Predicting the threats to ecosystem function and economy of alien vascular plants in freshwater environments

Literature review

by

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AquAliens

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Contents

Introduction

The spread of alien species is a large threat to global biodiversity. According to Wilcove et al. (1998), only habitat destruction poses a larger threat to biodiversity than biological invasions do. Biological invasions, as well as extinctions, are natural ecological processes, but with the mobility of humanity the invasion rates are far more rapid today than ever before (Vitousek et al. 1997). As an attempt to stop the threats to biological diversity, the Convention of Biological Diversity (CBD) was adopted in 1992 at the Earth Summit in Rio de Janeiro. Concerning alien species, this convention states that each contracting part shall, as far and as appropriate as possible prevent the introduction of those alien species that threaten ecosystems, habitats and species and put an effort in controlling and eradicating measures.

In aquatic environments, the threat to biodiversity from alien species is of extra concern for several reasons. Firstly, aquatic habitats are rather homogeneous in some senses, e.g. the variations in temperature are smaller than for terrestrial environments. This means that aquatic species easily can survive and possibly establish in other parts of the world than their native geographic range (Cook 1985), which is the case for some of the world's worst aquatic weeds (Cook 1990). Secondly, aquatic habitats are difficult to monitor. Because of the difficulties to monitor aquatic habitats, at the time when an introduced species is discovered, it might be impossible, or at least very costly, to control it. Finally, since water is an efficient vector for propagules, aquatic organisms are easily spread with currents to new sites.

Alien aquatic plants have caused both economic and ecological damage in many parts of the world. Among the approximately 700 aquatic plant species worldwide, fewer than 20 are considered to be major weeds (Spencer & Bowes 1990). The world's worse aquatic weed is generally considered to be the water hyacinth *Eichhornia crassipes* (Cook 1990). *E. crassipes* is a free floating plant within the family Pontederiaceae, and it is among the free floating plants that the most serious aquatic weeds are found. However, also plants classified as non-weeds can have severe impact on biodiversity, since the term weeds only refers to plants undesired by man (Les & Mehrhoff 1999).

The terms used in plant invasion biology literature have caused much confusion in the past, but a recommended terminology now exists (Richardson et al. 2000). This terminology will be used in this report. Alien plants are plants in a given area whose presence there is due to intentional or accidental introduction as a result of human activity. Other terms often used synonymous to alien plants are non-indigenous, exotic and non-native plants. Alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans are referred to as naturalized or established plants. If an established plant has rapid spread and is associated with impact, it is called invasive. The term weeds, sometime used in plant invasion biology, refer to plants growing where they are not wanted and which usually are associated with detectable economic or environmental costs.

Impact of alien freshwater vascular plants

Alien aquatic plants have caused both economical and environmental damage in many parts of the world. Examples of economic damage are clogging (e.g. navigation routes, water intakes and fishing equipment), reduced recreational values of rivers and lakes, and costs for controlling measures. The environmental damage of alien aquatic plants, i.e. loss of native biodiversity, can be caused by competition with rare native species or habitat modification. In the worst case, loss of endemic species and disruption of entire ecosystems can follow an introduction (Mack et al. 2000). There is also a possibility that the impact of alien plants will interact with other causes of global change, e.g. changes in land use (Vitousek et al. 1997), increased atmospheric carbon dioxide concentration (Richardson et al. 2000) or habitat fragmentation (Hobbs 2001).

Economical impact

Costs for losses, damage and control of alien species have been estimated to US$ 137 billions year^{-1} in the USA alone (Pimentel et al. 2000). For aquatic weeds, these costs were estimated to US$ 110 million on annual basis. Except for direct losses of valuable species, alien plants can modify their habitat to a less valuable state, as when rivers and lakes no longer can be used for recreation, navigation or sport fishing. The cost for loss of a native species by an alien can be calculated with a modelling approach, but today's models need to consider more complex interactions in order to predict indirect costs (Barbier 2001). One example of such indirect costs is when alien plants cause reductions in flow in drainage channels which increases the risk of flooding (Murphy et al. 1990). Typical problematic alien species in such systems in Europe are submerged plants (e.g. *Elodea canadensis* and *E. nuttallii*), but also the water hyacinth *Eichhornia crassipes* is considered as problematic in some southern Europe drainage systems. Invasions of the latter species can also be considered as a threat to human health, since it creates a suitable habitat for mosquitoes (Sculthorpe 1967). However, also large economic benefits are associated with alien species; for example, species introduced as food crops and livestock accounts for an annual value of US$ 800 billions, i.e. almost six times as much as the costs (Pimentel et al. 2000).

Environmental impact

Alien plants can cause both direct and indirect damage in their new environment, with loss of biodiversity as consequence. The environmental impact of alien species has by some been ranked as the second largest threat to biodiversity in the USA today (Wilcove et al. 1998). When first introduced, the alien plant contributes to increased biodiversity measured as number of species, but as soon as native plants decrease in number due to replacement from the alien, the net result is decreased diversity. This replacement of native species by competition is an example of a direct effect. Since introduced plants can interact with native ones through shared herbivores, parasites and pathogens, and many types of habitat modification, the possible kinds of indirect effects are enormous (Simberloff & Alexander 1998).

Competition with native plants is the most obvious way in which alien plants affect biodiversity. Exploitative competition among aquatic plants occurs for limiting resources, e.g. light, nutrients and suitable substrates (Barrat-Segretain 1996). In addition to competition for limiting resources, aquatic plants sometimes compete with allelopathy, i.e. actively suppressing their neighbours by release of chemical compounds (reviewed by Gopal & Goel 1993). Novel mechanisms of competition, such as allelopathy, can affect native plants to a much larger extent than the alien's natural competitors (Callaway & Aschehoug 2000). Reduction of native biodiversity due to competition from aliens can also make the ecosystem more vulnerable to other types of disturbances, as is the case with reduction of seed banks. Some submerged plants, e.g. such as those belonging to the family Hydrocharitaceae, do not produce seeds outside their native range. When these species replace native vegetation, the seed banks of the lake will be reduced both in density and diversity (De Winton & Clayton 1996). Since seed banks have an important role in the re-establishment of aquatic vegetation following disturbance, invasions of non seed producing plants followed by disturbance can cause vegetation free lakes.

Impact on native species can also take the form of hybridization or other genetic alterations. Hybridization events between alien and native plants pose a threat to the native species but may also create new even more alarming pests (Rhymer & Simberloff 1996). New pests can also be created by evolution events in the alien plant with the possible consequence of increased impact on the ecosystem. An example of this is the genetic change of the introduced macroalga *Caulerpa taxifolia*, which made an invasion in the Mediterranean possible (Wiedenmann et al. 2001). Like hybridisation, evolution as a consequence of introduction of alien plants, may also affect the native plants in a more direct way. As a response to an introduction the native species may evolve, e.g. to withstand competition from or adapt to the habitat changes created by an alien plant. This change, which might include traits associated with reduced fitness in the absence of the alien, is permanent and will affect the native organism if the alien is removed (Simberloff & Alexander 1998).

Alien species can alter ecosystem processes such as hydrology and water quality and thereby change the rule of existence for all species (Vitousek et al. 1997). The Eurasian watermillfoil *Myriophyllum spicatum* has in its alien range proven to be capable of reducing the water quality (increased nutrient loading, reduced dissolved oxygen and changes in water temperature), which in turn decreased the numbers and cover of native plant species and caused negative effects to fishes and other animals (Eiswerth et al. 2000). However, alien plants can also contribute to increased diversity of animals, which has been observed for macroinvertebrate communities living on alien populations of the water hyacinth *Eichhornia crassipes* (Masifwa et al. 2001).

The impact of alien plants is much more difficult to predict than impact from other types of environmental threats, e.g. chemical pollutions (Simberloff & Alexander 1998). Some of the factors accounting for this are: introduced species reproduce and multiply, they disperse in a way hard to predict, and their interactions with other biota are very difficult to foresee. Finally, although no negative effects are found on native flora and fauna from an introduced alien plant, there is always a chance that it evolves. It is impossible to predict which effects an evolution can have, since both mutations and crossing over are stochastic events.

Alien vascular plants in Swedish lakes and water-courses

In Sweden a total of 30 alien vascular plant species have been introduced into freshwater habitats or into habitats closely linked to the freshwater environment, both established and occasional species included (Wallentinus 2002). Vascular plants thereby represent one fifth of all introduced species in Swedish aquatic environments ($n \approx 150$). Of the established non-indigenous plant species, 18 are considered as obligate or facultative aquatic plants, of which half are considered as weeds somewhere in the world (Table 1). Some of these species are only established in a few small populations but others are widespread. Especially three water-plants cause considerable trouble as invaders in Sweden: *Elodea canadensis* – Canadian waterweed, *Elodea nuttallii* – Nuttall waterweed, and *Nymphoides peltata* – Yellow floating heart (Josefsson & Andersson 2001).

Although some of the established non-indigenous plants not are considered as weeds in their present Swedish range, introductions in other parts of the country may result in environmental and economical impact. This is also true for species indigenous to some parts of the country but non-indigenous to others. The Reed sweetgrass – *Glyceria maxima* – is an example of a native species that have been transplanted to parts of the country where it is non-indigenous (Lohammar 1955). In some of its new habitats, it forms large stands that suppress the native vegetation. Additionally, future climatic changes (i.e. global warming) can increase the impact from some established alien plant species, but also allow new species to invade. Invasions from species not present in the country today are of course possible without any changes in the climatic conditions, since it is unlikely that all species able to establish have been introduced.

Table 1. Aquatic non-indigenous vascular plants established in Swedish freshwater habitats. Occurrence is measured as number of 5x5 km areas in which one or more populations have been found in recent time. Occurrence data are collected from floral inventories in the southern 22 of the totally 25 historical provinces of Sweden (see Figure 1). Geographic codes from the system used by the Royal Botanical Gardens are 1 = Europe and North Africa, 2a = Asia Minor, 2b = Central Asia, 2c = East Asia, 3 = North America, 4a = Central America, 4b = Tropical South America, 4c = Temperate South America, 5a = Tropical Africa, 5b = Southern Africa, 5c = Madagascar, 6a = India, 6b = Southeast Asia, 6c = Pacific Ocean, 7a = Australia, 7b = New Zeeland (Cook 1985). References: 1) Wallentinus (2002), 2) Lohammar (1955), 3) Lohammar (1965), 4) Cook (1985), 5) Lönnberg (1896), 6) Anderberg (1992), 7) Lenfors & Nilsson (1987), 8) Jonsell (2001), 9) Jonsell (2000), 10) Hylander (1971), 11) Almborn (1983), 12 Carlsson (1976), 13) Bergengren (1960), 14) Niordson (1989), 15) Collinder (1909), 16) Bertilsson (2002), 17) Malmgren (1982), 18) Almquist (1965).

Species and family name	Weed status	Introduced or first observed	Occurrence	Native in
Araceae				
Acorus calamus L.	Weed[1]	15th – 16th cen. [2, 3]	981	2b, 2c, 3, 6a, 6b [4]
Lysichiton americanus Hultén & StJohn		1975 [7]	29	3 [1]
Orontium aquaticum L.	Weed[1]	1982 [7]	1	3 [1]
Azollaceae				
Azolla filiculoides Lam.	Serious weed[1]	1923 [9]	1	3, 4a, 4b, 7a, 7b [4]
Cabombaceae				
Cabomba caroliniana A. Gray	Serious weed[1]	1984 [8]	1	3 [4]
Hydrocharitaceae				
Elodea callitrichoides (Rich.) Casp.		1985 [16]	1	4c [4]
Elodea canadensis Michx.	Serious weed[1]	1870s [3, 18]	1458	3 [4]
Elodea nuttallii (Planch.) St. John	Weed[1]	1991 [6] (but see text)	78	3 [4]
Iridaceae				
Iris sibirica L.		1795 [10]	137	1, 6b [1]
Iris versicolor L.	Weed[1]	1960 [13]	21	3 [1]
Menyanthaceae				
Nymphoides peltata (S. G. Gmel.) Kuntze	Serious weed[1]	Late 19th cen. [5]	50	1, 2a [4]
Poaceae				
Glyceria grandis S. Watson		1975 [14]	17	3 [1]
Glyceria maxima (Hartm.) Holmb.		19th cen.[3] (but see text)	1855	1, 2a, 2b [4]
Glyceria striata (Lam.) Hitchc.		1975 [12]	7	3, 4a [4]
Polypogon monspeliensis L.	Serious weed[1]	1862 [17]	12	1, 2a, 2b, 2c, 5b [4]
Sarraceniaceae				
Sarracenia purpurea L.		1948 [11]	9	3 [1]
Scrophulariaceae				
Mimulus guttatus D.C.		1846 [10]	52	3 [1]
Mimulus luteus L.		1909 [15]	3	4c [1]

Elodea canadensis – the Canadian waterweed – is the species with the widest distribution in Sweden (Figure 1a). It originates from the North American continent and has spread to Europe during the 19th century (Birger 1910). In Sweden, where it first was recorded in the 1870s, it is today widely spread in meso-eutrophic alkaline lakes with fine-grained sediments in the southern and central parts, as well as in the coastal lowlands in the northern part of the country (Mossberg et al. 1997). Its invasive character is well documented in many other European countries (Wallentinus 2002). The main vector for its first introduction seems to be both planting and aquaria release, but also other sources of spreading has been reported (Birger 1910; Josefsson 1999). The further dispersal is facilitated by vegetative propagation, by an easy transport of fragments caused by wind and wave actions, and to human boating and fishing activities. Birds may also be a probable vector. *Elodea* species begin to grow from winter-dormant apices (buds) in the spring. Such dormant apices are produced in large numbers in the autumn just before the winter-season (up to 5000 have been recorded from 1 m^2 of sediment surface, Bowmer et al. 1984). The apices are dispersed through with wind and waves within a lake and downstreams with running waters. Floating winter-buds start to grow when they reach the bottom layers.

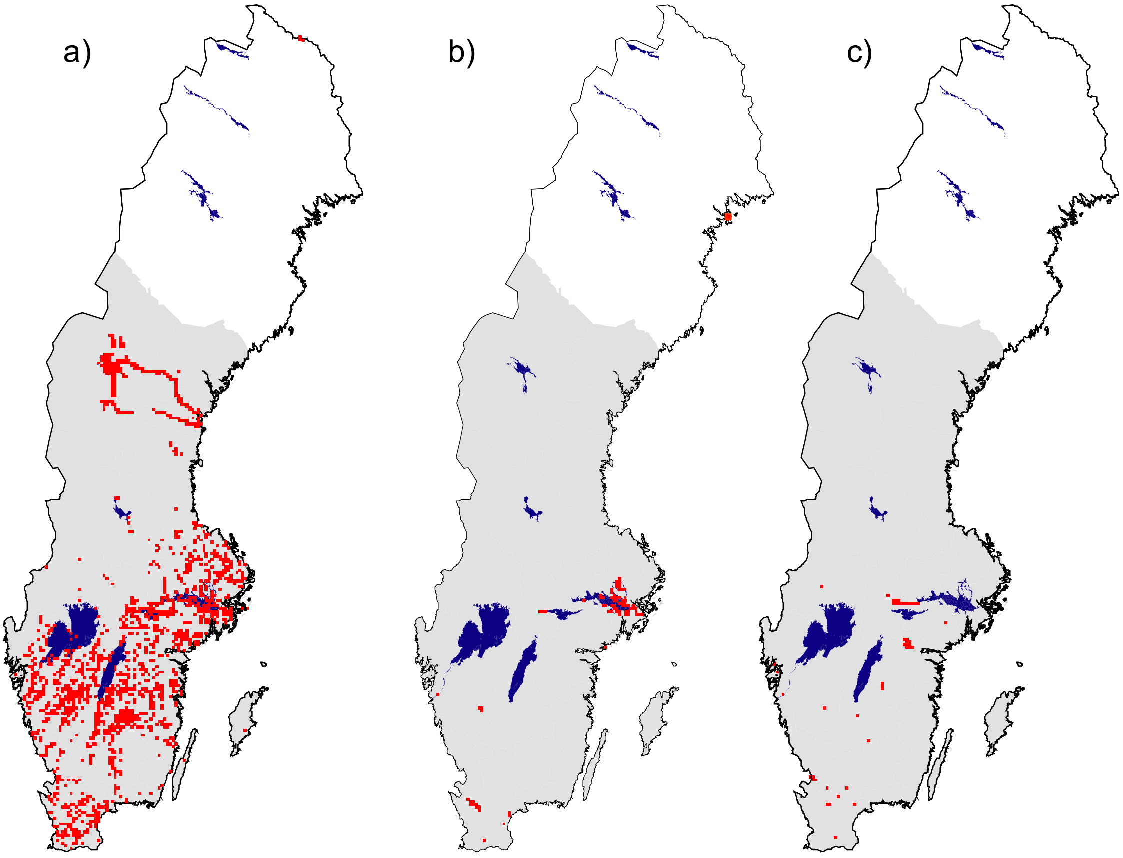

Figure 1. Present Swedish distribution of three non-indigenous water-plants associated with considerable environmental or economical impact: 1a) *Elodea canadensis*, 1b) *Elodea nuttallii*, 1c) *Nymphoides peltata.* Red squares represents occurrence within an economic chart (5x5 km). Areas of grey background are areas in which floral inventories have been performed by regional floristic groups, while only sporadically data have been collected from areas of white background. Data are collected from published regional floras (Andersson 1981; Danielsson 1994; Genberg 1992; Georgson et al. 1997; Malmgren 1982; Mascher 1990) as well as from botanical organisations databases.

Good water transparency is an important environmental factor mentioned in connection with *E. canadensis*. Bicarbonate as a carbon source and supply of iron in reduced form are other prerequisites (Spicer & Catling 1988). *E. canadensis* acts as a nutrient sink because it assimilates phosphorus from the water and the sediment while growing. During mineralization of large biomasses of *Elodea* considerable amounts of phosphorus are released to the water, favouring the growth of littoral and pelagic algae.

Elodea nuttallii - the Nuttall waterweed - also originates from North America and has during the 1990s invaded many waters in central Sweden. *Elodea nuttallii* was detected for the first time in Lake Mälaren, 1991 (Anderberg 1992), but according to herbarium material it occurred already in 1973 in the northern part of Lake Vättern where it by that time was mistaken as *E. canadensis* (Andersson unpublished). It seems to have the same preference for hardwater lakes as *E. canadensis*, but its distribution is still restricted in Sweden (Figure 1b). However, it has reached several sites in Lake Mälaren and occurs there in mass abundance and is a competitor to the Canadian waterweed (Anderberg 1992). There are indications that *E. nuttallii* has a competitive advantage between the two at high concentrations of NH_4-N (Dendène et al. 1993). *E. nuttallii* as well as *E. canadensis* have the potential to develop into dense submerged beds, which prevent the use of water for recreational and professional purposes. There is a need to investigate the vectors of dispersal and the differences between this recently introduced species and the Canadian waterweed both for competition and further spreading.

The floating-leaved invasive species *Nymphoides peltata* occurs in some twenty sites in southern and central Sweden's lowland areas (Mossberg et al. 1997, Figure 1c). Nuisance problems are related to the shading effects of the leaves to the underlying water and it is an obstacle to boat traffic, fishery and other recreational activities. It is dispersed via fragmented vegetative parts (stems and rhizomes). Rhizomes and roots survive mechanical harvesting, and as a consequence of such restorations, fragments can reattach elsewhere which increases its distribution. Its weedy character is especially annoying in the entire water system of the River Arbogaån which drains to Lake Mälaren, and outside the town of Kungsör in the western part of Lake Mälaren (Josefsson & Andersson 2001) as well as in a number of lakes within the drainage area of Motala Ström in the county of Östergötland, S. Sweden. The attractive appearance of this species has induced to planting with devastating effects. In Lake Väringen (in the water system of Lake Arbogaån) *N. peltata* was introduced for ornamental purposes in 1933 (Eckerbom 1940). Following the introduction of a single plant rapid establishment was observed, and today it not only covers a large area of Lake Väringen but is also spread and established in River Arbogaån and lakes therein (Figure 2, Löfgren 1993).

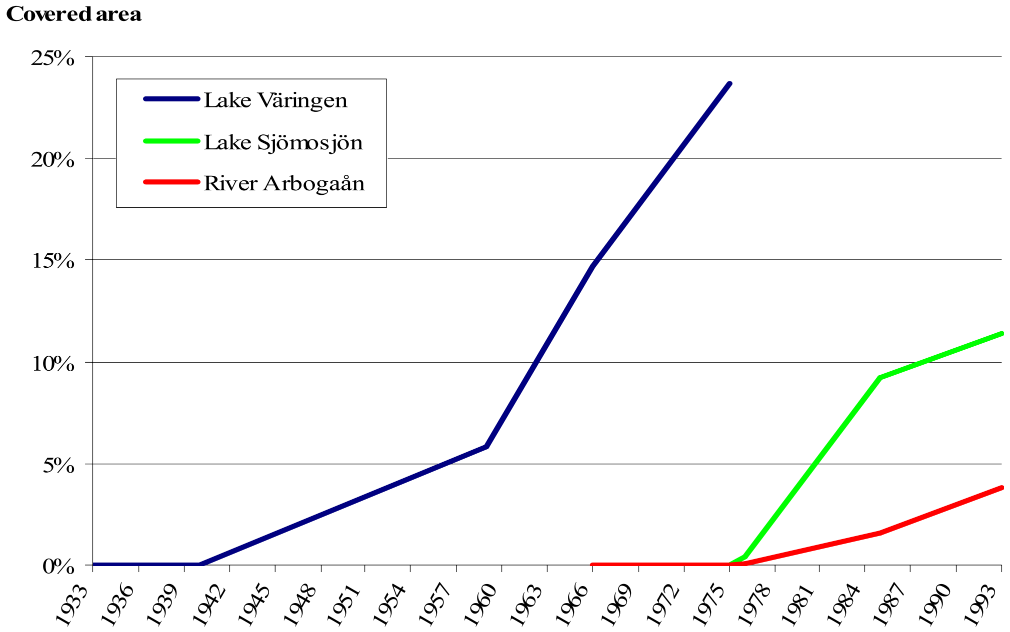

Figure 2. Invasion history of *Nymphoides peltata* in the drainage area of River Arbogaån (Löfgren 1993). The blue line represents the percentage area cover in Lake Väringen, where *N. peltata* was introduced in 1933; the red line represents the area cover in River Arbogaån; and the green line the area cover in Lake Sjömosjön, where *N. peltata* was first observed in 1969.

Predicting plant invasiveness

Far from all alien plants will become invasive. The tens rule (Williamson & Fitter 1996a) states that only 1 in 10 imported plant species become introduced in the wild, and only 1 in 10 of those introduced become established (Figure 3). It is only established species that can cause severe damage to an ecosystem on a local scale, but to be a regional pest the species also has to spread to new localities, which is done only by 1 in 10 of those established. Only plant species that succeed all three transitions (introduction, establishment and dispersal) may become pests. However, for those that do become pests, the effects on the natural ecosystems and the economy might be severe.

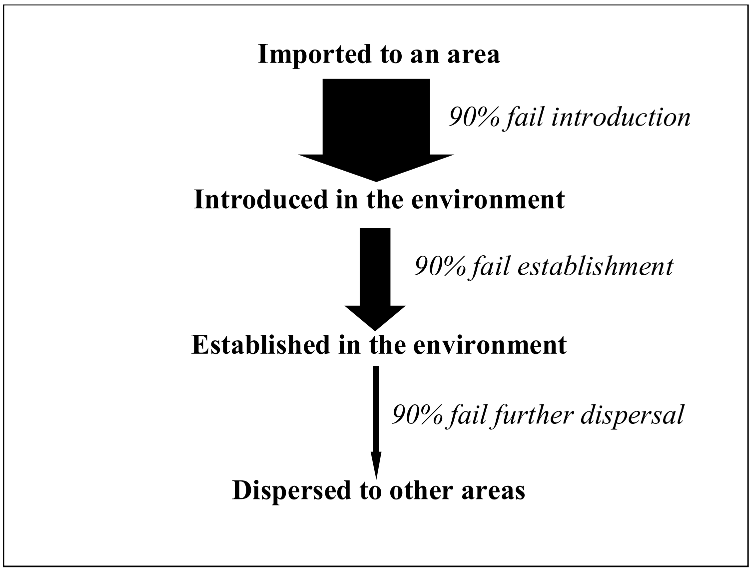

Figure 3. The tens rule (Williamson & Fitter 1996a). The proportion of plant species that succeeds each transition (i.e. introduction, establishment and dispersal) is approximately 10%.

It is of great concern for conservation biologists and decision-makers to be able to tell which alien plants that will become pests, so resources can be directed towards measures against those. The number of propagule movements is very large and it is impossible to prevent all introductions, and since political boundaries seldom are the same as biogeographical ones even such a drastic action as stopping all plant material from entering a country or a state, will not stop all future invasions. Also, one shall not forget that there are alien aquatic plants of economic value, e.g. those used in aquaculture, aquarium trade etc, therefore a total import stop may not be justified on the basis that some plants (1 in 1000 according to the tens rule) will become invasive. Several approaches have been suggested how to predict which alien plants will become invasive if introduced. Among the earliest attempts, lists of plants being invasive in other parts of the world were constructed. More recent attempts have tried to find characters differing invasive from non-invasive species (Grotkopp et al. 2002) or characters differing established alien species from non-established ones belonging to the same species pool (Prinzing et al. 2002).

Taxon-affinity

Many aquatic vascular plants occupy large geographical ranges and recently some have also extended their range and become serious pests in recently occupied regions (Cook 1985). The most straightforward approach for predicting future invaders is to use lists of species that are already invasive elsewhere. The most well-known list of worldwide invasive plants is probably the one compiled by Holm et al. (1977) containing almost 100 invasive weeds, mainly terrestrial, considered to be the world's worst. A list like this serves as an excellent tool for drawing attention to some problematic species, but its predictive value is small since it does not include species not yet introduced anywhere (Mack 1996).

There seems to be some overrepresentation for invasiveness by some plant families (Pysek 1998). Daehler (1998) found that species belonging to primarily freshwater aquatic plant families are more likely to be invasive than species from most other plant families. When taxonomic affinity was compared for invasive plants in three US states, some plant families tended to be overrepresented, but the total number of plants belonging to these families was only a fraction of the total number of the invaders (Lockwood et al. 2001). The use of an invasive family list alone as a risk assessment tool is by no doubt ineffective since most invasive plant species will not be predicted, but it might be useful in combination with other tools. Another disadvantage with such lists is that even if the proportion of invasive plants in a family is small, their impact may be severe.

Biological characters

Are there any traits that invasive plants have in common? Baker (1974) compiled a list of traits for an "ideal weed" that he believed should be beneficial for invasive species, e.g. continuous seed production, high overall seed output and lack of special requirements for germination. More recently, others have made predictions based on comparisons of characters between invasive and non-invasive species or between established alien species and their non-established congeners. Lately, several reviews have been written on how to predict future invaders based on the species traits they have in common (e.g. Kolar & Lodge 2001; Mack 1996; Rejmanek 2000). The basic approaches are listed below:

- Comparisons between native species in a community and alien species that successfully have invaded that community have been performed in the search for characters of successful invaders by Williamson and Fitter (1996b) among others. These comparisons help us understand the impact of alien species on natives, but they cannot answer the question why some species become invasive and others not (Prinzing et al. 2002). Another problem associated with this kind of investigations is that some of the plants classified as native might in fact be introduced (Carlton 1996). If these cryptogenic species (i.e. species with unknown origin) are included in a comparative study, the predictive power will be less.

- Invasive and non-invasive alien plants have been compared by others in hope to find characters separating successful invaders from non-successful ones. Relative growth rate, seed mass and mean generation time are traits that have proven to differ between invasive and non-invasive pine species (Grotkopp et al. 2002). The pine species serve as a well fitted study object, since many well documented introductions have taken place in most parts of the world because of economical interests. However, for most plant taxa, the information needed for this kind of comparative studies are not available (Prinzing et al. 2002).

- Some studies have compared the alien plants established in a region with their native non-established congeners. In a study by Goodwin et al. (1999) the question if invasiveness of plant species could be predicted from available biological information was examined in such a way. After comparing life form, stem height, flowering period, and geographical range (characters all available from floras) for 110 congeners, a model that significantly predicted invasive plants from non-invasive was constructed. More recently, an extensive study compared the alien flora of two Argentine provinces, indigenous to central Europe, with almost the entire species pool of central Europe (Prinzing et al. 2002). One trait was found more frequent in aliens than in their native congeners in both these studies. It was the geographical range of a species in its area of origin, which can be important for two reasons: species with larger native range more likely come in contact with vectors and more likely have larger tolerance spectrums than species with a more restricted distribution. Except for the importance of geographical range, the latter study did also find other traits more common in the aliens, such as frequent contact with and/or utilization by humans, a niche position within the native range near the abiotic conditions in the alien range, and a ruderal strategy. However, one drawback of this kind of study design is that all aliens are treated as one group; hence predictions based on the results will not tell which plant species that will affect native biodiversity if introduced.

The search for particular traits associated with invasiveness of plant species has proven difficult (Alpert et al. 2000). Traits that seem to best explain invasiveness are probably broad native range and rapid dispersal (Table 2). The most likely reason why this search for invasive traits has failed is that invasiveness depends more of the interaction between the alien plant and its new habitat than upon the characteristics of the species alone. This might also explain why many of the characters found to differ between invasive and non-invasive plants are those associated with the first transition step, introduction, which is habitat independent.

Table 2. Species characters associated with high plant invasiveness; empirical support.

Species character	Scientific approach	Species group	References
High relative growth rate	Successful vs. unsuccessful invaders	Pine	Grotkopp et al. (2002)
Small seed mass	Successful vs. unsuccessful invaders	Pine	Grotkopp et al. (2002)
Low generation time	Successful vs. unsuccessful invaders	Pine	Grotkopp et al. (2002)
Large native geographical range	Established vs. non-established alien species	Terrestrial vascular plants	Goodwin et al. (1999), Prinzing et al. (2002)
Frequent contact with humans	Established vs. non-established alien species	Terrestrial vascular plants	Prinzing et al. (2002)
Niche position as natives similar to the abiotic conditions in the alien range	Established vs. non-established alien species	Terrestrial vascular plants	Prinzing et al. (2002)
Ruderal strategy	Established vs. non-established alien species	Terrestrial vascular plants	Prinzing et al. (2002)

Predicting habitat invasibility

The number and impact of alien aquatic plants differ between different habitats, i.e. habitats differ in their invasibility. If an alien plant will establish in a new habitat depends both on the attributes of the species and on the properties of the new site. The observed phenomenon that some plants growing in small non-invasive populations in there native range become invasive when introduced elsewhere, might be explained by differences in habitat invasibility. The Eurasian watermillfoil *Myriophyllum spicatum* is one such example. *M. spicatum* is not considered invasive in its area of origin, but in North America it is considered as a pest with severe environmental and economical impact (Eiswerth et al. 2000). Differences in invasibility might be correlated with both biotic factors, e.g. competition or allelopathy from native plants, or presence of herbivores and pathogens, and abiotic ones, e.g. physical stress and disturbance (Table 3). It has proven easier to identify differences in habitat invasibility than to identify species characteristics associated with invasiveness (Alpert et al. 2000).

Table 3. Habitat characters associated with high habitat invasibility; theoretical or empirical support.

Habitat character	References
Biotic factors:	
Vacant niches	Herbold & Moyle (1986)
Absence of enemies	Clay (2003), Keane & Crawley (2002), Mack et al. (2000)
Low competitive resistance	Barrat-Segretain (1996), Callaway & Aschehoug (2000)
High biological diversity	Elton (1958), Kennedy et al. (2002), Levine (2000), Prieur-Richard et al. (2002)
Low biological diversity	Stohlgren et al. (1999, 2003), Wardle (2001)
Abiotic factors:	
Suitable climate, nutrient levels etc.	Rejmanek (2000)
Disturbance (water regime)	Moyle & Light (1996)
Disturbance (eutrophication)	King & Buckney (2000)
Immigration of humans	Lonsdale (1999)

Biotic factors affecting invasibility

Biotic factors such as competition, herbivory and pathogens in the introduction habitat can affect the introduction success of an alien aquatic plant. Some ecosystems may hold unutilized niches that alien species can invade without competition, as stated by “the vacant niches theory” (Herbold & Moyle 1986). However, actual demonstration of vacant niches has proven difficult (Simberloff 1995).

The lack of natural competitors, herbivores and pathogens (i.e. species that have evolved to compete with or prey upon the alien species) can be one explanation of invasion success for some immigrating species, according to the enemy release hypothesis (Clay 2003; Keane & Crawley 2002; Mack et al. 2000). This escape from natural enemies can give the alien species advantages in growth, longevity and fitness. Except for the direct advantage of loosing its enemies, the escape from specialist enemies allows the alien plants to allocate resources from defence to growth and reproduction (Blossey & Notzöld 1995). However, the advantages of resource allocation holds true only for escapes from specialist enemies (i.e. enemies that have co-evolved with the immigrant species) and not for generalist enemies, since such most certainly will be present also in the new habitat. If natural specialist enemies are absent, selection will occur for those individuals in the alien population with the least defence against these (Lee 2002). The time needed for these, in their new environment well fitted, individuals to dominate the alien population may be one reason for the often observed lag time between introduction and dispersal (Ellstrand & Schierenbeck 2000), but there may be other explanations such as stochastic extinction of propagules (Sakai et al. 2001).

The competitive resistance from native plants may differ between different communities. Exploitative competition among aquatic plants takes place for limiting resources, e.g. light, nutrients and suitable substrates (Barrat-Segretain 1996). In addition to competition for limiting resources, plants sometimes also compete by release of chemical compounds (allelopathy). If the native plants in the invaded community are not adapted to the type of chemical compounds released, the invasibility is greater than if they are (Callaway & Aschehoug 2000).

High biological diversity has been proposed to decrease the habitat's invasibility (Elton 1958). In high diversity habitats, both space and limiting resources are more efficiently used than in low diversity ones, which might be the reason for this possible relationship (Kennedy et al. 2002). As an indirect effect of highly plant diversity, herbivore diversity, and thereby herbivore pressure, might increase, which has been proposed as another explanation for the lower invasiveness in high diverse communities (Prieur-Richard et al. 2002). Except for the theoretical support for such a relationship, some empirical studies have also found that biological diversity may act as a barrier towards invasions (e.g. Kennedy et al. 2002; Levine 2000). However, other studies have shown the opposite to be more likely (Levine & D'Antonio 1999). An important factor when studying the relationship between biological diversity and invasibility may be the spatial scale. Stohlgren et al. (1999) found contrary relationships at different scales, but at landscape and biome scale, biodiversity increased invasibility. Besides the effects of scale, the results in many studies claiming biodiversity reduces invasibility may be effects of experimental designs (Wardle 2001). After all, habitats with high biological diversity are by definition habitats in which many species have established over time.

Abiotic factors affecting invasibility

Abiotic factors such as climate, nutrient levels and disturbance are also affecting the habitats invasibility. Even though many aquatic plants have wide geographic ranges, the climate has an important role as setting limits for aquatic plants to establish (Rejmanek 2000). However, other dispersal barriers than climate may exist, and when these are broken a species can spread to other climatic zones. Hence, it is dangerous to rely on climatic differences alone between the native and the introduction habitat when assessing risks for spreading of aliens.

Disturbed habitats have in several studies been shown to have greater invasibility than undisturbed ones, e.g. changes in water regime (Moyle & Light 1996) and eutrophication (King & Buckney 2000). The reasons for this greater invasibility of disturbed habitats may be either abiotic or biotic, since a reduction in biological resistance often follows a disturbance event. After a disturbance event, the altered conditions may be favourable for alien species adapted for the disturbance. In addition, the abiotic conditions may be so much altered that some species inhabiting the habitat before the disturbance event, no longer are able to persist. The sometimes observed relationship between invasibility and biological diversity may in fact be nothing more than a pseudocorrelation, since loss of native biodiversity and increased invasibility both are consequences of disturbances. So, the loss of species or individuals following a disturbance event generally contributes to increased invasibility because of less competition and vacant growing sites.

Differences in invasibility at larger spatial scales can be caused by movement of humans and trade routes across the world. On a global scale, the New World is significantly more invaded by plants than the Old World (Lonsdale 1999). The explanation for this can be that more people have immigrated to the New World than the opposite, and humans tend to bring their favourite species along.

Risk assessment of alien species

The risk that an alien species will cause harm to ecosystem function or economy can be calculated if impact, species invasiveness and habitat invasibility are known. However, the risk can be calculated for different scenarios (e.g. if the species is imported, if it is introduced, if it succeeds establishment etc.), and depending on which scenario chosen different data must be collected. The simplest risk models are the so called screening systems, which use various types of information in order to separate more harmful species from those that probably not will cause harm if they are introduced to a geographic region. More advanced risk models use mathematical equations to calculate the probability for specific economical or environmental damages on a single species level.

Complete screening systems have been developed for detecting of which alien plants that will be invasive if introduced. Such systems are usually applicable to a wide range of taxonomic groups but focused on specific geographic regions (Daehler & Carino 2000). These models combine various types of information (e.g. invasion history, life history, biogeography and habitat characteristics) to classify species invasiveness. A screening system for invasive plants developed for Australia did successfully predict all serious weeds and most minor weeds, while only 7% of the non-weeds were rejected (Pheloung et al. 1999). This model consists of 49 questions and based on the answers each species is assigned a numeric score. The numeric score decides which alien plants that can be imported without posing large environmental risks by classifying them into one of the three categories “accept”, “further evaluation”, or “reject”. When tested for Hawaiian conditions, the Australian model (with some minor modifications) successfully rejected more than 90% of the invasive species while the rest were classified in the “further study” category (Daehler & Carino 2000). Among the non-invaders, more than half were accepted, but a large fraction were classified as “further study” objects. This type of screening systems might serve as an important tool for water managers in the future given that the needed information is available for the plants to assess.

Mathematical risk models can, besides utilise field data, include stochastic information in order to simulate the probable outcome of an event (e.g. species introduction). In order to assess the total risk of a species introduction (R) the probabilities of establishment (E), further spread (S) and impact (I) needs to be considered:

$$R = E * S * I$$

Some experiences from the development of models for assessing the environmental risks of genetically modified organisms may be useful in the developing process of such models for alien species. However, both the construction and usage of mathematical risk models can be more time-consuming than screening systems are, hence the choice of method should be made depending on the purpose of the study; if lists of species that may cause harm if introduced are required screening systems are preferred, but if risks needs to be evaluated for a single or few species mathematical risk models provide a better result. However, the choice of method need also to be taken in consideration available information, since screening systems only can be constructed if relevant information is known for a large group of species.

Discussion

In order to fully understand how alien species pose a threat to ecosystem function and economy both species invasiveness and habitat invasibility must be considered. Much research has been performed since Elton published his ideas in 1958, but still accurate risk models for most organism groups and regions are missing. In the field of alien aquatic plants, a great deal of research is needed in order to understand the invasion process and make accurate risk models.

The search for characters associated with species invasiveness has proven difficult for most species groups, and for aquatic plants it may be an even harder undertaking. Both historical introduction data and basic biological knowledge are often more sparse for alien aquatic plants than for many other organism groups. Since historical data of introductions often are missing, it may be difficult to compare successful invaders with introduced species who failed to establish following introduction. It may be even harder to quantify any characters found to be associated with invasiveness, since such an assessment also requires a quantification of species invasiveness. Also, basic biological and ecological knowledge for many aquatic plants are missing, which means that even if introduction history is known and species invasiveness has been quantified for the successful invaders, invasiveness can not be tested against some species characters of interest. If a model is produced anyway, by including only species for which basic biological and ecological knowledge are known, it will be useless for assessing the risks of those species for which basic biological knowledge is lacking.

Habitat characters associated with invasibility have proven easier to identify and quantify, but still much research remains. Both biotic factors (e.g. escape from natural enemies) and abiotic ones (e.g. climate and disturbance) have been shown to affect the invasibility of the introduction habitat for a wide range of ecosystems. Some studies have been performed on the invasibility of freshwater environments, but few of these have focused on aquatic plants. However, although more research is needed in order to build accurate risk models, it may be rather easy both to identify and to quantify biotic and abiotic factors which affect the invasibility of freshwater habitats.

Since it has proven problematic to make comparative studies between groups of species of different invasiveness (e.g. those who successfully established versus those who failed establishment), it may be about time to start making mathematical risk models on a single species level instead of screening systems for groups of species, which most research has been focused on up to date. Such models will not just provide information of the risks for impact of the studied species, but also give a deeper understanding of how the invasion process works.

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