

General knowledge on invasive alien species

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■ Alien, non-native or exogenous species

A species, i.e. an individual or population, introduced intentionally or unintentionally by humans or their activities to areas outside its original distribution range. A species is said to be alien to a given biogeographic area over a given period when it was absent from the area at the start of the period, but subsequently colonised the area and established long-term populations. In other words, the species lives outside its natural distribution range.

■ Introduced species

A non-native species introduced intentionally or unintentionally to an area or part of an area where it had been absent up to that point.

■ Naturalised species

An introduced species encountering favourable ecological conditions for establishment that is sustainable over decades in the host area. The species reproduces and expands regularly in the new distribution range and maintains its presence over the long term, an example being *Hibiscus palustris* (see Figure 1). Specifically concerning plants, Richardson *et al.* (2000) proposed a fairly close definition, adding that these species can maintain their presence without any direct intervention on the part of humans or in spite of human intervention in natural, semi-natural or man-made ecosystems.

Figure 1



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Hibiscus or Crimsoneyed rosemallow (*Hibiscus palustris*). Originally from North America, this plant grows near water and has large, highly visible flowers during the summer. It has been established for decades on a few sites in the Landes and Pyrénées-Atlantiques departments (SW France). It is mentioned in the interministerial decision dated 20 January 1982, in the "list of plant species protected throughout the country".

■ Pervasive or proliferating species

A pervasive species is defined in ecological terms as a native or non-native species in a given territory, that develops in abundance locally and rapidly expands its range. Aboucaya (1999) added as an additional criterion that the species colonises natural or semi-natural habitats. The definition of a proliferating species is similar to that of a pervasive species, i.e. rapid development in the number of individuals to the point that the species comes to dominate a given area. Though this definition does not exclude the concept, it does not mention the damage caused by the species.

The causes of pervasion or proliferation vary significantly depending on the origin of the species. Native species may become pervasive or proliferate following environmental changes in the occupied biotope (development work, eutrophication, climate change) or the environmental changes may also contribute to triggering an invasion by non-native species.

Invasive or pervasive?

The terms “invasive” and “pervasive” do not have exactly the same meaning. Though they both pertain to the rapid development in the numbers of a species and its geographic expansion, the term “invasive” is generally used for populations that are not native to the given area, whereas the term “pervasive” can designate an introduced or a native species that suddenly begins to grow in numbers. In addition, certain experts speak of an invasive population only if it causes noticeable damage. Practically speaking, the two terms are often perceived as virtually synonymous, particularly given the fact that it is not always possible to determine if a population is native or the product of introduced individuals. (Pascal *et al.*, 2009).

Biological invasion

An invasion occurs when a species expands outside its natural distribution range and establishes one or more sustainable and autonomous populations, generally without any human assistance in the colonised environment. Three phases are generally observed, arrival, establishment and expansion (Kolar and Lodge, 2001).

Feral animal/population

A captive or domestic animal that has returned to a wild state. This definition is used particularly for mammals, e.g. feral pigs, goats, cattle, etc.

Table 1 shows the links between the various terms and can be used to compare two terms. For example, a native/indigenous species cannot be alien/non-native, introduced or naturalised. It may be pervasive or proliferating, but it cannot be invasive and alien.

Table 1 Possible combinations of terms. According to Thévenot, 2013.

If a species is...	Native or indigenous	Alien or non-native	Introduced	Naturalised	Pervasive or proliferating	Invasive alien
Can it be...						
Native or indigenous		No	No	No	Possible	No
Alien or non-native	No		Possible	Possible	Possible	Possible
Introduced	No	Yes		Possible	Possible	Possible
Naturalised	No	Yes	Yes		Possible	Possible
Pervasive or proliferating	Possible	Possible	Possible	Possible		Possible
Invasive alien	No	Yes	Yes	Yes	Yes	

Semantic difficulties

■ Terminology

The study of biological invasions has generated a highly diverse set of concepts that are still under debate in the scientific community as well as among stakeholders (Lévêque *et al.*, 2012). This multiplication of terms and concepts has been identified as one of the factors slowing improvements in knowledge on the ecology of biological invasions (Falk-Petersen *et al.*, 2006) and also constitutes an obstacle to the integration of these issues in public policies and to intervention strategies. In addition, certain terms were defined taking into account specific taxonomic groups. This is a direct result of the relative paucity of multidisciplinary research and the high specialisation of researchers and naturalists, which in some cases can result in difficulties in understanding. That is occasionally the case between the animal and plant spheres (Falk-Petersen *et al.*, 2006) or concerning micro-organisms.

There is often confusion between the concept of proliferation and the alien nature of a species (Lévêque *et al.*, 2012). For example, some native species that proliferate locally are occasionally thought to be alien species. That is the case for river water-crowfoot (*Ranunculus fluitans*, see Figure 2), that can form thick beds similar to water primrose or water cabbage (*Pistia stratiotes*, see Figure 3) and hinder navigation, or the Great cormorant (*Phalacrocorax carbo*), that can do significant harm to freshwater fisheries, but is nonetheless a protected, native species.

Figure 2



Native *Ranunculus* species, such as river water-crowfoot (*Ranunculus fluitans*), can colonise large areas in favourable, river biotopes, modifying water flows and hindering navigation.

Figure 3



Water cabbage (*Pistia stratiotes*), is a floating, alien plant that is highly appreciated as an ornament in fountains. It can proliferate very rapidly, as shown above in 2003 in a periurban river in the Gironde department (SW France).

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The distinction is, however, important. Above and beyond the underlying regulatory issues that arise when preparing management work, there are numerous interactions between native species that are the result of long co-evolution and the existing communities can be disturbed by the arrival of new species (Strauss *et al.*, 2006a and 2006b; Ricciardi and Atkinson, 2004). The absence of co-evolution between an alien species and the host communities can explain an invasion (due to the lack of any possibility to compete) or its failure. However, recent research has shown that rapid evolutionary processes may take place within introduced populations, a clear indication of the complexity and of the possible changes in the relations between native and alien species.

For aquatic environments, Ricciardi and Atkinson (2004) submitted the hypothesis that the impact of an introduced species can be determined by the evolutionary and phylogenetic history of the invaded ecosystem. For example, an introduced species from a genus that is absent or not frequent in the host ecosystem, and consequently has a different evolutionary history, may produce impacts that are seen as more negative than those of an introduced species from a genus already widely present in the same ecosystem.

■ Different geographic areas

The alien or native nature of a species may also depend on the geographic area under consideration. Theoretically, a species should be seen as introduced only in areas lying outside its past or present natural distribution range. A native species is thus considered alien when it is transported outside of its original range and even invasive if it proliferates in the new environment (Beisel and Lévêque, 2010). Introductions may take place between countries or within a single country, but between two distinct biogeographic regions. In both cases, the population is considered alien in the host environment. For this reason, a given species may be considered native or alien depending on the geographic area under consideration (Poulet, 2010).

That is the case, for example, of the marsh frog (*Pelophylax ridibundus*), whose natural distribution range spans a vast zone in Eurasia. In the western part of this range, in France, the species is considered native in the eastern section of the country around Lake Geneva and down the Rhône valley (Neveu, 1989). The species was also introduced to numerous French regions, including Bretagne (Brittany). As a result, the status of the marsh frog can change depending on the geographic area under consideration. It is native to Eastern Europe and a large part of continental France, but is alien in Bretagne.

A further example is the common nase (*Chondrotoma nasus*), a fish species native to Central Europe that is present in the Rhine basin. As early as 1860, the species could disperse, via navigation canals, to the Rhône, Seine and Loire River basins where it is considered alien (Keith *et al.*, 2011). That is also the case of the butterbur (*Petasites hybridus*, see Figure 4), that grows along rivers in the Massif Central and in the eastern section of France, but is considered a potential invasive species in Bretagne (Haury *et al.*, 2010; Quéré *et al.*, 2011).

Figure 4



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The butterbur (*Petasites hybridus*).



■ Introduction dates

In addition to the geographic factors, further criteria concern the dates and reference periods selected in determining whether a species is native or non-native to a given area. The distribution of a species at a given date or period serves as the reference point on the basis of which the movements of the species are then analysed in order to set their status. In continental Europe, transfers of species by humans, both intentional and unintentional, started several thousand years ago, a fact that can make it difficult to determine whether a species is native or non-native in a given area (Simberloff *in* Pascal *et al.*, 2006).

In continental France, numerous zooarchaeological studies on certain species have revealed whether they were present prior to the start of the Holocene (10 000 years ago), i.e. the end of the last glacial period and the start of the first known introductions (Pascal *et al.*, 2006). Selection of the Holocene as the reference point means that certain species are considered native, when in fact they are alien, for example house mice (*Mus musculus*) or the common pochard (*Aythya ferina*, see Figure 5).

Figure 5



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The common pochard (Aythya ferina) is an introduced species that has integrated so completely in the local fauna that many people think it is native.

In terms of flora, it is generally acknowledged that plants introduced intentionally or unintentionally by humans after the year 1500, the start of introductions from the Americas, are considered alien (Lacroix *et al.*, 2007; Pył ek *et al.*, 2009). It is more difficult to apply that particular date to Asian, Eurasian and Mediterranean species for which the date of introduction in France is often unknown (Toussaint *et al.*, 2007). In these cases, some species are considered native if an analysis of regional and national bibliographic data indicates that they were widely found and seen as growing spontaneously in a given area at the end of the 1800s (Lacroix *et al.*, 2007). On the other hand, rare species not commonly found at the end of the 1800s may be considered alien (Lacroix *et al.*, 2007).

■ Impacts

The inclusion of the concept of impacts in determining whether a species is alien is still a topic of debate. Not all the stakeholders in this field share the same perception of invasive species and the modifications that they cause in host ecosystems, nor concerning the effective or presumed disturbances (Lévêque *et al.*, 2012). For certain authors, the concept of impacts is indispensable in determining whether a species is invasive (Davis and Thompson, 2001). However, it is often necessary to precisely define the ecological impacts of a species in order to make this criterion less subjective (Daehler, 2001). This uncertainty explains why a species is occasionally categorised as an invasive alien species if it rapidly and extensively colonises a new ecosystem, before any impacts have been identified.

Similarly, for managers, impacts and an assessment of their severity can justify management work on a species. Definitions including the two criteria, i.e. the alien status and the ecological and/or socio-economic impacts identifying the species as invasive, constitute a more operational approach for management. Discussions with stakeholders in the horticultural sector have shown that a common definition integrating management and clarification of the objectives for the lists of species to be drawn up jointly are seen as the indispensable prerequisites for effective, preventive management (Mandon-Dalger *et al.* 2013).

However, waiting for a species to cause significant negative impacts before taking action runs counter to the precautionary principle whereby work should be undertaken as soon as the species has been detected and an assessment of the risks involved has been run (Menozzi, 2010), two major elements in the various strategies implemented (see for example, Matrat *et al.*, 2012).

If the precautionary principle is interpreted to mean that immediate intervention following detection is required, excellent predictive capabilities concerning the future behaviour of the recently detected species would be necessary. The starting point in the analysis would be the impacts caused by the species already observed in other nearby, biogeographic areas in order to assess the risks involved in its introduction to the new area, and an analysis of the biological traits of species for which background data is absent (see Box 2, page 27).

At any rate, it is necessary to include the concept of impacts and damages in the definition of invasive alien species, at least tentatively as species having the “potential” to cause damage. The type of damage would depend on the ecological characteristics of the species and on those of the living communities in the colonised habitat, as well as on how humans use the environment in question (see Figure 6). In this case, as soon as a species is deemed likely to cause clearly defined damages, management work could be undertaken taking into account the issues specific to the site in question.

Figure 6



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The clearest impacts concern how environments are used. In the photo, a thick bed of parrot-feather watermilfoil (*Myriophyllum aquaticum*) blocks the passage of anglers (Léon pond, Landes department, 1993).



Introduction of species

Reasons and vectors

The introduction of a species, whether intentional or not, can take place via many paths (transportation itineraries) and many vectors (transportation means) (see Table 2 and Figure 7). A majority of introductions are caused by human activities.

Tableau 2 Examples of introduction paths and vectors, both intentional and unintentional. According to Soubeyran, 2008.

Intentional introductions		Unintentional introductions
Direct introductions	Evasions following planting or captivity	
Agriculture	Evasions from botanic gardens	Sea and air cargo
Forestry	Private gardens	Ballast water
Horticulture	Garden stores / Pet shops	Fouling of hulls
Animal farming	Zoos	Transport and construction machinery
Restocking	Animal farms	Transported earth and landfill
Releases of mammals	Bee keeping	Road cutting and filling
Hunting	Aquaculture	Agricultural products
Biological control	Aquariums	Seeds
Soil improvement	New types of pets	Construction materials
Agricultural expansion	Research centres	Wood
	Restocking	Packing materials
		Postal packages
		Waste
		Canals (navigation)

Figure 7

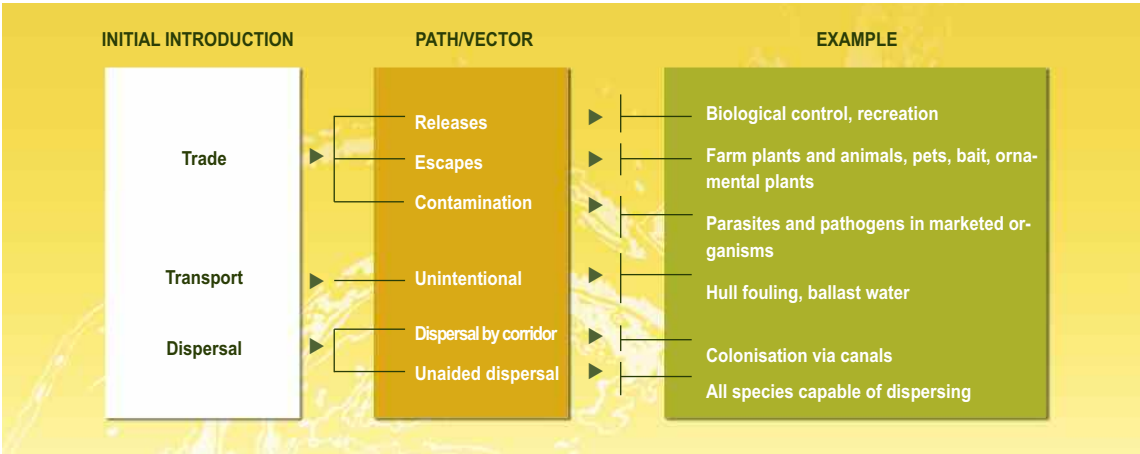


Diagram showing the various introduction paths and vectors. According to Hulme et al., 2007, in Poulet, 2010.

■ Intentional introductions

Certain species were introduced for the biological control of another species, e.g. the eastern mosquitofish (*Gambusia holbrooki*), a small fish introduced to limit mosquito populations. An analysis of its feeding habits has shown, however, that the species does not feed specifically on mosquito larvae, but also on other prey (aquatic insects and crustaceans) (Pascal *et al.*, 2006).

Plants have been introduced for ecological restoration, e.g. protection of soil and dunes, efforts to limit the erosion of river banks, etc. (Boudouresque, 2005). That is the case, for example, of the Hottentot fig (*Carpobrotus edulis*, see Figure 8) and the groundsel tree (*Baccharis halimifolia*). These two species are now considered extremely invasive along a major part of the coastline in continental France.

Figure 8



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The Hottentot fig.

Animal farming is the cause of the intentional or unintentional introduction of many species. For example, many mammals were introduced in Europe in the early 1900s for the fur industry, including coypus (*Myocastor coypus*, see Figure 9), muskrats (*Ondatra zibethicus*) and American mink (*Neovison vison*) (Léger 1999; Léger and Ruette, 2005). The same is true for the Red swamp crayfish (*Procambarus clarkii*) that was introduced for commercial production (Vigneux, 1993; Laurent, 1983).

Figure 9



a © Maurice, 1931
b © Le pêcheur français, 1984

Advertisements for a) a farm raising coypus in semi-liberty in the Eure department in 1931 and b) a farm raising signal crayfish in 1984.

Recreational hunting and fishing are also a source of direct introductions in the natural environment, examples being the largemouth bass (*Micropterus salmoides*), a carnivorous fish introduced for fishing, and Sika deer (*Cervus nippon*), introduced as game (Saint-Andrieux, 2006). It should be noted that restocking of fish for recreational fishing may result in unintentional introductions if the fish come from fish farms in ponds. That is the probable cause of the arrival in France of the topmouth gudgeon (*Pseudorasbora parva*) and the Albanian roach (*Pachychilon pictum*) (Pascal et al. 2006; Keith and Allardi, 1997).

The species imported for ornamental purposes and sold in garden stores, pet shops and plant nurseries have also been found in the natural environment. Water primrose (*Ludwigia* spp.) and parrot-feather watermilfoil (*Myriophyllum aquaticum*) were spread far and wide in ornamental pools (Dutartre, 1995). Numerous birds, e.g. Canada geese (*Branta canadensis*) and black swans (*Cygnus atratus*) (Fouque 2011a and 2011b), and certain fish, e.g. goldfish (*Carassius auratus*), have also been introduced for ornamental purposes in parks and gardens. Red-eared slider turtles (*Trachemys scripta elegans*, see Figure 10) were imported as pets (Dupré *et al.*, 2006).

Figure 10



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Red-eared slider turtles (*Trachemys scripta elegans*) can be easily identified by the red spots on the side of the head. They have rapidly colonised many aquatic environments, e.g. the Vistre River in the Gard department.

Indirect introductions are a further possibility. This is the case where animals held captive (farms, aquariums, zoos, pet owners) escape or are released to the natural environment by people unaware of the consequences. Examples are the sacred ibis (*Threskiornis aethiopicus*) (Clergeau *et al.*, 2005) and the red-necked Wallaby (*Macropus rufogriseus*) (Tillon and Lorvelec, 2004). Similarly, American mink (*Neovison vison*) and northern raccoons (*Procyon lotor*, see Figure 11) escaped from farms and have since firmly established themselves over large parts of continental France (Léger and Ruette, 2005). New types of pets, such as red-eared slider turtles (*Trachemys scripta elegans*) and Siberian chipmunks (*Tamias sibiricus*), have often been released to the natural environment by owners who no longer wished to keep them (Dupré *et al.*, 2004; Chapuis, 2005).

Figure 11



© C. Lemarchand

Raccoons escaped from farms prior to establishing feral populations in France.

■ Unintentional introductions

Certain species are transported unintentionally via water, on the hulls of boats. The phenomenon where organisms attach to hulls is called biofouling. Zebra mussels (*Dreissena polymorpha*) originated in the Black Sea and were introduced to Western and Northern Europe via canals and subsequently to North America by trans-atlantic shipping (see Figure 12). Intercontinental transport combined with biofouling is thought to be responsible for the introduction of over 60% of the invasive alien species (IAS) in marine environments (Molnar *et al.*, 2008).

Figure 12

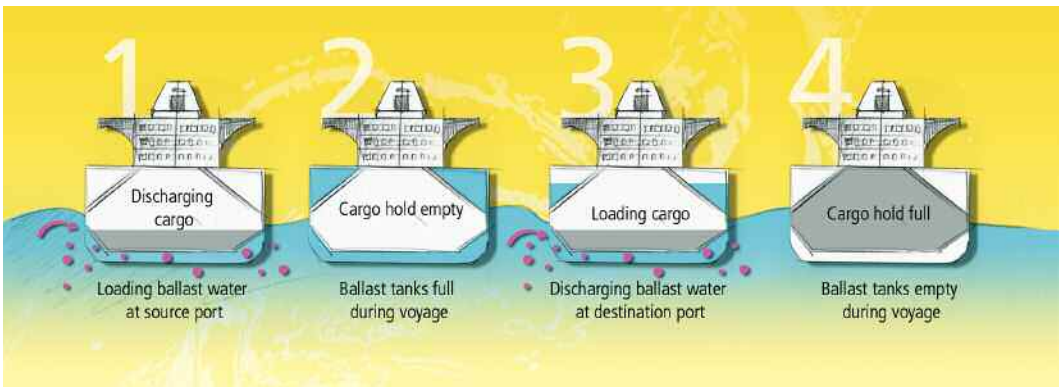


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Zebra mussels (*Dreissena polymorpha*) attached to the navigational instruments of a ship.

Ballast water, used to stabilise ships when travelling with no load, is subsequently pumped out in a port where cargo is loaded. As a result, enormous quantities of water containing local fauna and flora are transported from one ocean to another by ships serving as “giant aquariums” (see Figure 13). Ballast water thus constitutes one of the most effective vectors for the introduction of marine species as well as for freshwater species when ships travel to or from the Great Lakes in North America. Worldwide, Carlton and Geller (1993) estimated that between 8 and 10 billion tons of ballast water are transported annually and that at least 3 000 to 4 000 species travel around the world in this manner every day. An example is the Chinese mitten crab (*Eriocheir sinensis*) introduced to the United States, via California, in the ballast water of ships arriving from the Far East (Cohen and Carlton, 1997).

Figure 13



Cross-section of a ship showing ballast tanks and ballast-water cycle. Adapted from the Global Environmental Fund, United Nations Development Program, International Maritime Organisation, Global Ballast Water Management Program, 2007.

Unintentional imports can also occur during the transportation of goods (marine or air cargo) when species are inadvertently enclosed in containers. That is the case for the Asian hornet (*Vespa velutina*) that entered France through the Aquitaine region around the year 2000 via goods shipped from Asia (Villemant *et al.*, 2006) and for the narrow-leaved ragwort (*Senecio inaequidens*) whose seeds were lodged in imported sheep wool (Muller, 2004).

A further source of unintentional introductions is IAS-contaminated materials and machinery that travel around the country for development work (road construction, sanitation networks, river maintenance, transportation and reuse of landfill), to say nothing of the remains of invasive plants (Muller, 2004). Knotweed (*Reynoutria* spp.) has been widely dispersed by excavation machinery and landfill containing fragments of stalks and/or rhizomes. The wheels of cutting machines and the machines themselves (buckets, blades, dump trucks) cause unintentional introductions by transporting plants from one site to another unless they are properly cleaned after each job. Several examples of fragments of water-primrose stalks being transported by machinery working in aquatic environments have been noted. That is thought to be the case for the introduction of large-flower water primrose in the Brière regional nature park (Hauray and Damien, 2012).

Movements by certain types of people (anglers, boaters) from one aquatic environment to another can also result in the transport of species, generally over fairly short distances, in the form of plant fragments stuck to boats or trailers, animals attached to boat hulls, etc. (Anderson *et al.*, 2014) (see Figure 14).

Figure 14



Disinfection of recreational boats to avoid transporting invasive species to Ireland.

Finally, a further possibility consists of the transportation of plant propagules by animals, notably birds. It would seem certain that waterfowl³ are responsible for the colonisation of isolated lakes by *Lemna minuta*. The colonisation of isolated lakes by water primrose is probably due to the same cause.

In France, of introduced freshwater plant species, 38% were introduced for ornamental reasons and 29% are used in aquariums (Muller, 2004). In continental France, 44% of the 43 species of introduced freshwater fish have naturalised and among them, almost half were introduced for recreational fishing (Keith and Allardi, 1997). In Europe, the two main reasons for the introduction of fish are aquaculture and recreational fishing (Gozlan, 2008).

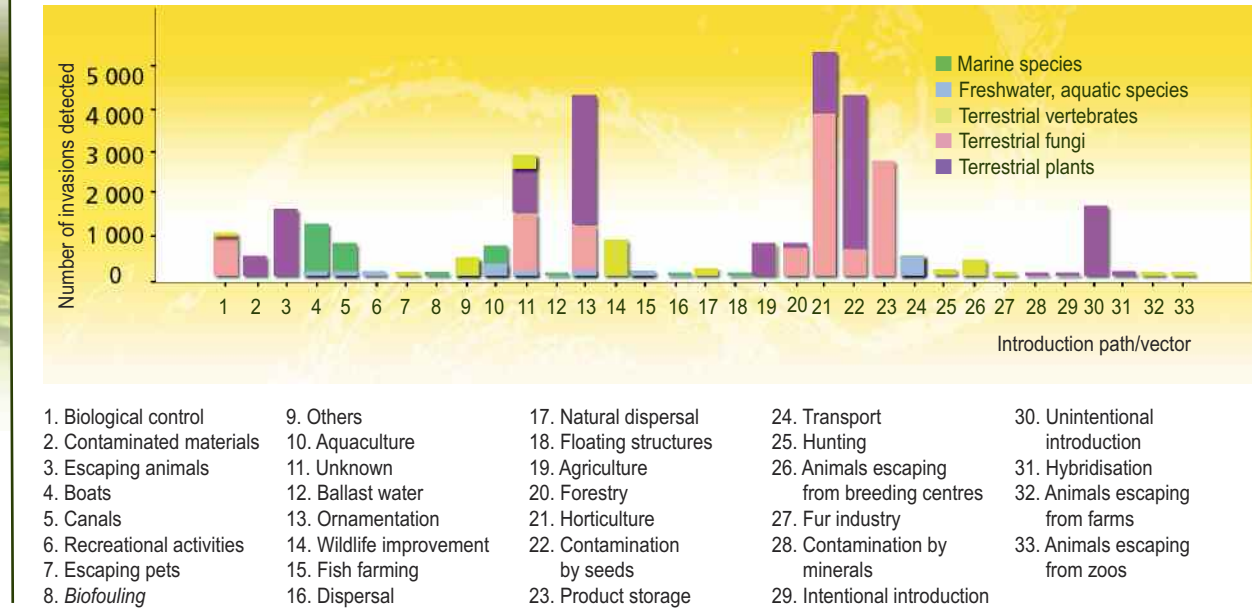
A study carried out on aquatic environments in Italy (Gherardi *et al.*, 2008) revealed that introductions of freshwater animal species from other continents were essentially the result of sport fishing and extensive fish farming (30%), intensive aquaculture (27%) and ballast water (25%). Ornamental uses in aquariums and basins represented a further 9% of introductions. The transported organisms can then colonise a new geographic area that in some cases is very far from their original range (see Table 3 and Figure 15 on the following page).

3. Waterfowl in this case consist of wildfowl, i.e. wild birds travelling significant distances.

Table 3 List of the introduction paths/vectors for the IAS discussed in the second volume of this book.

Species	Introduction path/vector
FLORA	
Curly waterweed - <i>Lagarosiphon major</i> , (Ridl.) Moss, 1928	Aquariums
Large-flowered waterweed - <i>Egeria densa</i> , Planch., 1849	Aquariums
Water pennywort - <i>Hydrocotyle ranunculoides</i> , L.f., 1782	Ornamental horticulture
Parrot-feather watermilfoil - <i>Myriophyllum aquaticum</i> , Verdcourt, 1973	Ornamental horticulture
Water primrose - <i>Ludwigia</i> spp.	Ornamental horticulture
New Zealand pigmyweed - <i>Crassulla helmsii</i> , (Kirk) Cockayne, 1907	Ornamental horticulture
Groundsel tree - <i>Baccharis halimifolia</i> , Linnaeus, 1753	Ornamental horticulture
Giant hogweed - <i>Heracleum mantegazzianum</i> , Sommier and Levier, 1895	Ornamental horticulture
Box elder - <i>Acer negundo</i> , Linnaeus, 1753	Ornamental horticulture
Knotweed - <i>Reynoutria</i> spp.	Ornamental horticulture, agriculture (fodder)
Goldenrod - <i>Solidago</i> spp.	Ornamental horticulture
Garden balsam - <i>Impatiens</i> spp.	Ornamental horticulture
Water finger grass - <i>Paspalum distichum</i> , Linnaeus, 1759	Agriculture (fodder)
FAUNE	
Signal crayfish - <i>Pacifastacus leniusculus</i> , Dana, 1852	Aquaculture
Red swamp crayfish - <i>Procambrus clarkii</i> , Girard, 1852	Aquaculture
Pumpkinseed - <i>Lepomis gibbosus</i> , Linnaeus, 1758	Fishing and aquariums
Red-eared slider turtle - <i>Trachémys scripta elegans</i> , Wied, 1839	Pets
African clawed frog - <i>Xenopus laevis</i> , Daudin, 1803	Raised for scientific research
American bullfrog - <i>Lithobates catesbeianus</i> , Shaw, 1802	Farming, ornamentation
Canada goose - <i>Branta canadensis</i> , Linnaeus, 1758	Ornamentation
Egyptian goose - <i>Alopochen aegyptiacus</i> , Linnaeus, 1766	Ornamentation
Ruddy duck - <i>Oxyura jamaicensis</i> , Gmelin, 1789	Zoos
Sacred ibis - <i>Threskiornis aethiopicus</i> , Latham, 1790	Zoos
American mink - <i>Neovison vison</i> , Schreber, 1777	Raised for the fur industry
Coypu - <i>Myocastor Coypu</i> , Molina, 1782	Raised for the fur industry
Muskrat - <i>Ondathra zibethicus</i> , Linnaeus, 1766	Raised for the fur industry

Figure 15 Main introduction paths/vectors of alien species in Europe. Source: DAISIE, 2009.



Spontaneous and subspontaneous invasions

■ Spontaneous invasions

Certain species can establish themselves in a new geographic area without any help from human activities. Such species are not, strictly speaking, invasive alien species (see the definitions page 10). Their invasion may be qualified as spontaneous or natural. It may occur when a physical or environmental barrier between two areas disappears, thus enabling the movement of the species to the new area via either biotic (animal) or abiotic (water current, wind, etc.) means of transportation (Ashton and Mitchell, 1989).

Spontaneous invasions are rare and little is known about them. The physical distance between the original range of the species and the new area is probably the most difficult barrier to overcome, particularly for freshwater, aquatic plants. The chances of these species succeeding in travelling to new areas are slight given that they cannot survive out of water over long periods and they react poorly to long stays in seawater (Haller *et al.*, 1974).

The greater dispersal capabilities of certain animal species put them in a better position to overcome these barriers. That is the case for the Eurasian collared dove (*Streptopelia decaocto*) that originally came from Asia minor and the Near/Middle East. It is thought to have spontaneously reached Constantinople and established large populations as early as the 1500s. Today, it has spread widely throughout continental France (Pascal *et al.*, 2006). Another example is the violet dropwing (*Trithemis annulata*) that is believed to have naturally migrated from Northern Africa to Southern Europe since the end of the 1900s. It is now settling progressively in France (Deliry, 2010), perhaps due to climate change.

■ Subspontaneous invasions

The opening of new passageways facilitates the movement of species from one geographic area to another. The term “subspontaneous invasion” is used when human activities bring into contact previously separate environments, thus indirectly making possible the arrival of a species in a new area. The construction of navigation canals linking previously isolated river basins made it possible for many aquatic species to expand their distribution range, either by using human means of transportation or their own means. For example, the construction of the Suez canal (see Figure 16) led to the introduction of 200 to 300 species from the Red Sea to the Mediterranean in what are called Lessepsian migrations (Ramade, 1993). Similarly, Wels catfish (*Silurus glanis*) and pikeperch (*Sander lucioperca*) benefited from the canal network in continental France, in addition to direct vectors such as aquaculture and recreational fishing. The Danube-Main-Rhine canal, opened in 1992, facilitated passage to Western Europe (Ponto-Caspian migration) for Ponto-Caspian fauna, e.g. for various goby species *Neogobius melanostomus*, *Ponticola kessleri*, *Proterorhinus semilunaris*, etc.) (Manné *et al.*, 2013) and aquatic invertebrates (Devin *et al.*, 2005) that are now firmly established in the Rhine basin.

Figure 16



© NASA MISR images

Satellite view of the Suez canal and the surrounding area.

Subspontaneous dispersal may also be caused by environmental changes, e.g. deforestation, or climate change. Increases in temperature, variations in hydrological regimes or rises in sea levels will have major consequences for water quality and the functioning of the environments in question and could lead to modifications in the dynamics of native and non-native species (Dutartre and Suffran, 2011). It should be noted that the recently adopted European regulation does not include among the invasive species “species changing their natural distribution range without human intervention, in response to changing ecological conditions and climate change”.

Colonisation dynamics and chronology

■ An array of natural barriers

Not all the species imported by humans become invasive. According to Richardson *et al.*, (2000), an alien species must overcome different geographic and/or environmental barriers (see Figure 17) before it becomes invasive. For each barrier overcome, the terms employed for the status of the species change and an invasion becomes more probable.

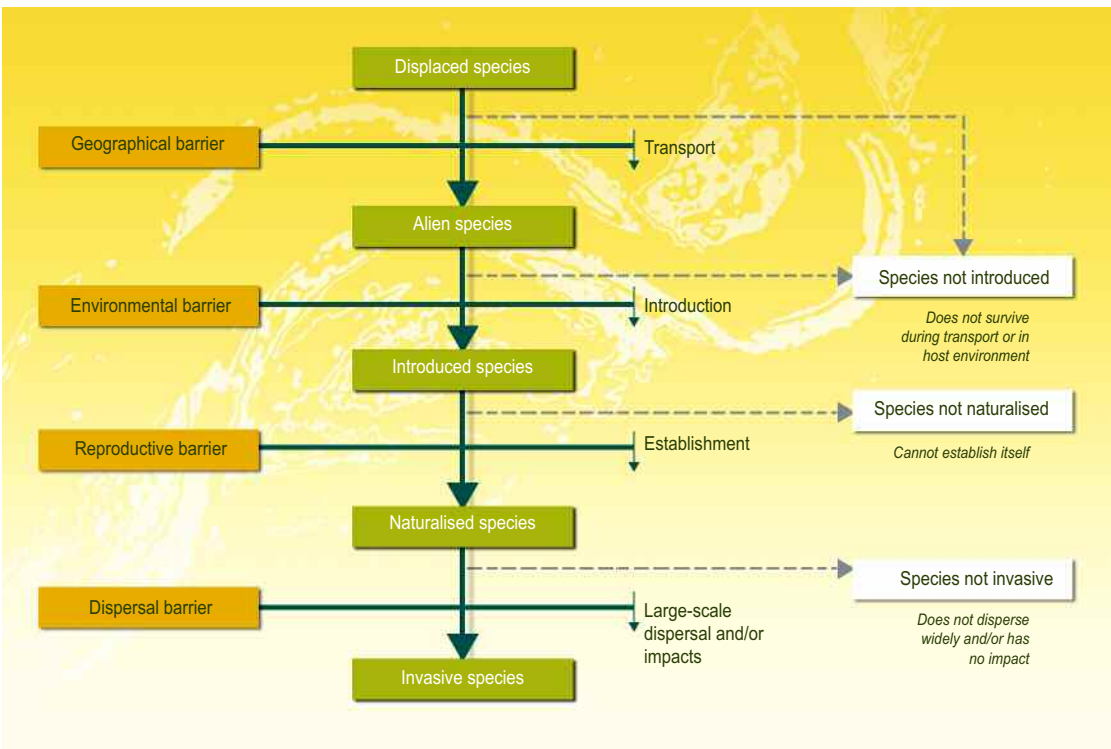
The first geographic barrier is generally overcome thanks to human intervention, i.e. via a means of transportation and intentional or unintentional introductions. This is the introduction phase.

The environmental barriers oblige the species to acclimate to the environmental conditions of the host site, i.e. the abiotic (climate, resources, habitats) and the biotic (predators, pathogens, trophic resources) conditions. This is the adaptation phase.

The third type of barrier deals with reproduction. The species must be capable of reproducing if it is to develop a viable population over the long term. This is the naturalisation phase.

Finally, the last barrier limits species dispersal. If overcome, the species can expand in the new area by colonising new habitats. This is the expansion phase.

Figure 17



The barriers that must be overcome before an alien species becomes invasive. This theoretical diagram showing the species dynamics leading to biological invasions should be used with caution because survival and dispersal may occur throughout this sequence. According to Richardson *et al.*, 2000. Diagram adapted by Mazaubert, 2013.

■ Success rate of biological invasions

Many species are not capable of successively overcoming the various barriers. Only a very small percentage of the species that are effectively introduced after overcoming a geographic barrier go on to become invasive and to have a negative impact on the environment and on human activities.

In 1996, Williamson proposed the “Three tens rule”. This rule starts with the number of imported species in a given area and postulates a reduction by a factor of ten first in the number of introduced species, then in the number of naturalised species and finally in the number of invasive alien species inhabiting the area.

For example, if 1 000 species are imported by humans, 100 would be introduced in the area, 10 would succeed in reproducing and a single species would become invasive (see Figure 18). These values are probabilistic and vary depending on numerous factors, i.e. the type of species, the type of site and host community, and the introduction conditions.

Figure 18

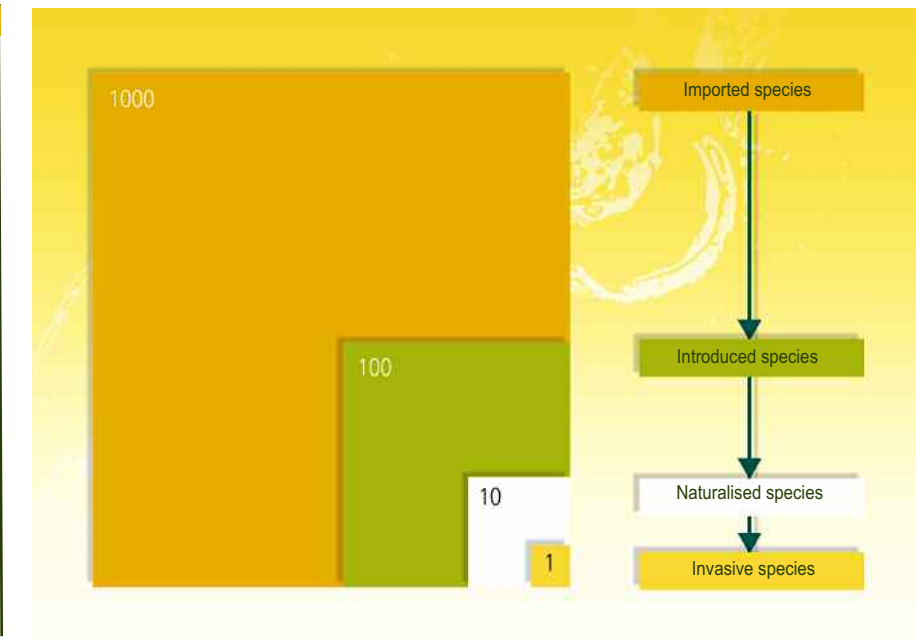


Diagram showing the “Three tens rule” developed by Williamson. According to Mazaubert, 2008.

This empirical rule turns out to be fairly accurate for plant species, however success rates for vertebrates are much higher and range between 15 and 50% (Jeschke and Strayer, 2005). For aquatic species introduced to Europe, a naturalisation rate of 63% has been estimated (García - Berthou *et al.*, 2005).

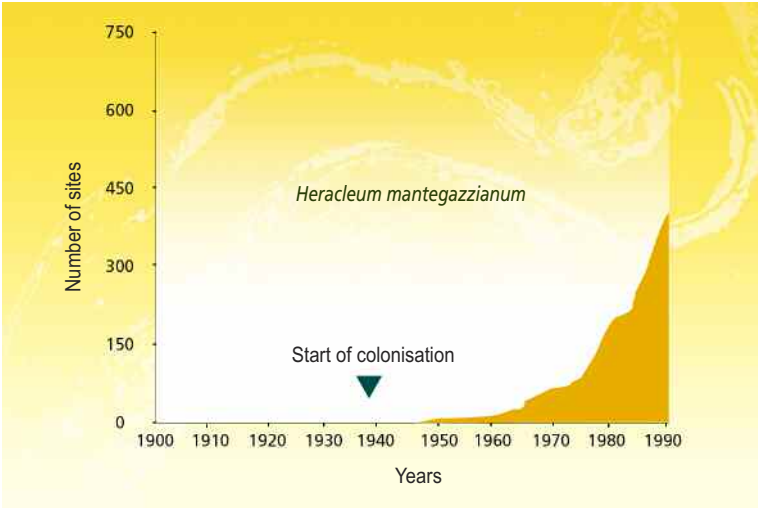
■ Une phase de latence

The transition over the environmental and reproductive barriers differs significantly among species. It may last several decades and even reach 150 years in some cases (Kowarik, 1995). An alien species can remain in a latent phase over very long periods in the host ecosystem without becoming invasive.

The invasion, when it occurs, may be triggered by ecological modifications in the environment (in some cases caused by human activities, in others not), by biological modification in the species (adaptation to the host environment) or when the species exceeds a population threshold enabling it to grow more rapidly, thus becoming invasive (Soubeyran, 2008).

For example, in their study on the invasion dynamics of giant hogweed (*Heracleum mantegazzianum*) in the Czech Republic, Pyšek and Prach identified a latent phase, following the introduction of the species in the 1800s up to the beginning of the 1940s, during which the population numbers remained very limited (see Figure 19). Subsequently, the number of sites increased sharply. According to the authors, this was due to modifications in the habitats of the species (Pyšek and Prach, 1993 in Muller, 2004).

Figure 19

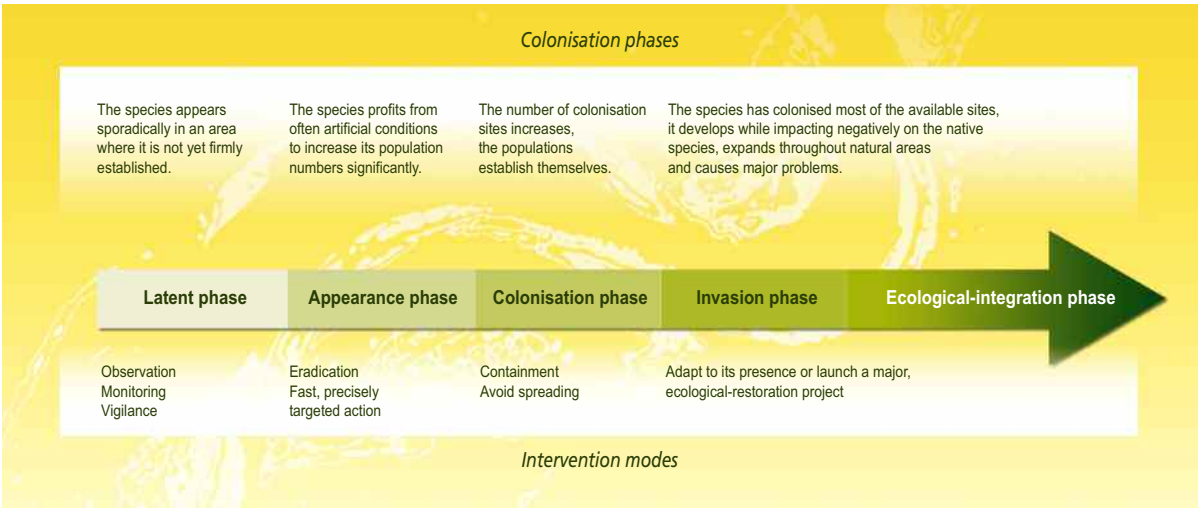


Graph showing the invasion of giant hogweed (*Heracleum mantegazzianum*) in the Czech Republic over the 1900s. According to Pyšek and Prach, 1993.

■ Colonisation phases

The invasion process results in successive colonisation phases in a given area, corresponding to the transitions over the barriers mentioned above. They range from the arrival of the alien species to the point where management difficulties caused by species proliferation are observed. Depending on the species, the potentially effective management techniques can vary according to the current phase and may become increasingly expensive in step with the successive stages in the colonisation process.

Figure 20



The different colonisation phases for an alien species and the corresponding management techniques. According to Mazaubert, 2008.

Before a species arrives in an area, prevention is without any doubt the best solution. An assessment of the risks and a reduction or even the elimination of species movements through improvements in regulations governing the sale of species worldwide, among other methods, would certainly limit the impacts of biological invasions.

Once an alien species has arrived in an area, the most effective and least costly management measures are clearly those taken during the initial phases of the colonisation process (i.e. rapid intervention). During the latent phase, it is difficult to determine whether the species will become invasive, however risk analysis can be carried out on the basis of the available information concerning its colonisation capabilities in other areas, thus making it possible to set up a preventive management strategy comprising, for example, measures to limit species dispersal by humans in the natural environment (raising awareness, restrictions on sales, etc.).

The appearance phase would seem to be the most decisive because eradication remains a feasible objective. The objective is to remove the species and its propagules from the host site in order to avoid any later dispersal. All available knowledge on the species biology and ecology can be of help in selecting the intervention techniques for each particular case.

During the colonisation phase (geographic expansion), any chance of eradication is rapidly lost. Two techniques may be used. The first consists of containing the species within the already occupied area. For the second, managers must monitor the zones around the infested area and set up warning systems in order to halt any progression in the colonisation through measures adapted to the area and the species in question.

During the invasion and ecological-integration phase, the species has firmly established itself, occasionally over vast areas, and its management becomes more difficult and generally expensive (see Box 2). Regular management work is nonetheless indispensable, the objective being to maintain the species within certain limits where the disturbances and/or damage are not overly serious or are deemed tolerable.

Box 2

The time factor in biological invasions

Biological invasions can take place over decades or occur relatively rapidly and often require, for certain species over unforeseeable time periods, expensive management work intended to reduce the perceived negative impacts or the assessed damage. What is the outlook for these situations? Will these species remain invasive for the foreseeable future and cause further disturbances?

It is obviously difficult to provide an answer to such a general question, given the great diversity of situations and the dynamics involved with the various species of fauna and flora. Each situation (a combination of the local area, the invasive species and the human factors) is relatively unique and the management approach must be closely adapted to the local situation if it is to succeed. Management work on certain invasive alien species has been undertaken as soon as the human resources were available for an organised intervention, even before taking into account the status of the species. Concerning plant species, the manual techniques used in agriculture were progressively replaced by mechanised methods that were then transferred to aquatic environments. This is particularly the case for mowing techniques created in the 1920s for lakes colonised by submergent plants, using cutter bars adapted from agricultural equipment and installed on boats (Dutartre and Tremea, 1990). Management of wildlife that damages crops is also well established and the techniques used to kill or trap are still in use today.

Even though a number of studies on the concept of biological invasions took place fairly early, following the work of De Candolle, Darwin and Thellung, actual scientific research on the topic is relatively recent and the book by Elton (1958), titled *The Ecology of Invasions by Animals and Plants*, is generally acknowledged as the first general review of the subject. Since then, a great deal of research has been carried out, but given the recentness of the work, very few projects have studied biological invasions over several decades.

Will the invasive species disappear or, on the contrary, will they integrate the living communities of their host area and play a functional role similar to the native species in these communities? If some of the invasive species are more adaptable to climate change, what would be the consequences on the functioning of ecosystems and on the related services? Could some of the invasive species become domesticated and farmed if the services offered are seen as a means to replace the receding native species?

One example concerning an aquatic plant has been well documented, namely Canadian waterweed (*Elodea canadensis*, Michaux, 1803). This submergent species originated in North America and was noted for the first time in Europe in 1840, near Dublin, then in 1842 in the U.K. and in Belgium and France starting in 1860 (Sculthorpe, 1967). The plant progressively spread throughout Europe, including Scandinavia, and after causing problems in numerous lakes in Western Europe up until the early 1900s, it would now seem to have stabilised and, to our knowledge, no longer causes difficulties, except in the northern countries (Hellsten, Oulu Univ., personal pub.) and on rare occasions (Haury *et al.*, 2010). Today, it is one of the hydrophytes widely prevalent in stagnant aquatic environments or in those with slow to moderate currents in Europe. The plant is still considered an IAS, but its geographic expansion would seem to have stopped. After having been invasive and seen as such for over 50 years, is the plant now an integral part of European hydrophyte communities?

Even when modified by human intervention, the population dynamics of living organisms can take decades to fully develop, an example being the latent phase of certain alien species before they effectively begin to invade. The integration (if it occurs) of invasive species in host communities can undoubtedly take decades as well, which can render an analysis of their evolution highly complex. Water primrose, which has been present in continental France for over 150 years and invasive for approximately 40 years, is regularly consumed by native invertebrates, for example *Ludwigia grandiflora* is consumed by the beetle *Altica lytrhi* (Petelczyc *et al.*, 2006) (see Figure 21). These opportunistic, plant-eating insects may be capable of exerting increasing pressure on the water primrose to the point of reducing its presence in biotopes to levels commensurate with those of native aquatic plants, but over what time frame?

In addition, the co-evolution processes continually at work within communities will also affect at least those invasive species that persist over the long term in their host communities. But how quickly will those processes proceed, what will be the consequences for future ecosystems and what will be the future needs in terms of management?

Figure 21



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Altica lytrhi is a small beetle that eats large-flower water primrose.

Factors contributing to the success of invasions

The success of an invasion depends on a combination of characteristics specific to the introduced species and to the more or less favourable environmental components in the colonised ecosystem, and on chance (Soubeyran, 2008). Environmental modifications, whether natural or anthropogenic, can also facilitate invasions. The countless number of combinations among these factors makes it very difficult, perhaps impossible, to predict an invasion, even if certain determinants have been identified.

■ Propagule pressures

The success of an invasion may depend on the incoming volumes and species introductions, i.e. the number of individuals introduced and the number of introductions, which have been defined as the “propagule pressure” (Williamson, 1996). The term “propagule” (or diaspore) covers any part of a plant or animal that can be dispersed and give birth to a new individual, for example stalk fragments of large-flowered waterweed (see Figure 22). It has been shown that propagule pressure is generally a factor explaining the success of species in naturalising and the degree of biological invasions (Williamson, 1996; Lockwood, 2005; Colautti, 2006; Dehnen-Schmutz, 2007; Pyšek *et al.*, 2009; Simberloff, 2009). This is because the greater the number of individuals and introductions in a given area, the higher the probability that the species will succeed in establishing itself.

Figure 22



© A. Dutartre, Istea

Plant fragments deposited on a beach of Parentis-Biscarosse Lake (Landes department). The stalks of certain submergent plants, e.g. curly waterweed or large-flowered waterweed, can survive in water over long periods and are easily transportable. Each fragment is a potential cutting.

■ Characteristics of the host environment

The host environment also plays an important role in an invasion. According to Williamson (1996), all communities may be invaded, but some are more likely candidates due to their fragility. It would seem that ecological disturbances in habitats are a factor contributing to biological invasions. The ecosystems in anthropogenised and artificialised environments have reduced levels of resistance and resilience⁴ to withstand invasions (Williamson, 1996; Mack *et al.*, 2000), thus paving the way for opportunistic, alien species. The same is thought to be true for ecosystems where ecological niches are vacant or those comprising a small number of species (Williamson, 1996; Mack *et al.*, 2000).

4. Resilience is the capacity of an ecosystem, confronted with major pressures, to self organise and trend back to its earlier evolutionary trajectory.

■ Biological profile of invasive alien species

A definition of the fundamental characteristics of an invasive species could theoretically make it possible to prevent future invasions and to enhance management strategies and regulations. Unfortunately, though certain invasive species would seem to have shared traits, there are numerous exceptions and the process is made complex due to the many interactions that exist between the characteristics of the species in question, those of the host ecosystem and the conditions under which the introduction takes place (Barbault *et al.*, 2010; Mack *et al.* 2000). For these reasons, it is virtually impossible to establish a “typical biological profile” of an invasive species, if only because there is never one invasion, but many.

Some authors have nonetheless identified certain biological traits that can contribute to the successful establishment of an IAS, such as high reproductive and resource-capture capabilities due to rapid and strong growth, high dispersal capability, good adaptation to disturbances (Pyšek *et al.*, 1995) and behaviour or population dynamics that fit well with human activities (Pascal *et al.*, 2006). These characteristics form the basis of methods to assess the risks of introduction (see Box 3).

For example, Hayes and Barry (2008) reviewed 49 studies testing 115 biological characteristics within seven groups of species. The characteristics that best explain the successful establishment of species have to do with the biogeographic similarity of the original and the new environments, and propagule pressures. Of less importance are the physiology and the morphology of species. Concerning plants, the study showed that the leaf surface area, the sexual reproduction system (dioecy, monoecy, hermaphroditism) and the size of the original distribution range play a central role in the successful establishment of species. For the seven species groups studied, the propagule pressure, also known as the introduction effort, plays a major role in the successful establishment of species and is often encouraged by humans via repeated, intentional introductions.

To date, attempts to predict which species, among a set of potential introductions, are likely to become invasive have met with highly limited success (e.g. Mack *et al.*, 2000). This is because the models used do not take into account the complexity of the analysed system. The biological and ecological profile of invasive species is still very difficult to establish and a prediction of the areas likely to be invaded is even more complex given that little is known about the colonisation capabilities of each species, the characteristics of ecosystems and the interactions between introduced species and each ecosystem.

In spite of the difficulties in attempting predictions, preventive measures remain necessary in the overall management procedures for invasive alien species, which means managers must be able to anticipate on the basis of an assessment of invasion risks.

■ Risk analysis and assessment

Prevention of biological invasions requires regulations making it possible to control the transfers of species on every possible geographic level. This means that an assessment of the invasion risks and of the impacts that a species may cause in a new area is required and must address both the species likely to be imported and those arriving inadvertently.

This risk assessment, taking into account the available knowledge on the biology and ecology of the species in question and resulting in a proposal to include the species in a particular list, i.e. confer upon it a status, should help in formulating the applicable management policy.

This aspect of the preventive measures has been the topic of research and analysis in many countries confronted with diverse types of biological invasions. Numerous procedures are currently available and present a set of characteristics and objectives offering a relatively wide choice, depending on specific context in which the preventive measures are implemented (see Box 3).

Some of the available risk-assessment methods

Weed Risk Assessment (WRA) (Pheloung *et al.*, 1999)

The purpose of this system, developed in Australia, is to accept or refuse species whose importation has been requested, on the basis of 49 questions concerning the biology, biogeography, colonisation history and ecology of the species. A score is given for each criterion and the final score determines whether the importation request is approved, rejected or requires more in-depth study.

Weber and Gut model (2004)

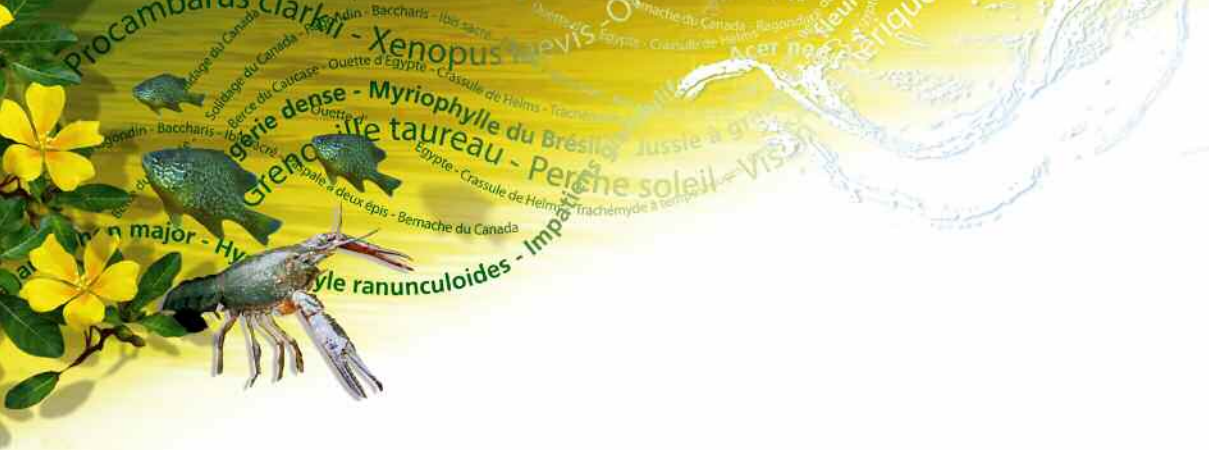
This protocol was developed to assess the risk of proliferation of all types of plants introduced in Europe. The answers to twelve questions on the species (distribution, taxonomy, growth rate, habitats, dispersion, population densities, climate similarity between the original distribution range and the introduction area, viability of seeds and their dispersal, etc.) result in a score ranking the species in different risk categories (low to high).

Pest risk analysis (Fried et Brunel, 2009, Mandon-Dalger *et al.*, 2012).

This is the method used by the European and Mediterranean Plant-Protection Organisation (EPPO). It determines the probability of a new species arriving in a given territory, naturalising there and producing impacts. Where necessary, it can also propose the most suitable control methods. This method can be used for all types of organisms, including plants, insects, bacteria and viruses. Its implementation is relatively long and costly, i.e. it is not easily applicable to all of the potentially invasive species already present in France or Europe. That explains the present need to develop simpler prioritisation tools in view of listing the invasive and potentially invasive species and determining those requiring an analysis of the plant-protection risks involved.

According to Mandon-Dalger *et al.*, 2012, Mazaubert and Dutartre, 2010.

With the above in mind, the French Ecology and Agriculture ministries requested that the State services rank the risks represented by the alien plant species in France and submit a list of the most dangerous species with the background information (Mandon-Dalger *et al.*, 2012). Various methods were then tested taking into account the different levels (regional and national) of management for invasive plants. The pest risk analysis and the Weber-Gut model were deemed the most suitable, however improvements and adaptations concerning the response typologies and the proposed thresholds were requested. An analysis to produce a ranking of habitats on the regional level is also indispensable in order to better determine the impacts that invasive alien species could cause by colonising those habitats (Mandon-Dalger *et al.*, 2012), it being understood that the results are simply a general indication that must be adapted to each particular situation.



Consequences of invasive alien species

The intentional introduction of new species is occasionally justified by the services that they can provide to humans (nutritional or ornamental value, agriculture, hunting, etc.).

However, when a species becomes invasive, the type and level of service provided no longer compensate the disadvantages caused by the proliferation. Not all alien species have consequences deemed serious in the host ecosystem, such as notable changes in status or functional conditions. But some of them produce major impacts, either direct or indirect, on different levels. In Europe, the Delivering Alien Invasive Species Inventories for Europe (DAISIE) programme has estimated that 11% of IASs have negative ecological impacts and 13% have negative economic impacts. The assessment of the annual costs incurred by damage and management work on IASs in Europe as a whole, carried out by Kettunen and his colleagues in 2008, exceeded 12 billion euros (Kettunen *et al.*, 2008).

IAS impacts can be grouped into five categories (Ciruna *et al.*, 2004):

- impacts on biodiversity;
- impacts on the ecological functioning of ecosystems;
- impacts on human health;
- impacts on human safety;
- socio-economic impacts.

In addition, it is important to note that the immediate impact must be put into perspective with the future impacts, or deferred impacts, given the need for mid to long-term management.

Harm to biodiversity

Worldwide, IASs are currently seen as one of the major threats to biodiversity and, according to IUCN, they are the second cause of documented species' extinctions and the third threat to species in danger of extinction (IUCN, 2014).

Over 54% of documented species' extinctions have been linked to IAS impacts and one extinction in five (20%) is directly caused by IASs (Clavero and García-Berthou, 2005). Similarly, Vié *et al.* (2008) estimated that 33% of threatened birds and 11% of threatened amphibians are impacted by IASs. In Europe, out of 395 threatened species, over 110 are directly threatened by IASs (Ciruna *et al.*, 2004). However, proof of extinctions directly linked to IASs are rare and have been documented primarily on islands. In many cases, species' extinctions are the result of a combination of pressures including IASs, but also habitat destruction, overuse, pollution, etc.

IASs can harm biodiversity in a number of ways, including genetics, species and ecosystems, but also communities by impacting their structure and composition (Randall *et al.*, 2009). These impacts are particularly destructive for ecosystems such as freshwater aquatic environments where IASs can cause cascading cumulative effects on the entire food chain.

■ Hybridisation

One form of impacts on genetic diversity is hybridisation where there is a transfer of genes between the introduced species and the native species. This phenomenon is particularly serious when the native species is rare and threatened.

Sterile hybrids can result in a decline in the populations of native species if they represent a majority of the descendants. For example, cross breeding of native Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) introduced to the Americas has produced sterile hybrids that reduce the population growth rates of Atlantic salmon (Garcia de Leaniz and Verspoor, 1989). Even on the infraspecific level, it is important to note that restocking using farmed brown trout has a negative impact on the genetic integrity of local populations (Berrebi *et al.*, 2000).

If the hybrids are fertile, they can breed among themselves and with the natives. That is the case, for example, of the ruddy duck (*Oxyura jamaicensis*) that breeds with the white-headed duck (*Oxyura leucocephala*), a protected species threatened with extinction and present in Spain (Caizergues and Fouque, 2008). In France, giant hogweed (*Heracleum mantegazzianum*) can hybridise with a subspecies of common hogweed (*Heracleum sphondylium* subsp. *pyrenaicum*) to produce a hybrid (*Heracleum x carbonnieri* Reduron) that proliferates along rivers in the Eastern Pyrenees. These genetic disturbances threaten the integrity of native species and can propagate genes that are poorly suited to the local ecological conditions, resulting in a gradual decline in the native population (Hulme, 2007). Another potential genetic impact takes place when hybrids have new characteristics enabling them to occupy ecosystems where their parents were absent and in which they can better develop. That is the case, for example, of *Reynoutria X bohemica* (see Figure 23), a generally sterile hybrid produced by cross breeding of Japanese knotweed (*Reynoutria japonica*) and giant knotweed (*Reynoutria sachalinensis*). Finally, hybridisation of individuals from the same species, but from different places can explain the high level of genetic diversity found in some invasive populations (sometimes higher than that of the native populations) and their success in invading an area (Kolbe *et al.*, 2004).

Figure 23



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Bohemian knotweed (*Reynoutria X bohemica*).

■ Predation and competition

Modifications in species' diversity may be qualitative (replacement or exclusion of a native species) and/or quantitative (reduction in population numbers) (Hulme, 2007). Examples of causes of changes in species' richness are interspecific competition for food and habitats or direct predation. Competition may reduce and in some cases totally eliminate native species over a more or less large part of their distribution range. In other cases, however, it can stimulate diversity and even encourage native species. An analysis of system evolution must address not only temporal, but also organisational aspects.

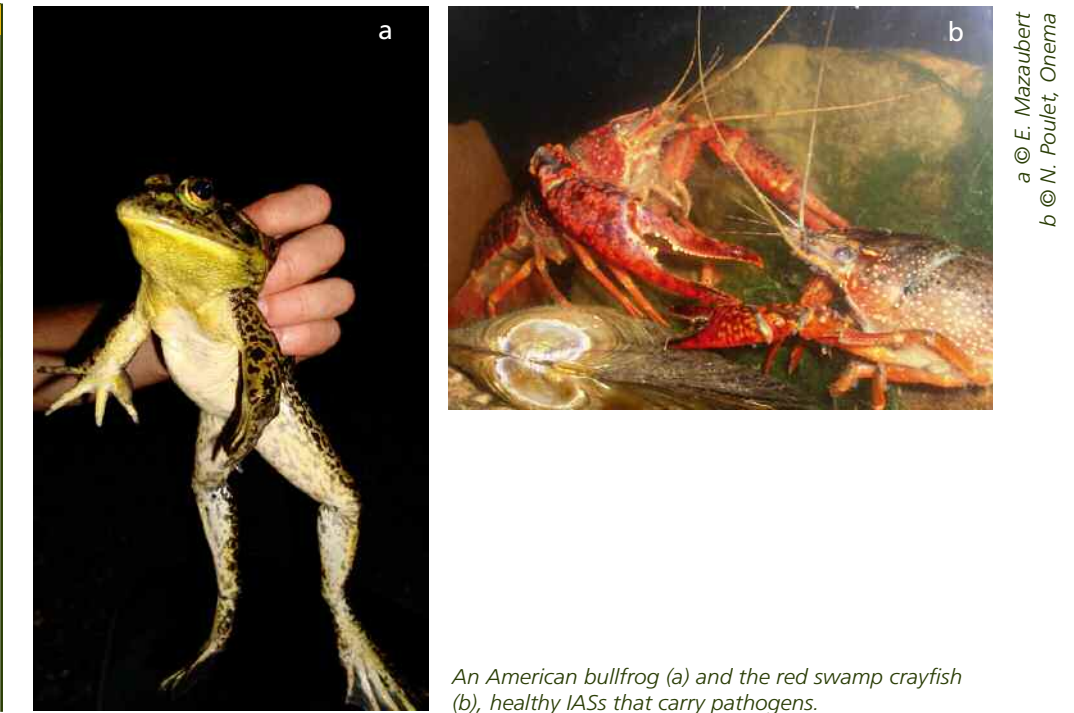
Invasive alien predators with opportunistic feeding habits (wide feeding spectrum) can have a serious impact on native populations. In the U.K. for example, the American mink (*Neovison vison*) is responsible for the decline in vole populations (*Arvicola terrestris*) (Bonesi *et al.*, 2006). Muskrats (*Ondatra zibethicus*) eat freshwater mussels and have often caused local extinctions (Jokela and Mutikainen, 1995).

Competition for resources between IASs and native species is often difficult to document or to quantify, notably for animals, for which the data are often based on discrete observations (Hulme, 2007). For plants on the other hand, competition for light, e.g. between box elder (*Acer negundo*) and white willow along rivers (Bottollier-Curtet *et al.*, 2012), and nutrients has been better documented (European Environment Agency, 2012). Similar to certain dominant native species, many invasive alien plant species end up forming a monospecific cover, thus leading to a major reduction in the richness of local species (Muller, 2004; Fried *et al.*, 2013).

■ **Transmission of pathogens and parasites**

Biological invasions may also have negative health consequences due to the direct introduction of pathogens, contaminated carriers or the emergence of new pathologies. American bullfrogs (*Lithobates catesbeianus*, see Figure 24a) and the African clawed frog (*Xenopus laevis*) are the healthy carriers of a parasite fungus, *Batrachochytrium dendrobatidis*, acknowledged as a major cause in the extinction of native amphibians (Berger *et al.*, 1999). That is also the case for the three native crayfish species in France, stone crayfish (*Austropotamobius torrentium*), noble crayfish (*Astacus astacus*) and white-clawed crayfish (*Austropotamobius pallipes*), that are sensitive to “crayfish plague” (aphanomycosis), a deadly pathology caused by a water mold (*Aphanomyces astaci*) carried by American crayfish, namely the Eastern crayfish (*Orconectes limosus*), signal crayfish (*Pacifastacus leniusculus*) and red swamp crayfish (*Procambarus clarkii*), that were introduced in the 1900s and are now widely present throughout France (see Figure 24b) (Diéguez-Urbeo and Soderhall, 1993).

Figure 24



An American bullfrog (a) and the red swamp crayfish (b), healthy IASs that carry pathogens.

When these species dominate, their overall impact can lead to a thinning of native biological communities and to a more or less significant transformation of ecosystems, which can in turn lead to more uniform environments and living communities.

Impacts on the ecological functioning of aquatic ecosystems

■ Modifications in food chains

One may reasonably assume that any introduction of an alien species is likely to modify the food chain in the colonised environment. Though that is not always the case (see the example of top-predator fish introduced into lakes, Boulétreau, 2012), there are some particularly striking examples where it is the case, e.g. for invasive bivalve molluscs such as the zebra mussel (*Dreissena polymorpha*) and Asian clams (*Corbicula* spp.). These organisms filter water (one to two litres per day for an adult mussel) in order to breathe and to feed on very small phytoplankton and zooplankton. All suspended matter in the water that is smaller in diameter than the inhalant siphon is drawn into the animal. This filtering activity creates a link between the water column and the river bed, i.e. between the seston (particles in the water column) and the benthos. When zebra mussels and clams proliferate, the living communities are subject to benthification, i.e. the filtration activity transfers the biomass (essentially phytoplanktonic) from the seston to the bed via the digestive waste. The sharp drop in phytoplanktonic and zooplanktonic biomass results in clearing of the water, grass beds grow and the other compartments (fish, invertebrates) chain react to the modifications. It may be tempting to see this situation as an improvement in water quality, however the consequences of bivalve invasions are complex (see the section on pH and dissolved oxygen below) (Beisel, 2014). For example, the composition of algal communities changes, in particular the type of dominant species. In some cases, green algae and diatoms gain the upper hand, in others cyanobacterial blooms, e.g. *Microcystis aeruginosa*. Another example is the red swamp crayfish. Its invasion in the Brière marshes resulted in a profound modification of the food chain by becoming the main link in the transmission of energy to fish (Paillisson *et al.*, 2012), a role probably played previously by various species of benthic invertebrates that have become very rare.

■ Temperature and gas exchange

In stagnant environments, the density of invasive alien grass beds can create temperature gradients having a negative impact on aquatic fauna and flora. This plant cover limits gas exchange with the atmosphere (Lejas, 2002) and is not specific to alien species. However, native species that develop in this manner generally cover small surface areas or special biotopes.

■ pH and dissolved oxygen

The proliferation of submergent plants, whether alien or not, can produce significant variations in the pH and dissolved-oxygen levels over the day that are detrimental to animals. Oxygen saturation levels can reach 200% at the end of the day, followed by extremely low saturation levels at the end of the night, and pH levels can change by a full two units (Dutartre *et al.*, 2009). The intensity of these nyctohemeral variations depends on the quantity of plant biomass and on the water renewal rate. The variations are particularly severe in stagnant environments. Among invasive alien species, the submergent Hydrocharitaceae, i.e. tape grasses (*Elodea* spp., *Egeria densa*, *Lagarosiphon major*) are capable of producing such variations.

Bivalve molluscs filter water in order to feed and to draw oxygen. The decomposition of organic matter falling to the bed also consumes oxygen. During the summer, the period of low-flow levels and high temperatures, the effect of bivalve molluscs on oxygen levels can lead to a lack of oxygen detrimental to other compartments, notably fish (Beisel, 2014).

When oxygen levels in water fall below 2 mg/litre, no fish species can survive. That can occur when water primrose (*Ludwigia* spp.) or parrot-feather watermilfoil (*Myriophyllum aquaticum*) proliferate in stagnant environments. Their dense beds cover the water and block oxygen exchanges.

■ Light

The growth of grass beds, whether alien or native, that are highly productive at the water surface can lead to a drop in light levels and consequently to a reduction in the potential development of other plants. This phenomenon may represent a risk of uniformity when the shade impacts one or more species, thus limiting the overall biological richness of the habitat. This can occur following the development of dense beds of submergent plants that rise to the surface or of floating plants. For example, among the submergent alien species, a bed of large-flowered waterweed (*Egeria densa*) blocks the penetration of light at one metre depth to 1% of the incident light (Nakanishi *et al.*, 1989). The same is true for duckweed (*Lemna* spp.). Among the alien species, least duckweed (*Lemna minuta*, see Figure 25) and red duckweed (*Lemna turionifera*) can reduce the incident light in water by 80% and cause the elimination of submergent plants (Peltre *et al.*, 2002). Invasive fauna, such as the common carp (*Cyprinus carpio*), can also cause aquatic plants to disappear through grazing, but also through their agitation which results in high levels of suspended matter that limit light penetration into water (Weber and Brown, 2011).

Figure 25



© E. Mazaubert

Duckweed (*Lemna* spp.).

■ Undermining of river banks and infrastructure

When digging their burrows, coypus (*Myocastor coypus*), Eastern crayfish (*Orconectes limosus*) and red swamp crayfish (*Procambarus clarkii*), can destabilise river banks and provoke their collapse. An example from the plant kingdom is Japanese knotweed (*Reynoutria japonica*), which can facilitate winter erosion of banks along some rivers because it eliminates the native vegetation, but provides no cover for the banks (Ciruna *et al.*, 2004). In addition, its roots can penetrate concrete, a risk for structures installed in and along rivers. These impacts are not limited to IASs, but their colonisation capabilities means they can produce those impacts over large areas.

■ Uniform landscapes

When certain species, such as knotweed (*Reynoutria* spp.) or garden balsam (*Impatiens* spp.), spread rapidly over large areas along rivers, the result can be uniform landscapes and environments. The same is true for water primrose (*Ludwigia* spp.) that has colonised dozens of hectares of wet meadows, thus modifying the perception of marshes such as those in the Brière region (Hauray and Damien, 2012). Once again, these impacts are not limited to IASs, but their speed of colonisation can significantly modify a landscape in just a few years.

■ **Modifications in flows and sedimentation**

When an aquatic plant proliferates, the growth in plant biomass can slow the flow of water in rivers. This slowing of the current and the density of the plants can temporarily trap sediment in the plant beds. The vast quantities of biomass and the sediment can reduce the bankfull cross section in rivers and lead to an elevation in water levels in the affected areas, resulting in some cases in spring flooding without any increase in the river discharge. This phenomenon can also cause flooding during the first high-water events in the fall (Peltre *et al.*, 2002). The very high levels of biomass produced by certain invasive plants such as waterweeds can significantly contribute to these phenomena in rivers even if some native species are also capable of provoking local flooding, e.g. river water-crowfoot (*Ranunculus fluitans*).

Impacts on human health

Similar to various native mammals, certain alien mammals can transmit diseases, for example coypus (*Myocastor coypus*) and muskrats (*Ondatra zibethicus*) can transmit via water numerous diseases to humans, including leptospirosis and echinococcosis, which can also be transmitted to livestock (Waitkins *et al.*, 1985). The Siberian chipmunk (*Tamias sibiricus*, see Figure 26), a new, authorised pet, can carry the bacteria causing Lyme disease (Chapuis *et al.*, 2010). The pollen produced by a number of plant species can also create more or less serious risks for human health, including allergies. That is the case for native species such as birch trees and grasses, but some IASs are also well known in this field, e.g. giant hogweed (*Heracleum mantegazzianum*), where a simple contact can cause serious dermatitis (Lagey *et al.*, 1995) and, above all, common ragweed, whose pollen can cause allergies in many people. Allergies to common ragweed were treated for approximately 230 000 people in 2011 in the Rhône-Alpes region alone, costing between 14.2 and 20 million euros (Observatoire régional de la santé Rhône-Alpes, 2012).

Figure 26



© J.L. Chapuis

The Siberian chipmunk can carry the bacteria that cause Lyme disease.

Impacts on human safety

A number of vertebrates, both native (wild boar, deer) and alien, can cause accidents on the road or in the air. Alien species that have caused problems in this field are, among others, in the Netherlands the Egyptian goose (*Alopochen aegyptiacus*) and in the U.K. the Canada goose (*Branta canadensis*), whose large flocks hinder the take-off of planes from airports (Gyimesi and Lensink, 2010; Watola and Allan, 1999).

The rapid growth of certain aquatic plants in large rivers, both native such as river water-crowfoot and alien, e.g. waterweed, can result in safety problems for nuclear power plants, in particular on the Loire and Rhône Rivers, where masses of plants floating down the river block the pumping intakes for cooling water. Some molluscs, such as the Zebra mussel (*Dreissena polymorpha*, see Figure 27), can colonise the intakes in numbers, causing the same problems (Khalanski, 1997).

Figure 27



© USGS

Dreissena polymorpha.

Economic impacts

The impacts of invasive alien species do not concern biological functions alone, they can affect a number of economic sectors. This may have several consequences.

■ Loss of production for certain industries (commercial sea fishing and aquaculture)

For example, the *Mnemiopsis leidyi* (see Figure 28), a North American carnivorous ctenophore inadvertently introduced to the Black Sea via ballast water, caused the collapse of commercial anchovy fishing, with losses estimated at over one billion dollars (Ivanov *et al.*, 2000). Agricultural losses due to the eating of crops along aquatic environments by rodents such as coypus and muskrats have also been frequently mentioned (Panzacchi *et al.*, 2007).

Figure 28



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Mnemiopsis leidyi, a North American carnivorous ctenophore introduced into the Black Sea and recently observed in the Thau Lake (Hérault department, France).

■ Reduced availability and accessibility of water for industrial companies due to blocked pipes, air vents, water inlets/outlets

In addition to the safety risks, the accumulation of zebra mussels (*Dreissena polymorpha*) can have a functional impact on certain nuclear power plants in France, such as Cattenom on the Moselle River, Golfech on the Garonne River or Bugey on the Rhône. The installations must be cleaned when they are pulled out of the water or divers can even be required for cleaning in some cases (Khalanski, 1997).

■ A physical hindrance for fishing and recreational boating

The formation of dense beds of invasive macrophytes such as curly waterweed (*Lagarosiphon major*), large-flowered waterweed (*Egeria densa*), water primrose (*Ludwigia* spp.) and parrot-feather watermilfoil (*Myriophyllum aquaticum*, see Figure 29) can limit navigability on lakes and rivers (Nepveu and Saint-Maxent, 2002) and justify repeated macrophyte harvesting (Dutartre *et al.*, 1989; Haury and Bouron, 2012). In some cases, the presence of large numbers of birds on sites used by humans can provoke significant disturbances. For example, a large population of Canada goose (*Branta canadensis*) and eutrophication of bathing water caused by their waste made it necessary to close a recreational centre in the Paris region (Fouque *et al.*, 2011c).

Figure 29



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Manual removal of parrot-feather watermilfoil.

■ Direct damage to infrastructure

Coypus (*Myocastor coypus*) cause major damage. Their burrows destabilise river banks and dikes, resulting in repair costs of several million euros in some cases (Panzacchi *et al.*, 2007).

These impacts have major economic consequences, but remain difficult to assess, even if they are better perceived, evaluated and taken into account than the ecological impacts, given their monetary value.

An assessment of IAS impacts on ecosystem services (see Table 4 on the next page), which would constitute a useful addition to the analysis of the damages effectively caused by biological invasions, requires significant further work (Vilà *et al.*, 2010).

Table 4  *Impacts of invasive alien species on ecological services in Europe. According to Vilà et al., 2010.*

Supply services	Regulatory services	Support services	Cultural services
<ul style="list-style-type: none">■ Loss or gain of food, material, fibres■ Threats to native species■ Alteration of genetic resources	<ul style="list-style-type: none">■ Alteration of biological control functions■ Modification of pollination services■ Pathogen transmission■ Protection against natural hazards■ Modification of erosion functions■ Water purification and regulation■ Bioaccumulation	<ul style="list-style-type: none">■ Modification of soil and sediment composition■ Alteration of nutrient cycles■ Changes in communities■ Modifications in primary production	<ul style="list-style-type: none">■ Effects on ecotourism■ Changes in landscape perception■ Aesthetic impacts■ Changes in local habits

In continental France, little is known on the consequences of invasions in the environment, due to a lack of sufficient experimentation and suitable research (Haury *et al.*, 2010). Gaps in knowledge concerning historical data on species distributions and ecosystem functioning must be filled in if progress is to be made in this field. The absence of untouched control sites for comparative analysis and the difficulties encountered in setting up long-term monitoring systems constitute two more major handicaps in pursuing assessments.

Sociological aspects

Here an obvious characteristic makes itself felt again, i.e. we are confronted with highly diverse biological invasions and not simply with a single process to which an overall analysis can be applied. Depending on the causes of their introduction and the more or less perceptible negative impacts, IASs, as defined in terms of the management needs of the concerned ecosystems, can be seen by the public in totally different, even opposing ways.

Ranging from dramatic, doomsday predictions to the behaviour of certain urban dwellers toward coypu populations in cities, as noted by Olivier Sigaut (2012) in his text *City coypus vs. country coypus*, there are many perceptions concerning alien species and biological invasions.

The vision of a “stable and harmonious world” (Maris, 2010), which was still dominant at the start of the 1800s, progressively gave way following the work of Darwin and many other researchers, and eventually became more realistic and less influenced by religious certainties. An example is a book published in 1867 by George P. Marsh, a naturalist and diplomat, who noted that “*man is everywhere a disturbing agent. Wherever he plants his foot, the harmonies of nature are turned to discords. The proportions and accommodations which insured the stability of existing arrangements are overthrown. Indigenous vegetable and animal species are extirpated, and supplanted by others of foreign origin. Spontaneous production is forbidden or restricted, and the face of the earth is either laid bare or covered with a new and reluctant growth of vegetable forms, and with alien tribes of animal life.*”

Well before the work by Elton (1958) and obviously prior to the emergence of the term “biological invasion”, studies addressed these issues of species transfers, the negative impacts in some cases and management requirements. The initial reactions and management efforts concerned the alien species having direct impacts on agricultural production and were thus focussed on areas and their surroundings with significant human activities.

In this context, the work was planned and implemented as a battle to eliminate the damage to agricultural production and the regulations that were progressively established also contributed to this protective approach.

Changes then occurred that completely modified this approach to the management of invasive species:

- a vast increase in the numbers of introductions, due in part to increasing demand for ornamental plants and pets (particularly “new pets”);
- dispersal of these species to non-agricultural environments, i.e. urban and rural areas;
- increases in environmental disturbances, including in the aquatic environments, facilitating certain dispersals;
- better understanding and acknowledgement of the ecological functioning of ecosystems and a widening of management objectives to include all environments;
- etc.

IAS management efforts progressively spread to more “common” environments, originally seen as having no particular use value, contrary to agricultural land. They took on importance in step with the disturbances caused by these species in the functioning of environments and with the development of new activities, often corresponding to a “need for nature” that it was possible to satisfy. More recently, it became necessary to expand the work to protecting biodiversity, for which the biological invasions constitute a disturbance.

Part of IAS management remains focussed on the studies and approaches that originally dealt with crop protection, clearly in view of eliminating “weeds” and “harmful” animals, terms which also apply to native species. That is even today a common theme in efforts to inform the general public on IASs. However, the expansion of management to different environments and ecosystems, for different needs, should inspire us to renew our analysis of current work, not necessarily in view of modifying the objectives, but perhaps in order to better assess the issues, expectations and, in some cases, the practical work conditions.

The relation to nature of the general public and the stakeholders in IAS management, as well as the aesthetic properties and visibility of species (Dalla Bernardina, 2010) largely determine perceptions. Very popular ornamental plants, e.g. the water hyacinth, see Figure 30) and fashionable pets are initially seen in a positive light. Then, when the plants escape from their basins and become disturbances in “natural” landscapes or when animals proliferate, opinions change from interest to rejection and requests for intervention. The increasingly frequent information on IASs in the media and the management work undertaken have contributed to convincing of the need for interventions, but it is interesting to note that the objective of eradicating species is more rarely mentioned. It would seem that the information disseminated by researchers, experts and the managers themselves has in fact been understood by the mainstream media.

Figure 30



© A. Dutartre, Istea

The beautiful flowers of the water hyacinth (Eichhornia crassipes) have contributed considerably to its dispersal over the entire planet.

A further difficulty in this field arises from the fact that perceptions can differ extremely between plants and animals, particularly as concerns mammals and birds. These two groups of animals are generally seen, at least initially, in a much more favourable light than the other IASs. A part of the public is attached to the aesthetics of

birds and the behaviour of mammals similar to that of farm animals or pets, which may explain certain negative comments on, for example, the programme to eradicate the sacred ibis and the shooting of Canada goose on sites visited by the public.

Though the alien origin of IASs is generally mentioned in the media, it is less often explicitly seen as the main reason for the damages caused by these species. On the other hand, that origin has been used by certain researchers to criticise management programmes, accusing them of nativism (a political opinion found in countries with many immigrants, such as the U.S., and opposed to any new immigration), xenophobia and even racism, in reference to the fears aroused by globalisation, thus creating a degree of confusion concerning management objectives (“eliminate the foreigners”). On this topic, Simberloff (2003) reviewed many of these opinions and demonstrated that this criticism of work to control biological invasions often neglected the ecological and economic impacts of IASs. He was of the opinion that *“These impacts ... constitute a cogent, ethical basis for management of introduced species”*.

This ethical basis cannot, however, confer indisputable and permanent legitimacy on all interventions. This is because IAS management objectives and conditions are directly confronted with a number of limits, socio-economic (the perceptions and financial decisions of societies), scientific (current knowledge) and technical (intervention possibilities), in a world and environments subject to rapid and uncertain dynamics. What do we know of the future and the potential roles played by certain invasive, currently regulated species in ensuring the functions of aquatic environments in a context of climate change (Dutartre *et al.*, 2012)? This ethical basis is but one of the elements requiring regular reappraisal in terms of management objectives and how they should be implemented.

But perceptions concerning IASs and the resulting relations do not consist solely of these management issues. In an increasingly urban world, the relations between city people and nature are evolving rapidly and the “need for nature” can occasionally take on strange forms. The example of coypus in urban areas (Sigaut, 2012), where they are welcomed and fed by people, whereas their populations are regularly trapped in rural areas, illustrates the diversity of the existing perceptions (see Figure 31).

It also explains why, in a periurban recreational centre in the Paris region, trapping and shooting of the many coypus causing various damages had to be planned at times when families bringing bread were not present on the site, in order not to shock the children and their parents (B. Breton, personal pub.).

Figure 31



© N. Poulet, Onema

Coypus are a true attraction in urban areas.

This inherent complexity in the relations between humans and biological invasions should inspire us to continuously maintain an analytical attitude toward management policies, with regular reappraisals of the issues, objectives, intervention conditions, as well as how communication is carried out with the other stakeholders, including the general public. Awareness of all aspects of management must be maintained if we are to improve it.



Further research

In spite of the significant progress made over the last few years, a great deal of research is still required on numerous aspects of invasive alien species. To enhance IAS management, research must be pursued on various issues, targeting different objectives, including species biology and ecology, invaded environments, monitoring and surveillance methods, intervention techniques, economic assessment of damage and intervention programmes, etc. Research programmes clearly addressing IAS management have yet to be developed in view of encouraging partnerships between researchers and managers. It should be noted, for example, that the INVABIO programme set up by the Ecology ministry from 2002 to 2006 funded approximately 30 research projects of which only one-third addressed management issues.

Need for taxonomic progress

People are not always fully aware of or understand taxonomy, which makes it more difficult to set up monitoring programmes and quarantines. Better information on the numbers and identity of introduced species will require further taxonomic research. Similarly, because some IASs are immediately identifiable but other are not, efforts to identify the taxonomic criteria of use for routine work are required in view of developing a permanent monitoring network across the country. In addition to standard identification based on species morphology, work on genetics, including research on environmental DNA (Miaud *et al.*, 2012), should produce major improvements in this field.

Pursue research on species biology and ecology

It is clear that invasion mechanisms must be better understood in order to better anticipate them. In particular, IAS effects on ecological processes such as the structure of food webs, energy flows and IAS dispersal conditions also require a great deal of work.

Improvements in surveillance methods and systems, in early detection of invasions and monitoring systems are required. Solutions must be developed to rapidly draw up species inventories that are reliable and cost effective. They are indispensable components in establishing early-detection and monitoring networks that make possible rapid interventions. Innovative technologies for inventories, such as the molecular methods capable of detecting DNA in aquatic environments (method used to detect American bullfrogs and currently being developed for the African clawed frog, Dejean *et al.* (2012)), must be perfected and the corresponding marker banks must be expanded.

The development of technical solutions for management requires excellent knowledge of species biology and ecology, notably for trapping, the use of biocides and for biological control. Population dynamics, parasite interactions and species ecophysiology are some of the fields that research must address.

Other research issues that merit work include:

- what are the short and long-term impacts of hybridisation and genetic-introgression phenomena following the establishment of IASs?
- how can IAS impacts be distinguished from the consequences of other forcings, such as habitat loss, pollution in aquatic environments and modifications in hydrological connectivity?
- what are the key factors in ecosystem resistance and resilience when confronted with biological invasions?
- what processes can facilitate the integration of certain invasive species in host communities?
- how can invaded ecosystems be stabilised and over what time frame?
- what forecasts can be made concerning the future relations between biological invasions and climate change?

Study and quantify the ecological, health and economic impacts

The ecological and socio-economic impacts caused by most IASs are generally not well documented locally. Policy makers and managers nonetheless need information on the costs of the damage incurred by IASs and cost-benefit analyses for their management, in view of setting priorities for action. The economic and financial information, i.e. the costs of interventions, constitute the only available data and are not sufficient for prioritisation. Existing studies generally concern the species having major economic impacts and there are few studies on IAS impacts on ecological services. Studies are often launched fairly late, when introductions have already occurred and data on the initial status are no longer available, which makes it difficult to determine the ecological and economic impacts of a species.

Invasive alien species and the human and social sciences

Socio-cultural impacts are rarely addressed in studies on how invasions are perceived by local communities, whose opinions in some cases can differ from those of researchers and managers (Menozzi and Pellegrini, 2012).

Research on the links between socio-economic and environmental sectors, including the feedback loops between them, must be developed to assist in creating better decision-aid tools. Communication strategies designed to prevent invasions must also be devised to raise the awareness of stakeholders and the general public.

Generally speaking, the emergence of these problems on the international level raises the question of how human societies relate to the non-human species making up “nature”. This question involves numerous aspects, philosophical, ideological, etc., that should induce a major cultural shift, i.e. the change from being consumers of nature to managers and caretakers.

Research and management

Applied research, in close partnerships with the managers of natural areas, should make it possible to improve control and restoration methods, and to assess the technical and economic feasibility of a project (Dutartre, 2010). Among the research topics that should be developed to provide managers and policy makers with the critical tools required to set up effective management strategies, we should mention (Soubeyran, 2008):

- improvements in surveillance methods, in early-detection and monitoring systems;
- ranking of the ecological and socio-economic impacts by different stakeholders, thus putting the managers of natural areas and policy makers in a position to set priorities for action;
- development of control and eradication techniques for invasive species;
- increased production and marketing of native species for the ecological restoration of aquatic environments, that could also serve for the landscaping and ornamentation of sites;
- enhanced knowledge to improve the operational management of species in terms of inventories, distribution, geographic dynamics, evolutionary factors, impact factors, etc.;

■ support for and contribution to the formulation of regulations, to public awareness and information, on the basis of confirmed scientific data.

It should be noted that IASs are a cross-cutting topic due to the different biological mechanisms governing their appearance in an area, their installation and their spatial and temporal dynamics. These issues must be taken into account in conjunction with other global issues such as environmental degradation and climate change. Financial support for research programmes would thus appear indispensable for all effective management strategies based on solid scientific data and addressing invasive alien species.

