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Running title: Invader impacts in Europe

How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment

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Abstract

Recent comprehensive data provided through the DAISIE project (www.europe-aliens.org) facilitate the first pan-European assessment of the impacts on ecosystem services of alien plants, vertebrates and invertebrates in terrestrial, inland aquatic and marine environments. Ecological and/or economic impacts were documented for 1094 (11%) and 1347 (13%) alien species, respectively. The two taxonomic groups with most taxa causing impact are terrestrial invertebrates and plants. The Mediterranean Sea is the maritime region suffering most impacts. Across taxa and regions, ecological and economic impacts are highly correlated. For invertebrates, economic impacts are more evident than ecological impacts, while for plants the reverse is true. Alien species from all taxonomic groups affect supporting, provisioning, regulating and cultural services and interfere with human well-being. Terrestrial vertebrates represent the taxon with the highest number of impact types, and the most widely distributed impacts across Europe. A review of the monetary costs is presented as the first step towards an estimate of the economic significance of alien species in Europe.

In a nutshell

- Ecological and economic impacts of alien organisms are usually studied separately, but they are likely to be highly correlated.
- Information on impacts is scarce and thus prone to underestimation for species-rich taxa or large regions.
- While aliens impact all ecosystem services, current economic valuations focus primarily on provisioning services due to a scarcity of data relating to impacts on other ecosystem services. Nature conservation, agriculture, forestry and fisheries are the main economic sectors where alien species cause marked direct costs in Europe.
- Europe represents the continent with the most up-to-date information on numbers of aliens and their impacts but lags behind North America in the knowledge of mechanisms underlying impacts. Researchers from both continents can profit from each other's experiences and work towards reliable and comparable estimates of costs from alien species invasions.

Key words: ecosystem services, ecological impacts, economic impacts, Europe, invaders, nature conservation.

Introduction

Biological invasions cause problems to the conservation of biodiversity and ecosystem integrity worldwide. Invasive species threaten biological diversity at various levels, by reducing genetic variation and eroding gene pools, through the extinction of endemic species, and by altering habitat and ecosystem functioning (Hulme 2007; Table 1). Biological invasions also cause economic impacts that can be valued as monetary costs based on expert extrapolations of high profile alien pests (Pimentel *et al*. 2001, 2005; Born *et al.* 2005; Collautti *et al.* 2006; Olson 2006; Lovell *et al*. 2006).

However, ecological and the economic impacts are rarely compared either for individual geographic regions or taxonomic groups. Thus even with increasing information on ecological and economic impacts, we still do not know the extent to which ecological and economic impacts are correlated, how taxonomic groups differ in the impacts they inflict, and which biomes suffer most. This information is essential to prioritize management action.

Biological invasions have subtle socio-economic consequences, which are difficult to assess using traditional monetary approaches and market-based models (Binimelis *et al.* 2007). To address this added complexity, we base our analysis of impacts on the Millennium Ecosystem Assessment (2005) that allows us to link ecological and economic impacts by assuming that the effect of any ecological change influences ecosystem services, and in turn human well-being. The ecosystem services approach attributes values to ecosystem processes and functions as the basis for providing all human needs. Ecosystem services are classified into four categories: supporting (i.e., major ecosystem resources and energy cycles), provisioning (i.e., production of goods), regulating (i.e., maintenance of ecosystem processes) and cultural (i.e., non-material benefits). The ecosystem assessment approach requires multidisciplinary collaboration in environmental management (Meyerson *et al.* 2005). Yet, a thorough analysis of the impacts of alien species on ecosystem services has not been completed for any continent, and requires harmonization of data on impacts with information on the taxonomic identity and distribution of the species concerned (Crall *et al.* 2006).

Here, we provide the most comprehensive review of the ecological and economic impacts caused by alien species in Europe, based on data generated by the EU-funded project DAISIE (Delivering Alien Invasive Species Inventories for Europe; Panel 1). The results represent the first continent-wide assessment of impacts on ecosystem services by all major alien taxa: plants, vertebrates and invertebrates in terrestrial, inland aquatic and marine environments. Our aims are to (1) estimate the number of alien species known to have ecological and/or economic impacts in Europe, (2) identify the most widespread species causing impacts and those with the broadest spectra of impacts, and finally (3) summarize available information on the monetary costs of alien species in Europe.

General trends

Ecological and economic impacts

More than 10,000 plant and animal species alien in Europe are registered in the DAISIE database (Panel 1), yet ecological and economic impacts are only documented for 1094 and 1347 species, respectively. Not surprisingly, the most species-rich taxa (terrestrial invertebrates and plants) have the highest number of species with recorded impacts. Thus while absolute numbers may not be informative, examination of proportions reveals terrestrial vertebrates and inland aquatic species to be of particular concern with more than a third of species known to cause impacts (Table 2). The Mediterranean Sea is the marine region with the highest number of aquatic alien species known to cause ecological and economic impacts; however, it is the smaller marine basins such as the Barents, Baltic and Black Seas that harbour the highest proportions of species with impacts (Table 3). Although overall more species cause impacts in marine than aquatic inland ecosystems, they represent a smaller proportion of all alien recorded.

Although the impacts arising from species in smaller taxonomic groups such as vertebrates and inland aquatic invertebrates may be better studied than in groups with two orders of magnitude more species (plants and terrestrial invertebrates) the higher proportional impacts may be more than a sampling effect. One reason is the preponderance of predatory or omnivorous taxa among alien vertebrates and aquatic invertebrates. The introduction of vertebrate predators has been the most severe cause of extinction globally especially on islands (Blackburn *et al.* 2004); and the cause of cascading effects in freshwater ecosystems. Freshwater ecosystems are more vulnerable to introduced predators than terrestrial and marine ecosystems due to generally lower levels of defense among native taxa and greater naivity to novel predators (Cox and Lima 2006).

In general, there are more species known to cause economic than ecological impacts, since the former are more easily perceived and immediately reported by stakeholders. Economic pests are likely to attract more scientific attention. For example, the Argentine ant (*Linepithema humile*), an economic pest in citrus and olive groves of the Mediterranean, is among the most studied alien organisms (Pyšek *et al*. 2008) and has been the subject of 14% of the studies on the impact of alien insects worldwide (Kenis *et al*. 2008).

Across the different regions in Europe (i.e., individual countries, major islands or administrative units) there is a significant positive relationship between the percentage of species with ecological impacts and those with economic impacts (Figure 1). For vertebrates and aquatic species, the percentage of ecological and economic impacts are more or less similar. In contrast, for terrestrial invertebrates, more species are known to cause economic than ecological impacts. Many introduced insects cause impacts to agriculture or forestry, which are sectors with well developed methods for estimating damage. For plants, the reverse is true, with ecological impacts more frequently documented than economic impacts even though these are less tangible and cannot be estimated as market-based costs. (Figure 1).

Most widespread species causing impacts

The taxonomic groups with impacts documented across the highest number of regions in Europe are terrestrial vertebrates and invertebrates (Figure 2). For example, the muskrat (*Ondatra zibethicus*) and the raccon dog (*Nyctereutes procyonoides*) are known to cause impacts in more than 50 European regions. Several insects such as the thrips *Frankliniella occidentalis* and *Heliotrips haemorrhoidalis* are also documented to cause impacts on crops in more than 30 regions. The most widespread aquatic organisms with impact are crustaceans such as the Chinese mitten crab (*Eriocheir sinensis*, 20 regions) and molluscs, for example the zebra mussel (*Dreissena polymorpha*, 20) and the Pacific oyster (*Crassostrea gigas*, 18). In contrast, alien terrestrial plants with known impacts are rarely widespread, often documented in only one region (Figure 2). Since many of these alien plants are widespread in Europe (Lambdon *et al.* 2008), this finding illustrates that the perception of impacts can be quite localised. Tree of heaven (*Ailanthus altissima*), black locust (*Robinia pseudoacacia*) and Japanese knotweed (*Fallopia japonica*) are the plant species with the most widespread impacts.

Are species with economic or with ecological impacts more widespread? For terrestrial vertebrates and aquatic taxa there is no difference, but for invertebrates those with economic impacts are more widespread while for plants it is those with ecological impacts (Figure 2).

A myriad of impacts on ecosystem services

Using a representative list of 100 of the worst European invasive species as designated by DAISIE (Panel 1) we classified taxa in relation to different types of impacts on the four main ecosystem services (Figure 3): supporting (5 types of impacts), provisioning (3), regulating (10) and cultural (4). As might be expected, a single invader may affect several different ecosystem services and have many impacts (Binimelis *et al.* 2007).

There are significant differences among taxonomic groups in the number of ecosystem services and different impact types affected by alien species (Figure 4). Terrestrial vertebrates exhibit the widest and invertebrates the narrowest range of different impact types (Figure 4). The coypu (*Myocastor coypu*) exemplifies best how a terrestrial vertebrate causes many different impacts since it damages crops, strongly disturbs riverine vegetation by grazing, undermines riverbanks by burrowing and transmits leptospyrosis (Bertolino and Genovesi 2007).

Aquatic invaders also exhibit a high number of impact types per species (Table 4), with nine reported for the American crayfish *(Procambarus clarki*), the zebra mussel and the brook trout (*Salvelinus fontinalis*). In invaded temperate freshwater ecosystems, introduced crayfish represents the largest invertebrates and as omnivores they have cascading impacts on foodwebs. In addition the diet of many vertebrates now depends upon the crayfish, changing completely the trophic structure of the invaded community (Gherardi 2007). Similarly, as in other parts of the world, the zebra mussel changes supporting, regulating and ultimately provisioning services in aquatic ecosystems through alteration of water quality and bioaccumulation. The brook trout has been introduced into more than 20 European countries for sports fishing and it causes impacts on all four main ecosystem services. It impacts populations of native salmonids through hybridization and reduces the abundance of other freshwater taxa. It also alters primary production and benthic resources of former oligotrophic lakes.

In summary, it appears that alien taxa often have several different types of impacts, rarely restricted to a single ecosystem service. The more impacts a species causes, the more ecosystem services are affected ($r^2 = 0.60$, $p<0.0001$).

Monetary costs to ecosystem services

Despite some invaders having clear economic impacts, there are only a handful cost-benefit analyses applied to aliens in Europe, few cross-taxa cost estimates at the national level and no cost estimates for highly widespread and harmful invaders across the whole of Europe. This is quite a different perspective than in North America. In Europe, most monetary expenses refer to management costs including eradication, control, monitoring and environmental education programmes targeting emblematic natural areas for which there was specific funding. For example, over 100 EU LIFE conservation projects aimed at eradicating alien vertebrates on islands to protect marine birds resulted in expenditure totalling more than 27 million € (Scalera and Zaghi 2004). Expenditure has also gone towards controlling widespread invasive alien plants such as ice-plant (*Carpobrotus* spp.) in the Mediterranean litorral or giant hogweed (*Heracleum mantegazzianum*) in temperate Europe (Table 5). Through extrapolation from herbicide sales, Williamson (2002) has estimated that the cost for chemical control for 30 alien weeds in the UK would be more than 150 million € per year.

Besides management costs, information on losses to provisioning services is sometimes available, but primarily for agriculture, forestry and fishery sectors. In the UK, annual crop losses due to alien arthropods are estimated at 2800 million €, which together with the impact inflicted by pathogens and vertebrates adds up 3800 million € per year (Pimentel *et al*. 2001). In Germany it is estimated that the minimum costs of losses in stored grain attributable to only three damaging arthropods might be as much as 12 million € per year (Reinhardt *et al*. 2003). In the Milan region (Italy) an attempt to eradicate populations of an invasive Asian long-horned beetle (*Anoplophora chinensis*) resulted in the removal of 2000 trees at a cost of 1.06 milllion €, apparently without success (van der Gaag 2007). A cost-benefit analysis conducted in Italy has shown that even an active control plan for coypu (*Myocastor coypus*) over 5 years has not decreased costs arising from its damage to agriculture and riverbanks (Panzacchi *et al.* 2007).

Marine fisheries highlight the complexity arising from both costs and benefits to provisioning services following the introduction of an alien species. For example, some Erythrean fishes (i.e., introduced through the Suez Canal) have become part of the Levantine fisheries (Galil *et al.* 2009) but others such as the blue-spotted coronetfish (*Fistularia commersonii*) have a low market value and prey on commercially important native fishes such as the picarel (*Spicara smaris*) and bogue (*Boops boops*). However, fewer than a handful of studies have estimated costs of alien species to fisheries and the estimates depend on the model assumptions. For instance, from the mid 1980’s to early 1990’s, invasion by the combjelly (*Mnemiopsis leidyi*) contributed to 10% losses of the commercial anchovy (*Engraulis encrasicolus*) fishery in the Black Sea. This decline is estimated at between 12.3 mio € (Knowler 2005) to 16.9 mio € per year (Travis 1993), depending on the underlying fisheries model.

The introduction of crayfish is often assumed to contribute positively to local economies by developing new aquaculture activities. This is the case for farmed American crayfish in southern Spain (Gherardi 2007). An integral cost-benefit analysis of alien species in fisheries or aquaculture is lacking and would be complex to undertake. For example, losses to commercial fisheries due to the Chinese mitten crab might range from 73.4–84.7 million € since 1912 during intermittent mass occurrences in German waters (Fladung, pers comm.). However, the crabs are sold as food and between1994–2004 this amounted to sales of 3-4.5 million €. This amount needs to be deducted from impact costs arising from their burrowing activity that increases erosion of dikes, river and lake embankments (Gollasch and Rosenthal 2006, Gherardi 2007).

Finally, costs from damages to aquatic infrastructures, especially by fouling, can be high. The great shipworm (*Teredo navalis*), a bivalve, has destroyed dykes and flood protection installations in the Baltic and North Sea (Leppäkoski *et al*. 2002). Similarly, damages to seawater intake pipes in power plants in the Levantine coast by the Erythrean nomadic jellyfish (*Rhopilema nomadica*) cost 36,530 € per year (Galil and Zenetos 2002). Unfortunately, there are only a few published studies on actual or projected costs from individual countries or maritime basins for widely distributed aquatic invertebrates known to have high economic impacts.

The non-material benefits people obtain from ecosystems are also influenced by alien species but are more difficult to quantify as most evidence is anecdotal (Bardsley and Edwards-Jones 2006). Changes in the recreational use of natural areas or impacts on ecotourism activities are described but not evaluated. In the 1970s, the Erythrean nomadic jellyfish entered the Mediterranean through the Suez Canal. Local municipalities in the Aegean and Levantine coast reported a decrease in holiday-makers frequenting the beaches because of their concern over the painful stings inflicted by the jellyfish (Galil and Zenetos 2002). In contrast, many alien plants are considered to be emblematic species in certain landscapes. The Japanese rose (*Rosa rugosa*) grows on Danish beaches and sand dunes in such abundance that it is a problem for beachgoers since it forms impenetrable thorny thickets (Weidema 2006). Despite this nuisance, blooming thickets are displayed in tourist brochures and on postcards. In Mediterranean coastal areas, the American *Opuntia* and *Agave* species are typical floral elements and attract the attention of tourists looking for “Wild West” landscapes (Vilà 2008).

Many invaders cause health problems. Nearly 100 (ca. 6%) of the alien invertebrate species in Europe affect human and animal health (Roques *et al*. 2009). Biting insects, which can potentially transmit diseases, include seven mosquitoes and more than 30 ectoparasites. More than half of the 47 introduced nematodes are endoparasites of humans or cause zoonosis (an infectious animal disease that can be transmitted to humans) in cattle and game animals. Some aliens that pose a health risk to humans live in or around buildings, including two recluse spiders (*Loxosceles* spp.) from America that have necrotic bites and the venomous redback spider (*Latrodectus hasselti*) from Australia (Kobelt and Nentwig 2008). Several alien plants produce allergenic pollen and increase the prevalence of hay fever (Belmonte and Vilà 2004), giant hogweed produces sap that causes skin lesions (Pyšek *et al.* 2007). The estimated medical costs of invaders are only available for known expenditures to treat the induced allergic reactions to *Ambrosia artemisiifolia* in Germany (Reinhard *et al.* 2003).

Conclusions

Our survey has revealed that in Europe there are over one thousand alien species known to cause ecological or economic impacts. While these findings reflect the current state-of-the-art, they are liable to change as more information is gathered in the future.

Many invaders cause multiple impacts over a large area in Europe. The overall impact of invaders depends upon their area of distribution, local abundance and per capita effect (Parker *et al.* 1999), but these three components are difficult to quantify. A harmonized database such as that produced through DAISIE enables the identification of the most widespread species causing impact as well as those with the widest range of impacts types on ecosystem services. Using the Millennium Ecosystem Assessment approach to quantify the services most at risk from invasive species should help rank different species as well as prioritise management procedures (Hulme 2006). This approach is a crucial first step to find indicators of ecosystem service disruption (Meyerson *et al.* 2005) but, as yet, ecosystem services are still not well integrated into conservation assessments (Egoh *et al.* 2007).

We have identified that the monetary costs of invasions in Europe can be grouped into their harmful consequences on provisioning services and response actions in managing alien species populations. Besides conservation, the sectors of agriculture, forestry, fisheries and health seem to be the main economic sectors where alien species lead to significant monetary costs. Yet, the economic evaluation of aliens cannot be based solely on market-based costs and should include indirect and non-use value costs (Born *et al.* 2005).

These results drawn from DAISIE should establish a European benchmark upon which further research on impacts can develop. With evidence of increasing numbers of alien species introductions to this region in the last few decades (Hulme et al. 2008) such assessments should become a regional priority.

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Panel 1: The DAISIE project (www.aliens-europe.org)

DAISIE (Delivering Alien Invasive Species Inventories for Europe) was funded by the European Commission (2005-2008) to create an inventory of alien species that threaten European terrestrial, fresh-water and marine environments in order to understand the environmental, economic, social and other factors involved in invasion (Hulme *et al.* 2009).The project was executed by an international team of leading experts in the field of biological invasions and an extensive network of European collaborators and stakeholders. In addition to collating one of the most comprehensive databases worldwide on introduced species, DAISIE aimed to raise awareness by producing factsheets on 100 of the worst European invasive species as well as mobilise researchers through a European registry of expertise in invasions.

The DAISIE database has collated information for fungi, plants, vertebrates, invertebrates, marine and inland aquatic organisms from up to 63 countries/regions (including islands) and 39 coastal and marine areas including regions adjacent to Europe. Over 248 datasets constituting more than 45,000 individual species records alien to (i.e. native outside Europe) or in (i.e. native somewhere in Europe) Europe were assembled and verified by experts. This represents the largest database of alien species in the world. The database includes information on ecological and economic impacts of alien species in particular regions, documented not only by standard international sources but also by exploring gray literature, local journals, books and check-lists written in non-English languages. The major findings, factsheets and species list are summarised in DAISIE (2009).

The DAISIE database follows the classification of species based on invasion status proposed by Occhipinti-Ambrogi & Galil (2004) and Pyšek *et al.* (2004). Alien species are those introduced by humans that colonize outside their natural range and dispersal potential, while invasive species are those alien species which spread over a large area and attain high local abundances. The DAISIE database includes only neophytes (i.e. species introduced after 1500 A.D.).

Panel 2. Lessons from and for North America

There are at least 1000 scientific case-studies published on the impact of invasive species on one or more ecosystem services (Table 1). While 53% of the studies have been conducted in North America, the similarly sized continent of Europe contributes only 16% . These published studies are essential to understand the ecological mechanisms underlying the impacts of invasive species. However, to translate the ecological information into monetary terms for individual continents, it is necessary to know the number of alien species causing ecological and economic impacts. This is now well known for Europe due to DAISIE, but as yet not for USA and North America as a whole. Such an analysis requires a comprehensive assessment of the numbers of species that have naturalised in North America and of the proportions that have resulted in economic or ecological impact. The groundwork for such an assessment , at least in the USA, exists. A total of 319 datasets on alien species, over half of which are online, have been identified in the USA (Crall *et al.* 2006; Graham *et al.* 2008) and while the taxonomic composition, geographic balance and extent of additional information might be variable this still represents a significant platform from which to launch an initiative equivalent to DAISIE on the other side of the Atlantic.

Although DAISIE reflects the foresight of the European Commission in identifying the need for an inventory of alien species, Europe lags behind North America in the direct quantification of monetary impacts. For example, the publication of Harmful Non-Indigenous Species in the United States (OTA 1993) played a pivotal role in raising awareness of the ecological and economic impacts of biological invasions. This document reported $97 billion in damages from 79 exotic species during the period from 1906 to 1991. This value has subsequently been updated to $120 billion per year (Pimentel *et al.* 2005) after inclusion of more species. In Canada, the projected costs of 11 invasive species to fisheries, agriculture and forestry has been estimated to be $13-34 billion Canadian (CDN) per year (Colautti *et al.* 2006). Monetary costs across regions are difficult to compare (Born *et al.* 2005), especially if different sectors are examined. This explains the differences between the US and Canada estimates where the higher value in the former reflects the inclusion of feral domestic animals and human diseases in the calculations. For Europe DAISIE has identified the monetary costs of relevant plants and animals affecting nature conservation, agriculture, forestry and fisheries (See Table 5 for some examples) from which an overall European cost estimate is underway for the development of an EU Strategy on Invasive Alien Species.

Table 1. Representation of publications (%) for Europe and North America in global reviews of ecological impacts of alien species. See Figure 3 for impact type code. Sample size represents the total number of publications screened in each review.

Reference	Taxonomic group	Impact types	Sample size	Europe	N America
Desprez-Loustau *et al.* 2007	Fungus	R4; S1, 3; P2	77	28.57	58.44
Vilà *et al.* 2000	Plants	P3	20	35.00	45.00
Ehrenfeld 2003	Plants	S1-3, 5	77	10.39	50.65
Vilà *et al.* 2004	Plants	P1	29	6.90	82.76
Levine *et al.* 2003	Plants	S2-3; P2; R2, 5, 7, 9	152	6.58	57.89
Liao *et al.* 2007	Plants	S1-2, 5	88	20.45	60.23
D'Antonio *et al.* 1999	Terrestrial plants & vertebrates	S1; R8-10	52	0.00	50.00
Traveset & Richardson 2006	Terrestrial plants, insects & vertebrates	P2; R1-2	38	26.32	10.53
Kenis *et al.* 2008	Insects	S1-3; P2-3; R2-4, 9	403	5.21	62.28
Long 2003	Mammals	S; P1-3; R1, 4, 6-9	339	30.97	20.35
Ciruna *et al.* 2004	Aquatic inland species	P2; S1, 3; R3, 9; C1	94	22.34	43.62
Grosholz 2002	Marine species	S3, 5; P3; R1, 3-4	31	0.00	93.55

Table 2. Total number and percentage of alien species known to have an ecological or economic impact for different taxonomic groups in Europe.

Taxonomic group	Total	Ecological impact (%)	Economic impact (%)
Terrestrial plants	5789	326 (5.6)	315 (5.4)
Terrestrial invertebrates	2481	342 (13.8)	601 (24.2)
Terrestrial vertebrates	358	109 (30.4)	138 (38.5)
Aquatic inland flora and fauna	481	145 (30.1)	117 (24.3)
Marine flora and fauna	1071	172 (16.1)	176 (16.4)

Table 3. Total number and percentage of marine alien species having an ecological and economic impact by marine basin in Europe.

Basins	Area (km2)	Total	Ecological impacts (%)	Economic impacts (%)
European Atlantic Ocean	3,700,000	675	100 (14.8)	145 (21.5)
Azov Sea	37,555	8	0 (0)	0 (0)
Baltic Sea	377,000	257	107 (41.6)	82 (31.9)
Barents Sea	1,400,000	2	1 (50)	0 (0)
Black Sea	436, 400	37	20 (54.1)	15 (40.5)
Caspian Sea	371,000	24	0 (0)	0 (0)
Mediterranean Sea	2,500,000	1313	229 (17.4)	171 (13.0)
North Sea	570,000	420	95 (22.6)	95 (22.6)

Table 4. The top-ten invasive species identified by DAISIE (Panel 1), with the highest number of different impact types on ecosystem services in Europe. The number of impacts is indicated by S: supporting, P: provisioning, R: regulating and C: cultural services. See Figure 3 for the classification of impact types.

Species	Taxonomic group	Impacts	Native range
Oxalis pes-caprae	Terrestrial plant	2P, 4R, 2C	S Africa
Branta canadensis	Terrestrial vertebrate	2S, 2P, 2R, 2C	Neoarctic N America
Cervus nippon	Terrestrial vertebrate	3S, 1P, 3R, 2C	E Asia
Myocastor coypus	Terrestrial vertebrate	3S, 1P, 3R, 2C	S America
Dreissena polymorpha	Aquatic inland invertebrate	1R, 1P, 4R, 3C	Black, Caspian and Aral Seas
Procambarus clarkii	Aquatic inland invertebrate	1S, 2P, 5R, 1C	Mexico and S-central USA
Salvelinus fontinalis	Aquatic inland vertebrate	3S, 3P, 1R, 2C	N America
Codium fragile	Marine alga	3S, 1P, 4R	Japan
Undaria pinnatifida	Marine alga	2S, 2P, 4R	NW Pacific
Balanus improvisus	Marine invertebrate	1S, 1P, 6R	Atlantic

Table 5. Alien species in Europe generating some of the highest costs (million € per year). Values are actual expenditures and not estimates or extrapolations. See Supplementary material for a full list of examples.

Species	Biome/taxa	Country	Extent	Cost item	Period	Cost	Reference
Carpobrutus spp.	Terrestrial plant	Spain	Localities	Control/eradication	2002-2007	0.58	Andreu & Vilà 2007
Anoplophora chinensis	Terrestrial invertebrate	Italy	Country	Control	2004-2008	0.53	Van der Gaag 2007
Cervus nippon	Terrestrial vertebrate	Scotland	Localities	Control		0.82	White & Harris 2002
Myocastor coypus	Terrestrial vertebrate	Italy	Localities	Control/damages	1995-2000	2.85	Gosling & Baker 1989
Sciurus carolinensis	Terrestrial vertebrate	UK	Country	Control	1994-1995	0.46	White & Harris 2002
Azolla filiculoides	Aquatic inland plant	Spain	Protected area	Control/eradication	2003	1.00	Andreu & Vilà 2007
Eichhornia crassipes	Aquatic inland plant	Spain	River basin	Control/eradication	2005-2007	3.35	Andreu & Vilà 2007
Oxyura jamaicensis	Aquatic inland vertebrate	UK	Country	Eradication	2007-2010	0.75	Scalera & Zaghi 2004
Chrysochromulina polylepis	Marine algae	Norway	Country	Toxic bloom		8.18	Hopkins 2002
Rhopilema nomadica	Marine invertebrate	Israel	Coast	Infrastructure damage	2001	0.04	Galil & Zenetos 2002

Figure legends

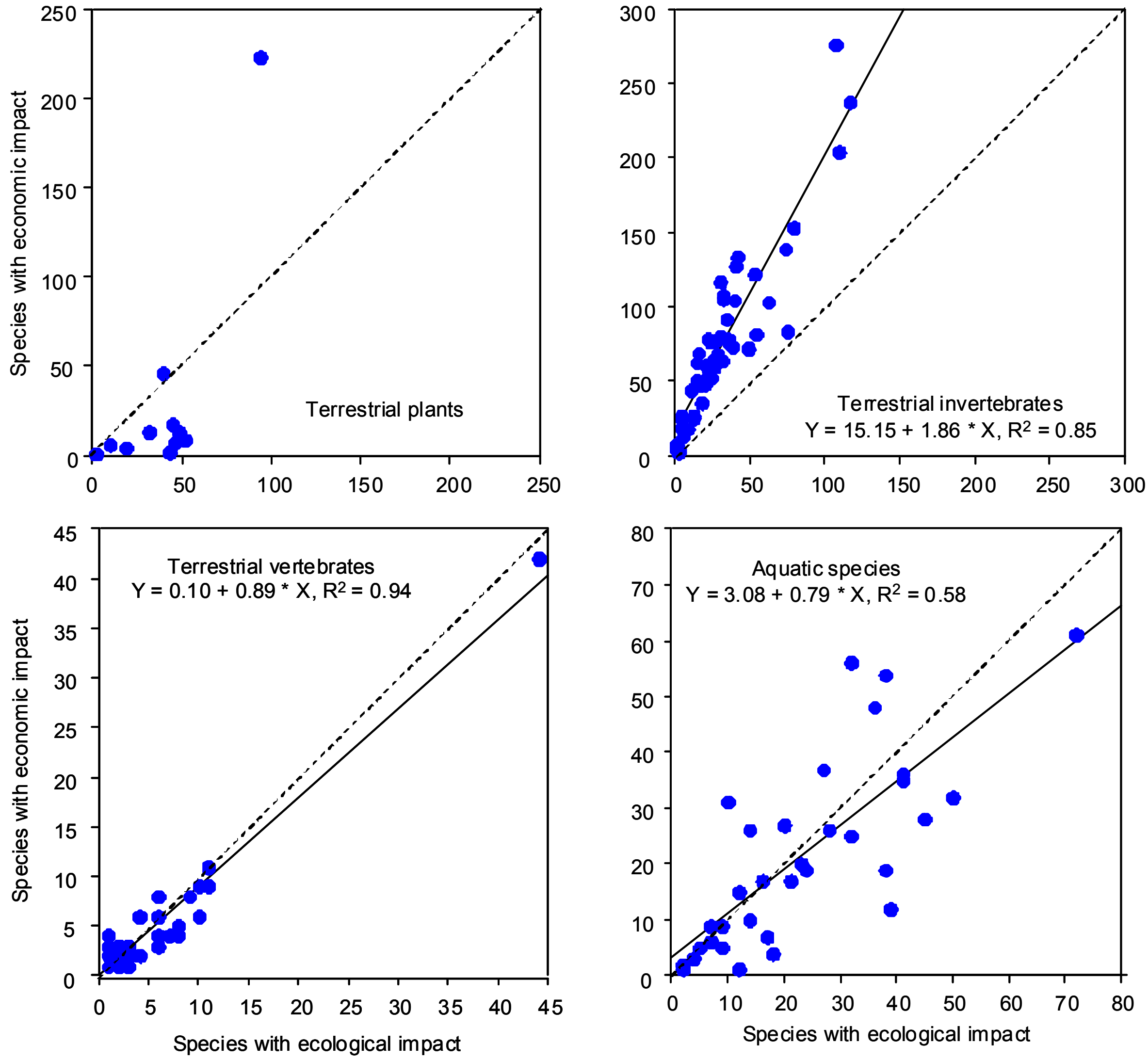
Figure 1. Relationship between the number of alien species with ecological and economic impact per region for different taxonomic groups in Europe). Each data point represents an individual country, major island or administrative unit (n = 63). The outlier in terrestrial plants and vertebrates represents the United Kindom. The lineal regression for plants is not shown. The line of unity is dashed. Data from the DAISIE database (Panel 1)

Figure 2. Frequency distribution of alien species with ecological and economic impacts in European regions. Significant differences between the distribution of species with ecological and economic impacts are indicated by χ^2-tests. The mean and maximum number of regions per taxonomic group are given in parentheses. Data from the DAISIE database (Panel 1)

Figure 3. Examples of impact types of invasive species in Europe classified in four categories of ecosystem services based on Binimelis *et al.* (2007).

Figure 4. Average (±S.E.) number of ecosystem services (i.e., supporting, provisioning, regulating and cultural) and number of impacts affected by different taxonomic groups based on information on 100 of the worst European invasive species (excluding the data for three fungal species). See Figure 3 for the identity of impacts. Data from the DAISIE database (Panel 1).

Figure 5. The American crayfish (*Procambarus clarki*), the common slider (*Trachemys scripta elegans*), the prickly-pear cactus (*Opuntia maxima*) and the muskrat (*Ondatra zibethicus*) are invasive species in Europe causing a variety of impacts on ecosystem services. Photo credits: top: H. Garrido/EBD-CSIC; bottom left: M. Vilà; bottom right: Veli-Matti Väänänen.



Species with economic impact
Terrestrial plants
Terrestrial invertebrates
Y = 15.15 + 1.86 * X, R2 = 0.85
Terrestrial vertebrates
Y = 0.10 + 0.89 * X, R2 = 0.94
Aquatic species
Y = 3.08 + 0.79 * X, R2 = 0.58
Species with ecological impact

FIG 1

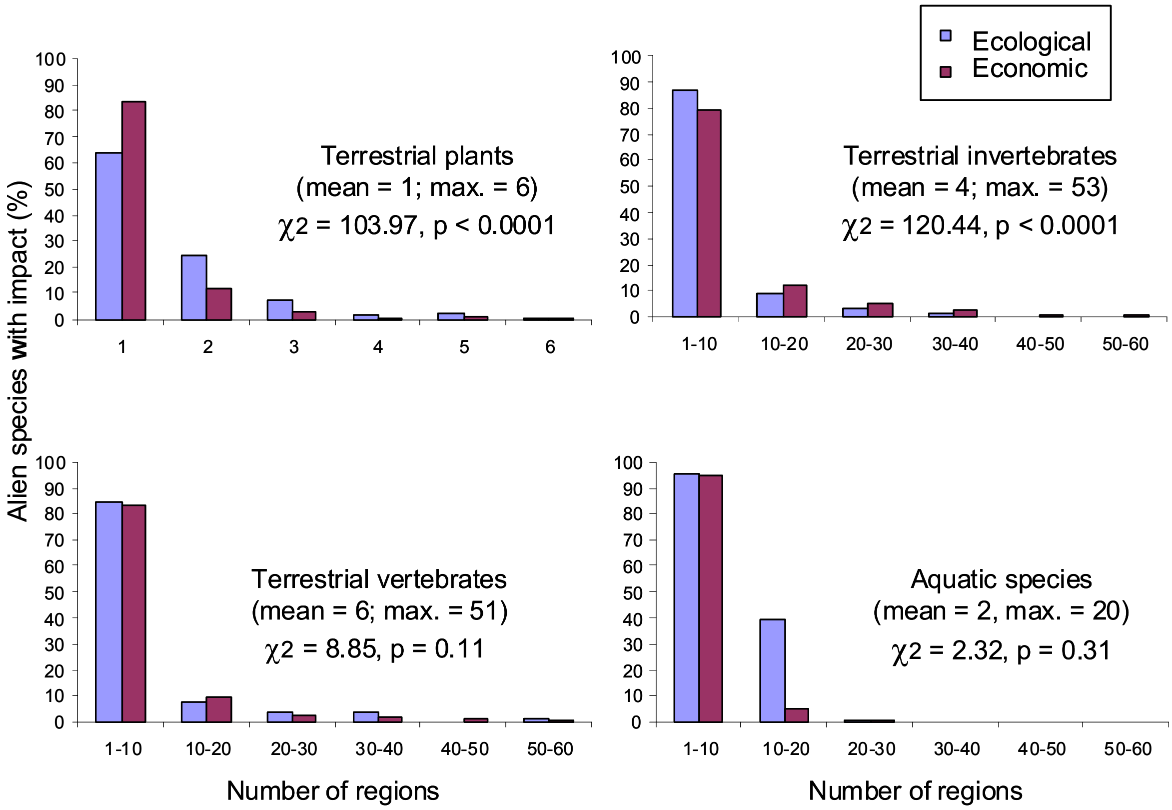
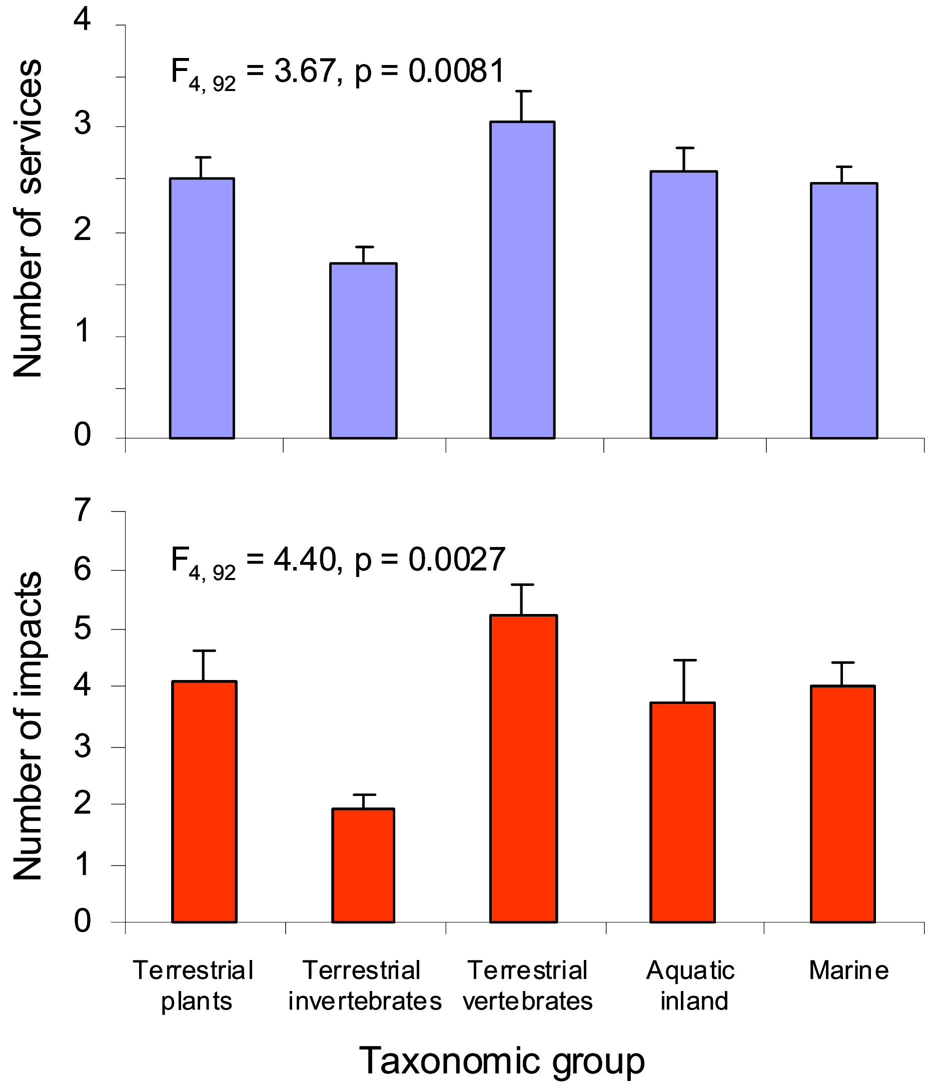

Ecological
Economic
Alien species with impact (%)
Terrestrial plants
(mean = 1; max. = 6)
χ2 = 103.97, p < 0.0001
Terrestrial invertebrates
(mean = 4; max. = 53)
χ2 = 120.44, p < 0.0001
Terrestrial vertebrates
(mean = 6; max. = 51)
χ2 = 8.85, p = 0.11
Aquatic species
(mean = 2, max. = 20)
χ2 = 2.32, p = 0.31
Number of regions
Number of regions

FIG 2


PROVISIONING
P1.Loss or gain in food, fuel or fiber (*Anophora chinensis*)
P2. Threat to endangered native species (*Trachemys scripta*)
P3. Alteration of genetic resources (*Oxyura jamaicensis*)
SUPPORTING
S1.Modification of soil and sediments (*Spartina anglica*)
S2. Alteration of nutrient cycling (*Dreissena polymorpha*)
S3. Community changes (*Procambarus clarkii*)
S4. Refugia changes (*Caulerpa taxifolia*)
S5. Changes in primary production (*Coscinodiscus wailesii*)
REGULATING
R1. Alteration of biological control (*Harmonia oxyridis*)
R2. Changes in pollination services (*Opuntia stricta*)
R3. Infection to native fauna and flora (*Aphanomyces astaci*)
R4. Vectors of diseases (*Aedes albopictus*)
R5. Production of toxic substances (*Chattonella verruculosa*)
R6. Causing injuries (*Ambrosia artemisifolia*)
R7. Natural hazard protection (*Cortaderia selloana*)
R8. Alteration of erosion regimes (*Myocastor coypus*)
R9. Water regulation and purification (*Elodea canadensis*)
R10. Bioaccumulation (*Ensis americanus*)
CULTURAL
C1. Changes in recreational use (*Heracleum mantegazzianum*)
C2. Affectation to ecotourism (*Rhopilema nomadica*)
C3. Changes in the perception of landscapes (*Rosa rugosa*)
C4. Aesthetics (*Cameraria ohridella*)

FIG 3



Number of services
4
3
2
1
0
F4, 92 = 3.67, p = 0.0081
Number of impacts
7
6
5
4
3
2
1
0
F4, 92 = 4.40, p = 0.0027
Terrestrial plants
Terrestrial invertebrates
Terrestrial vertebrates
Aquatic inland
Marine
Taxonomic group

FIG 4

Appendix I: List of DAISIE partners:

Pavlos Andriopoulos, Margarita Arianoutsou, Sylvie Augustin, Nicola Baccetti, Sven Bacher, Jim Bacon, Ioannis Bazos, Pavel Bolshagin, François Bretagnolle, François Chiron, Philippe Clergeau, Pierre- Olivier Cochard, Christian Cocquempot, Armelle Cœur d'Acier, Jonathan Cooper, Darius Daunys, Matej David, Pinelopi Delipetrou, Viktoras Didžiulis, Franck Dorkeld, Franz Essl, Bella Galil, Jacques Gasquez, Kyriakos Georghiou, Zigmantas Gudžinskas, Ohad Hatzofe, Martin Hejda, Mark Hill, Vojtěch Jarošík, Salit Kark, Stefan Klotz, Manuel Kobelt, Yannis Kokkoris, Mladen Kotarac, Ingolf Kühn, Phil Lambdon, Eugenia Lange, Carlos Lopez-Vaamonde, Marie-Laure Loustau, Arnald Marcer, Michel Martinez, Mathew McLoughlin, Alain Migeon, Dan Minchin, Maria Navajas, Pierre Navajas, Irina Olenina, Richard Ostler, Irina Ovcharenko, Vadim E Panov, Eirini Papacharalambous, Michel Pascal, Jan Pergl, Irena Perglová, Andrey Phillipov, Joan Pino, Katja Poboljsaj, Wolfgang Rabitsch, Jean-Yves Rasplus, Natalia Rodionova, Helen Roy, Daniel Sauvard, Riccardo Scalera, Assaf Schwartz, Ondřej Sedláček, Susan Shirley, Valter Trocchi , Marten Winter, Annie Yart, Artemios Yiannitsaros, Pierre Zagatti, Andreas Zikos.

Supplementary material: Examples of monetary costs (million € per year) of alien species invading Europe.

Species	Biome/taxa	Country	Extend	Cost item	Cost	Reference
Carpobrotus spp.	Terrestrial plant	Spain	Localities	Control/eradication	0.29	Andreu & Vilà 2007
Eucalyptus spp.	Terrestrial plant	Spain	Localities	Control/eradication	1.58	Andreu & Vilà 2007
Fallopia japonica	Terrestrial plant	UK	Localities	Eradication	0.81	Child et al. 2001
F. japonica, F. bohemica, F. sachalinensis	Terrestrial plant	Czech Rep.	Localities	Control/containment	0.02	Křivánek 2006
Heracleum mantegazzianum	Terrestrial plant	Czech Rep.	Localities	Control/containment	0.01	Křivánek 2006
H. mantegazzianum	Terrestrial plant	Denmark	Localities	Control	0.08	Nielsen et al. 2005 REF???
H. mantegazzianum	Terrestrial plant	UK	Country	Control	0.19	Shaw 2003
H. mantegazzianum, F. japonica, F. bohemica, F. sachalinensis, Impatiens glandulifera, Rudbeckia laciniata	Terrestrial plant	Czech Rep.	Localities	Control/containment	0.02	Křivánek 2006
Pennisetum setaceum	Terrestrial plant	Spain	Localities	Control/eradication	0.62	Andreu & Vilà 2007
Pinus strobus, Larix decidua	Terrestrial plant	Czech Rep.	Protected area	Control/containment	0.05	Hentschel & Hentschelová 2003
Rhododendron ponticum	Terrestrial plant	UK	Protected area	Control	66.26	Gritten 1995
Anoplophora chinensis	Terrestrial invertebrate	Italy	Country	Control	0.53	Van der Gaag 2007
Branta canadensis	Terrestrial vertebrate	Germany	Country	Eutrophication	1.02	Gebhart 1996
C. nippon	Terrestrial vertebrate	Scotland	Localities	Control	0.82	White & Harris 2002
Chrysolophus pictus	Terrestrial vertebrate	Germany	Country	Damages	1.28	Gebhart 1996
Felis catus, Rattus sp.	Terrestrial vertebrate	Italy	Small islands	Eradication	0.19	Scalera & Zaghi 2004
F. catus, Rattus sp.	Terrestrial vertebrate	France	Small islands	Eradication	0.21	Scalera & Zaghi 2004
F. catus	Terrestrial vertebrate	UK	Localities	Control	3.62	White & Harris 2002
Hystrix hodgsoni	Terrestrial vertebrate	UK	Localities	Eradication	0.03	Smallshire & Davey 1989
Muntiacus reevesi	Terrestrial vertebrate	UK	Localities	Control	0.02	White & Harris 2002
Mustela vison	Terrestrial vertebrate	UK	Country	Eradication	0.55	Moore et al. 2003
M. vison	Terrestrial vertebrate	Estonia	Country	Eradication	0.12	Scalera & Zaghi 2004
Myocastor coypus	Terrestrial vertebrate	UK	Country	Eradication	0.45	Gosling & Baker 1989
M. coypus	Terrestrial vertebrate	Italy	Localities	Riverbank damages	2.14	Panzacchi et al. 2007
M. coypus	Terrestrial vertebrate	Italy	Localities	Agricultural damages	0.19	Panzacchi et al. 2007
M. coypus	Terrestrial vertebrate	Italy	Localities	Control	0.52	Panzacchi et al. 2007
Oryctolagus cuniculus	Terrestrial vertebrate	Germany	Country	Control	5.11	Gebhart 1996
O. cuniculus	Terrestrial vertebrate	UK	Localities	Control	41.18	White & Harris 2002
O. cuniculus, Rattus sp, M. coypus, M. vison	Terrestrial vertebrate	France	Small islands	Control/eradication	0.29	Scalera & Zaghi 2004
Lithobates catesbeianus	Terrestrial vertebrate	UK	Locality	Eradication	0.01	Adrados & Briggs 2002
Rattus norvegicus	Terrestrial vertebrate	UK	Small islands	Eradication	0.28	Scalera & Zaghi 2004

Sciurus carolinensis	Terrestrial vertebrate	UK	Country	Control	0.46	White & Harris 2002
Azolla filiculoides	Freshwater plant	Spain	Protected area	Control/eradication	1.00	Andreu & Vilà 2007
Crassula helmsii	Freshwater plant	UK	Localities	Control	0.88	Shaw 2003
Eichhornia crassipes	Freshwater plant	Spain	River basin	Control/eradication	3.35	Andreu & Vilà 2007
Dreissena polymorpha	Freshwater invertebrate	Spain	River basin	Infrastructure & boat damage	2.00	Alonso 2006
Oxyura jamaicensis	Freshwater vertebrate	Spain	Protected area	Eradication	0.06	Cevallos pers comm
O. jamaicensis	Freshwater vertebrate	UK	Country	Eradication	0.75	Scalera & Zaghi 2004
Chattonella spp.	Marine algae	Norway	Country	Toxic bloom	7.43	Hopkins 2002
Chrysochromulina polylepis	Marine algae	Norway	Country	Toxic bloom	8.18	Hopkins 2002
Cercopagis pengoi	Marine invertebrate	Fidland	Gulf	Decline fish catches	0.02	Panov et al. 1999
Rhopilema nomadica	Marine invertebrate	Israel	Coast	Infrastructure damage	0.04	Galil & Zenetos 2002

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