bark stripping by grey squirrels (*Sciurus carolinensis*) on forestry production. The western corn rootworm (*Diabrotica virgifera*) was accidentally introduced in the 1990s into Serbia and is an important pest of maize and leads to yield losses. Preliminary studies on the potential of establishment of the western corn rootworm show that this pest is likely to survive and develop wherever maize is grown in Europe. Leaving aside introduced pests and diseases affecting agriculture, alien parasites such as *Gyrodactylus salaris* (an ectoparasite of Atlantic salmon) and *Anguillicola crassus* (swimbladder nematode of eels) have led to dramatic decreases in fisheries sector incomes in several Nordic countries. The American oyster drill (*Urosalpinx cinerea*) is an important gastropod pest of the cultured oyster industry as it feeds preferably on oyster spat and is recorded as consuming more than half the oyster spat in certain European estuaries (Cole 1942). The muskrat (*Ondatra zibethicus*) and coypu (*Myocastor coypus*), both introduced by the European fur industry, damage river banks through digging and have increased the risk and severity of floods in many central and southern European countries. Notorious invasive

alien weeds are of major economic significance e.g. Mexican tea (*Chenopodium ambrosioides*), knotgrass (*Paspalum paspaloides*), Canadian horseweed (*Conyza canadensis*), Bermuda buttercup (*Oxalis pes-caprae*). While other alien plants act as hosts of plant pathogens e.g. rescuegrass (*Bromus catharticus*) as host for barley yellow dwarf virus and wheat stem rust. Invasive alien species can also affect human health, e.g. phytophotodermatitis through contact with giant hogweed (*Heracleum mantegazzianum*), asthma and hay-fever arising from the pollen of annual ragweed (*Ambrosia artemisiifolia*), poisoning of humans through consumption of toxic fruit, e.g. American pokeweed (*Phytolacca americana*), silverleaf nightshade (*Solanum eleagnifolium*) or leptospirosis spread by the brown rat (*Rattus norvegicus*).

In addition, invasive alien species may also have profound environmental consequences, exacting a significant toll on ecosystems (European Commission 2004). These range from wholesale ecosystem changes e.g. colonisation of sand dunes by *Acacia* spp. and extinction of native species, e.g. threats to endemic coastal plants following expansion of iceplant (*Carpobrotus edulis*) to more subtle ecological changes and increased biological homogeneity. For example, rhododendron (*Rhododendron ponticum*) reduces the biodiversity of Atlantic oakwoods and the American mink (*Mustela vison*) is held partially responsible for the decline in water vole (*Arvicola terrestris*) populations in the UK. The freshwater Asiatic clam (*Corbicula fluminea*) is a phytoplankton feeder, its dense populations may affect the structure of planktonic communities, competing with native clams, reducing fish stocks, and shifting primary production to benthic communities. It is a major macrofoulant of power-generating plants, and industrial and municipal water systems. A subtler, but potentially more serious impact of alien species is the possibility of hybridization with native species. Hybridisation has occurred between alien sika (*Cervus nippon*) and native red (*C. elaphus*) deer, the alien ruddy (*Oxyura jamaicensis*) and native white-headed (*O. leucephala*) ducks as well as between native and alien oaks (*Quercus* spp). Hybridisation may introduce maladaptive genes to wild populations or result in a vigorous and invasive hybrid.

Several biological invasions now threatening Europe might have been prevented by a higher level of awareness of invasive species issues and a stronger commitment to address it e.g. the spread of the killer alga (*Caulerpa taxifolia*). Current inaction in many, though not all, countries is becoming increasingly disastrous for the region's biodiversity, health and economy (Hulme 2007). European states should recognise the risk that activities within their jurisdiction or control may pose to other states as a potential source of invasions and take appropriate individual and cooperative actions to minimize that risk. This is particularly important within Europe as species introduced into the territory of one state can easily spread to neighbouring States, especially with its shared coastline, transboundary mountain ranges and international watercourses. It is also critical with regard to Europe's trading partners. Yet, historically the number and impact of harmful invasive

alien species in Europe have been chronically underestimated, especially for species that do not damage agriculture or human health. Comparable estimates for Europe would play a pivotal role in informing policy and identifying resource priorities, yet until recently these data have not been available for any European region.

3.2 Rationale

Historically, invasive alien species issues have relatively low visibility in the European Community, outside specialist circles. However, in the late 1990s increasing awareness of the impact of biological invasions in Europe arose from clear evidence of impacts reported in regional environmental audits (Stanners and Bordeau 1995; European Environment Agency 1998; 2003). By 1998, the Community Biodiversity Strategy identified invasive alien species as an emerging issue of environmental importance (European Commission 1998) and in March 2002, the European Council (Environment) recognised that the introduction of invasive alien species was one of the main recorded causes of biodiversity loss and the cause of serious damage to economy and health (European Commission 2002). The European Council supported the use, as appropriate, of national, transboundary and international action. These include, as a matter of priority, measures to prevent such introduction occurring, and measures to control or eradicate those species following an invasion. Subsequently, under the auspices of the Bern Convention, the European Strategy on Invasive Alien Species was launched in 2002 (Council of Europe 2002).

With increasing awareness of the problem there followed recognition of policy and legislative commitments. A significant number of international policies and directives encompass alien species legislation in Europe (reviewed in detail by Miller *et al.* 2006). For example, Article 196(1) of the 1982 United Nations Convention on the Law of the Sea (UNCLOS) provides, that “*States shall take all measures necessary to prevent, reduce and control pollution of the marine environment resulting from the use of technologies under their jurisdiction or control, or the intentional or accidental introduction of species, alien or new, to a particular part of the marine environment, which may cause significant and harmful changes thereto*”. More generally, the European States have a commitment “*to strictly control the introduction of non-indigenous species*” (Bern Convention on the Conservation of European Wildlife and Natural Habitats) and “*eradicate those alien species which threaten ecosystems, habitats or species*” (UN Convention on Biological Diversity). The EU policy for the implementation of these conventions states that the European Community “*should take measures pursuing to prevent that alien species cause detrimental effects on ecosystems, priority species or the habitats they depend on and establish measures to control,*

manage and wherever possible remove the risks that they pose". This legislation also forms an integral element of the EU Habitats Directive which similarly contains provisions to ensure invasive alien species introductions do not prejudice the local flora and fauna. More recently, the EU Biodiversity Strategy (European Commission 1998) states that: *"The presence or introduction of alien species or sub-species can potentially cause imbalances and changes to ecosystems. It can have potentially irreversible impacts, by hybridisation or competition, on native components of biodiversity. Applying the precautionary principle, the Community should take measures to prevent that alien species cause detrimental effects on ecosystems, priority species or the habitats they depend on and establish measures to control, manage and wherever possible remove the risks that they pose"*.

Despite the Bern Convention efforts, Europe's practical programmes and coordination on invasive alien species lag behind many other regions of the world. Difficulties arise in the standardisation of the status of alien species. National studies often have access to far more detailed data, but classification of species may differ among countries. This is especially true in terms of the treatment of varieties, hybrids, reintroductions, translocations, feral species and naturally expanding populations. Guidelines for the classification of species status have only recently been suggested and have yet to be widely implemented (IUCN 2000) and the origin of ancient introductions prior to detailed floristic and faunal records is often uncertain. The heterogeneity in the degree to which different European nations are exposed to biological invasions may limit recognition of the risk that activities within their jurisdiction may pose to other nations. Species prioritised for management differ across Europe such that concerted actions should be planned at sub-regional scales. Finally, alien species in one European nation may be native in another. This poses considerable complexity on the development of regulations regarding trade within Europe. Whilst Europe's characteristics arguably make it harder to develop and implement common trade and movement policies, this should not be used as an excuse for failing to take decisive action (Council of Europe 2002).

Effective control of invasive alien species has been hampered in Europe by the lack of (a) monitoring for alien species at frequent enough intervals in regions of concern; (b) a means to report, verify the identifications, and warn of new sightings; and (c) risk assessments that predict the likelihood of a particular species becoming invasive. Information on the invasive alien species present in Europe is incomplete, and that which is available is scattered in a variety of published and unpublished accounts and databases. Anticipating invasions by alien species is difficult, because access to information on their previous invasive ability (one of the best predictors of whether a new species will become invasive) is mostly unavailable. A key recommendation of the European Strategy on Invasive Alien Species is the development of a regional inventory of alien species recorded in the wild (Council of Europe 2002).

The European Commission, under its 6th Framework Programme of support to Community activities in research and technological development, launched a call in 2003 for an inventory of alien invasive species. The call was precise and exhibited considerable foresight and understanding of the needs of end-users and scientists alike:

Create an inventory of invasive species that threaten European terrestrial, fresh-water and marine environments and to provide the basis to prevent and control biological invasions through the understanding of the biological, social, economic and other factors involved. The inventory should be established using common definitions and criteria, and aims to cover all taxa known to be invasive, and all European countries, water bodies and seas. Where possible, the distribution of known invasions should be presented graphically. The work should also assess the ecological, economic and health risks and impacts of biological invasions in Europe as well as indicators for early warning.

As a result of competitive bidding among several different research proposals, the contract for the alien invasive species inventory was awarded to a consortium of leading researchers of biological invasions in Europe, drawn from 18 institutions across 15 countries. The resulting project, DAISIE (Delivering Alien Invasive Species Inventories for Europe), was launched in February 2005 and ran for the three subsequent years with a European Commission contribution of 2.4 M€ The general objectives of the project were:

1. To create an inventory of alien species that threaten European terrestrial, fresh-water and marine environments
2. To structure the inventory to provide the basis for prevention and control of biological invasions through the understanding of the environmental, social, economic and other factors involved.
3. To assess and summarise the ecological, economic and health risks and impacts of the most widespread and/or invasive species in Europe
4. To use distribution data and the experiences of the individual Member States as a framework for considering indicators for early warning

By achieving these objectives, DAISIE aimed to deliver a European “one-stop-shop” for information on biological invasions in Europe.

3.3 Implementation

The European Strategy on Invasive Alien Species (Council of Europe 2002) encouraged the development of a pan-European inventory of invasive alien species to mobilise existing expertise for species inventory and review, link and integrate existing databases, include potentially invasive alien species that have a high likelihood of introduction or spontaneous spread from neighbouring countries, and identify priority species. Where available, information should include: species taxonomy and biology, date and place of introduction, means of arrival and spread, range and spread dynamics, risk of expansion to neighbouring countries, invaded ecosystems, population size and trends, impacts recorded and level of threat, other data relevant for risk analysis and, early warning systems, prevention, mitigation and restoration methods and their efficiency, references and contact details. In response to these requirements, DAISIE focused on four major areas of information gathering and dissemination:

1. The European Alien Species Expertise Registry: a directory of researchers and research
2. European Alien Species Database: including all known alien species in Europe
3. European Invasive Alien Species Information System: descriptions of key alien species known to be invasive in Europe that includes distribution maps of key invasive alien species in Europe known or suspected of having environmental or economic impacts.

Each of these activities is briefly described below and they have been integrated together as a single internet portal for information on European alien species (www.europe-aliens.org).

3.3.1 European Alien Species Expertise Registry

Current expertise in biological invasions is distributed across research organisations throughout Europe and is funded mainly by national programmes. The European Expertise Registry represents a fundamental step towards linking these organisations and individuals in ways that provide added value at European level and provide the critical mass of expertise in invasive alien species research to meet European-scale requirements. The European Expertise Registry facilitates the clustering and information sharing among different national programmes targeting the same invasive alien species, helps establish teams of experts who can, once a new alien incursion has been reported, assess the situation and prepare an action plan for the invasive alien species at a particular site and enables the current breadth and scope of European knowledge on alien species to be assessed. The registry contains information on the field of expertise (distribution, conservation, ecology,

economy, genetics, legislation, management, pathways, physiology, risk assessment, and taxonomy) and on the taxonomic and geographic structure of the expertise.. Within 12 months of its launch, the Registry contained information on 1500 experts from nearly 90 countries for almost 3000 higher taxa (family level or higher) and numbers have steadily increased since. These data already highlight a general paucity of expertise in the larger eastern European nations, under-representation of expertise in alien fungi, moss and invertebrate species, especially insects.

3.3.2 European Alien Species Database

An up-to-date inventory of all alien species known to inhabit Europe is essential to building an early detection and warning system for the Europe's environmental managers. This critical step represented the major activity in DAISIE and involved compiling and peer-reviewing national lists of hundreds of species of fungi, plants, invertebrates, fish, amphibians, reptiles, birds and mammals. Data were collated for all 27 European Union member states, and where these states had significant island regions, data were collated separately for these as well. In addition, data were collated for European states that are not in the European Union such as Andorra, Iceland, Liechtenstein, Moldova, Monaco, Norway, Russia, Switzerland, Ukraine as well as former Yugoslavian states in the Balkans. Finally, marine lists were referenced to the relevant maritime state and thus to have full coverage of the Mediterranean, marine data were included for North African and Near East countries. For each species, an attempt was made to gather information on native range, date of introduction, habitat, known impacts and population status. Considerable effort was required to ensure synonyms were accounted for accurately and all national lists were independently reviewed by experts. Records of over 10,000 alien species are included in the database (February 2008), the majority of records are for vascular plants with invertebrates also a significant component (see Olenin et al. 2008).

3.3.3 European Invasive Alien Species Information System

The provision of selected species accounts covering high profile alien species not only delivers end users with relevant details for species identification and management but also helps raise public awareness of the issue of invasions. Accounts for representative sample of 100 invasive alien species have been produced and each includes information on biology, ecology, distribution, management information, references, links and images. The aim was to generate brief factsheets that might appeal to the general reader with links to more detailed information for specialists. The accounts cover 3 fungi, 18 terrestrial plants, 16 terrestrial invertebrates, 15 vertebrates, 16 inland

and 32 coastal aquatic species invading natural and semi-natural habitats. Selection was based on ensuring a broad spectrum of life forms and functional types, a range of invaded ecosystems and clear examples of different impacts on European biodiversity, economy and health (see Vilà et al. 2008). A key requirement for the effective management of invasive alien species is the ability to identify, map, and monitor invasions in order to assess their extent and dynamics (Hulme 2003). Unfortunately, there are no common global standards in terms of sample units (e.g. points, systematic grids, political boundaries), data collected (e.g. species occurrence, both species presence and absence, relative abundance), spatial extent (e.g. regional, national or continental) and resolution of the maps thus generated. This absence of common standards leads to a profusion of different maps that rarely facilitate comparison. Furthermore, biological invasions are dynamic, large scale phenomena and the spatial resolution and extent of a species map determine the degree to which the data are of use in addressing key issues in invasion ecology (Hulme 2003). This is especially of concern in the many attempts to characterise the spatial pattern of invasive alien species, identify invasion hotspots and predict rates of spread. DAISIE therefore had as an objective to establish a common European standard for the graphical presentation of the invasive alien species data as distribution maps. The Common European Chorological Grid Reference System with the size of the mapping grid *ca* 50 × 50 km, depending on the latitude/longitude was used to produce distribution maps. This scheme employs a reasonably detailed resolution for Europe and is commonly used for species mapping. Data sources included European-wide and national atlases as well as regional checklists. The following data were plotted for each species: (a) known presence of the species; (b) known absence. Where known, additional information on (c) species previously present but eradicated and (d) native distribution, was also considered. Where precise information on distribution was missing but the species was known to occur in a country/region/district, the distribution in these administrative units was recorded and mapped by using hatching. A different format was adopted for mapping invaders in aquatic habitats where linear distributions or maritime areas needed to be recorded. Distribution maps were generated for the 100 species for which accounts were produced and can be found in Vilà et al. (2008).

3.4 Impact and implications

It is hoped that the inventory, accounts, and distribution maps will provide a qualified reference system on invasive alien species in Europe, available online for environmental managers, legislators, researchers, students and all concerned. It should also encourage the exchange of data among different geographical regions and thereby to serve a node in the Global Information System for Invasive Species. Documenting current invasions, predicting new invasion sites, and preventing

invasions are vital to the protection of biological diversity in Europe. Prediction of, and rapid response to, invasive alien species requires ready access to invasive alien species knowledge bases from many countries. It follows that internet-accessible knowledge bases are a precious tool which can provide crucial information for the early detection, eradication, and containment of invasive aliens—which are most possible for species that have just arrived. With direct access to national knowledge bases throughout Europe, managers and policy-makers addressing the invasive alien species challenge should easily obtain data on which species are invasive or potentially invasive in particular habitats, and use this information in their planning efforts. Agencies responsible for pest control can quickly determine if a species of interest has been invasive elsewhere in Europe. Importers of new alien species (e.g. nurseries, botanical gardens, the pet industry) can access data to make responsible business choices. Land managers can learn about control methods that have been useful in other areas, reducing the need to commit resources for experimentation and increasing the speed at which control efforts can begin.

The information available in the database also presents an outstanding resource to synthesise current knowledge and trends in biological invasions in Europe. The data will help identify the scale and spatial pattern of invasive alien species in Europe, understand the environmental, social, economic and other factors involved in invasions, and can be used as a framework for considering indicators for early warning. Describing in detail how these data can be applied to these questions is beyond the scope of this chapter. However, two examples of how these data may be mined to deliver policy relevant information and to disseminate information of invasion risk rapidly to stakeholders, policy makers and the public are presented below:

A key impact of the invasive species inventory is that it will provide an up-to-date view of the current status and distribution of alien taxa in Europe. Comparison between the estimates derived from previous datasets and those from the current inventory helps to identify major trends (Fig. 1). First, the distribution of alien species is heterogeneous across nations and this remains the case with the current data. The trends in numbers are not strongly correlated between the historic and current datasets samples. There is some indication that numbers of alien taxa are correlated with national GDP but this only explains part of the international variation (Hulme 2007). However, the more recent data reveals a consistent increase in the average numbers of alien plants, birds and mammals found across Europe (but only statistically significant for vertebrates). This probably reflects a more thorough assessment in the recent data rather than a sudden increase in recently established alien in Europe. These new data and their availability online will not only assist many European nations in the preparation of their National Strategy on Invasive Alien Species, but also herald the opportunity for discussion with neighbouring countries regarding regional and coordinated approaches for combating biological invasions.

Signatories to the Convention on Biological Diversity (CBD) have committed to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level (European Commission 2006). To facilitate the assessment of progress towards 2010 and communication of this assessment, a clear set of indicators have been proposed. The CBD has recognized an urgent need to address the impact of invasive alien species and has included 'Trends in invasive alien species' in the list of indicators to be developed and used for assessing global progress towards the 2010 target. The European Union (EU), in responding to the process for review of the EU Biodiversity Strategy and Biodiversity Action Plans, endorsed a first set of EU Headline Biodiversity Indicators in 2004 to monitor and evaluate progress towards the 2010 targets, including a general indicator 'Trends in invasive alien species in Europe'. A levelling off in the current increase in numbers of alien species and a reduction in the rate of establishment of alien species in new countries/regions, and/or a shrinking distribution of these within Europe would be a signal that this target is addressed successfully. The current inventory highlights that the rate of new naturalisations has consistently declined for some taxa most notably vertebrates such as inland fish, birds and mammals, while consistent increases are found for many invertebrates in both aquatic and terrestrial biomes (Fig. 2). However, even where rates of establishment are declining, the cumulative number of alien taxa is increasing and for plants, marine invertebrates and terrestrial insects, current rates of increase are over 10 new taxa per year. The pan-European inventory of alien species created through DAISIE provides a platform for European reporting on biodiversity indicators and highlights areas where Europe will need to direct resources to manage biological invasions.

3.5 Future opportunities

Biological invasions are dynamic phenomena both in time and space and while DAISIE has assembled the most comprehensive dataset on alien taxa that Europe has ever seen, there is still a pressing need to update regularly the information on alien species, their biology, vectors of introduction, spread, impacts on environment and economy. The European Environment Agency (EEA) is responsible for environmental information exchange and dissemination and plays a key role in awareness-raising. It hosts the European Community Biodiversity Clearing-House Mechanism (EC-CHM), a regional CHM established in support of the CBD. This aims to make biodiversity-related information of Community institutions more easily accessible not only to these institutions but also to member states and the public. In its 2004-08 strategy, the EEA identifies as priorities both biodiversity information gathering under the 2010 process, and the need to build on strong partnerships with NGOs and the science community for such data and information gathering

(European Environment Agency 2004). In delivering these priorities, the EEA collaborates with the European Topic Centre on Nature Protection and Biodiversity, which maintains and develops EUNIS (EEA Information System on Nature in Europe). The Topic Centre has intended to link EUNIS to the CBD/GISP system of interoperable databases and also to subregional or specialised databases and research networks in Europe on alien species. The infrastructure established by DAISIE would fit well with the aims of both the EEA and the Topic Centre. If, as is hoped, DAISIE acts as a catalyst to generate greater awareness of alien species in Europe it is likely that data management will become increasingly complex. The future of the inventory may increasingly see a move away from a single database to the integration of national databases across the same infrastructure. The inventory will then become a tool that integrates different data sets as a seamless resource. This should allow users to access and use multiple separately owned sources of invasive species information and for data owners/custodians to control who they give access to within their own rules/terms and conditions. There will certainly be political and logistic challenges in updating and delivering such information across a region the size of Europe, DAISIE is just a first step in the right direction.

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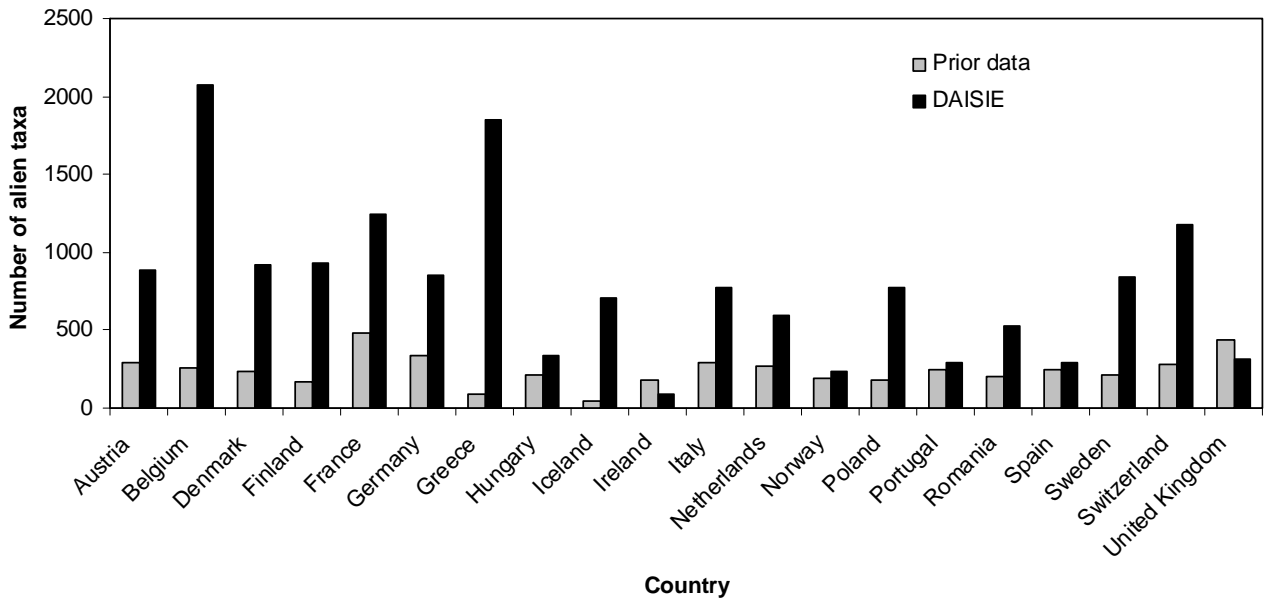
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Figure Legends

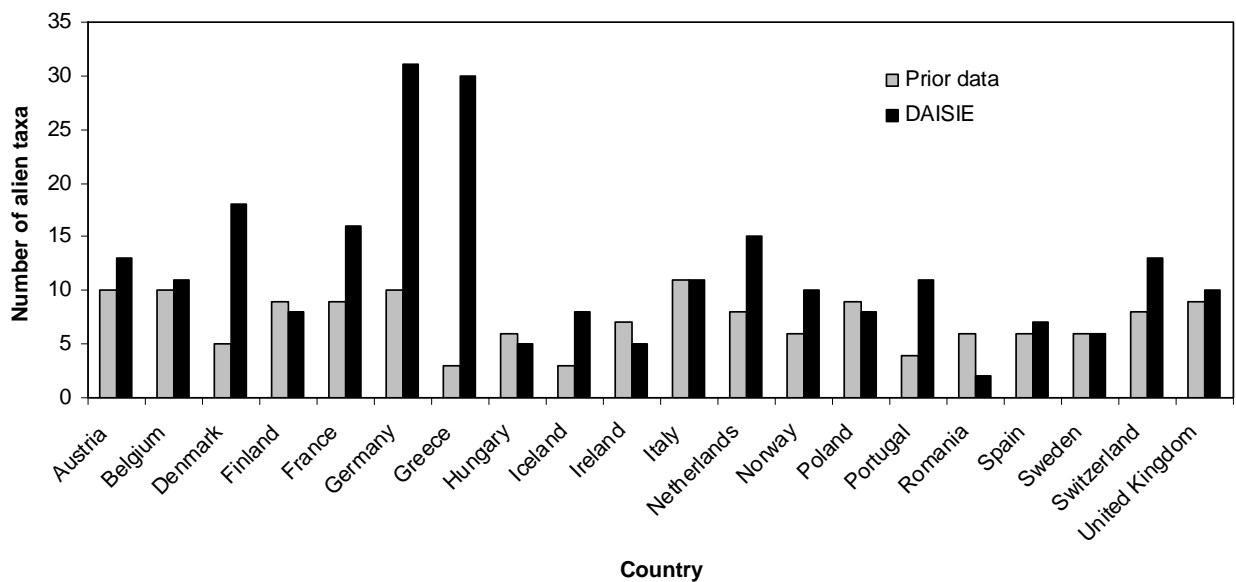
Figure 1. National trends for 20 European states in the number of naturalised alien taxa in datasets pre-dating the DAISIE inventory (for sources see Hulme 2007) and datasets from the current (October 2007) DAISIE database a) higher plants, b) birds, and c) mammals. The two datasets are not significantly correlated for plants ($r_s = -0.0129$, $df = 18$, $p > 0.05$) and ($r_s = 0.030$, $df = 18$, $p > 0.05$) but not mammals ($r_s = 0.097$, $df = 18$, $p > 0.05$).

Figure 2. Pan-European trends in the average number of new alien plants, invertebrate, fish, birds and mammals naturalising in Europe per year in three time periods 1951-1970; 1971-1990 and 1991-2007 in a) aquatic and b) terrestrial environments.

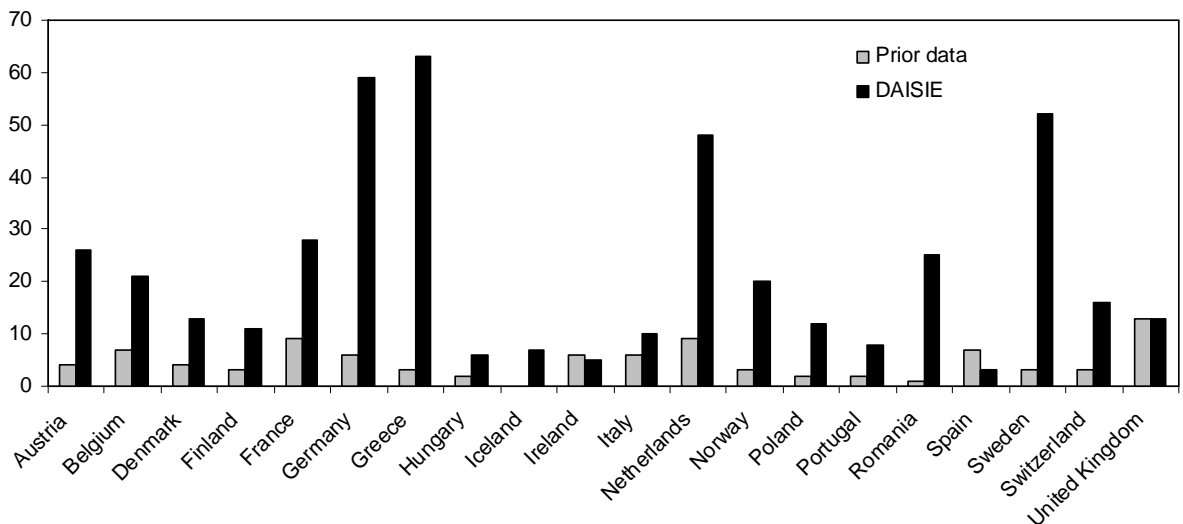
a)



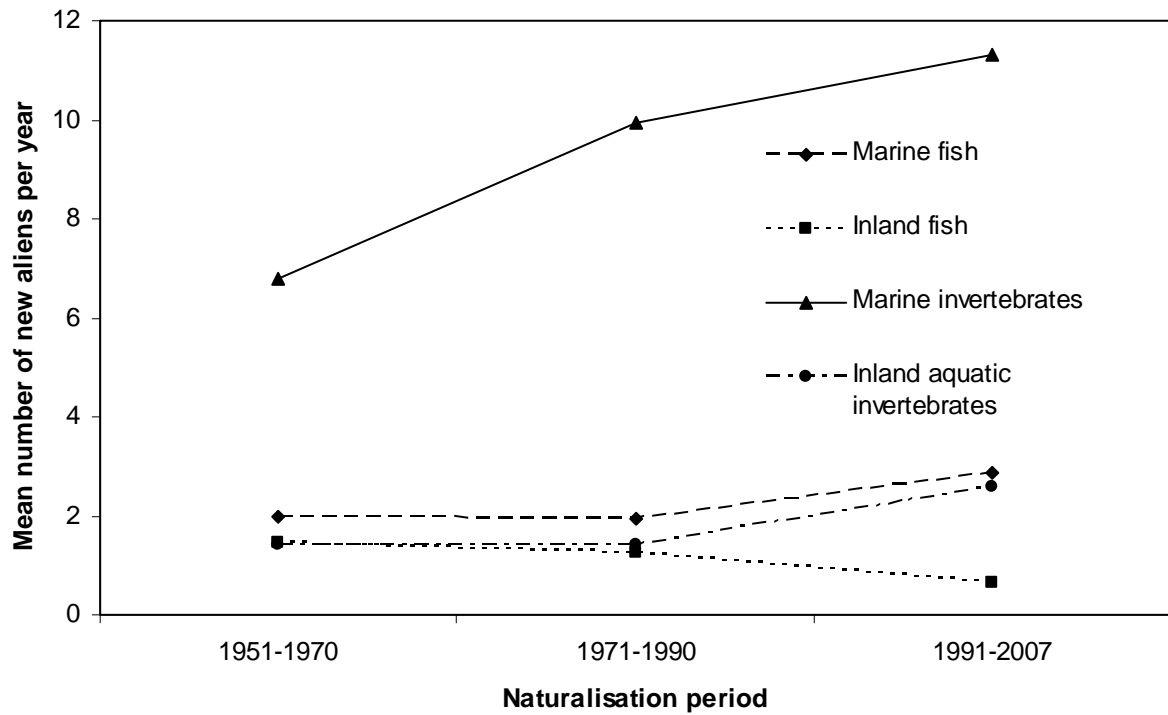
b)



c)



a)



b)

